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# Can Group-functional Behaviors Evolve by Cultural Group Selection?

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## An Empirical Test<sup>1</sup>

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by Joseph Soltis, Robert Boyd,  
and Peter J. Richerson

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Functionalists believe that social and cultural variation results from adaptation at the group level. Such explanations are controversial for two reasons: (1) Extensive analysis of mathematical models of group selection by evolutionary biologists suggests that group selection is unlikely to be important. (2) Group extinctions are too rare to generate sufficient evolutionary change. Boyd and Richerson have proposed a new model of group selection based on cultural variation that is theoretically more plausible than group selection on genetic variation. In this paper we present data on patterns of group extinction, group formation, and between-group variation in New Guinea which are consistent with the operation of this model. Observed rates of group extinction suggest that a minimum of 500 to 1,000 years would be required for the spread of a single group-beneficial trait under the influence of group selection. This result implies that group selection cannot explain cultural changes that take less than 500 to 1,000 years. It does not, however, preclude a role for group selection in explaining the evolution of human societies over the longer run.

JOSEPH SOLTIS is a doctoral candidate in the Department of Anthropology of the University of California, Los Angeles (Los Angeles, Calif. 90024, U.S.A.). Born in 1962, he received his B.A. from UCLA in 1988 and his M.A. in 1991. He is currently a visiting research student at the Primate Research Institute of Kyoto University, where he is studying female mate choice in Japanese macaques.

ROBERT BOYD is Professor of Anthropology at UCLA. He was born in 1948 and has a B.A. in physics from the University of California, San Diego (1970), and a Ph.D. in ecology from the

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University of California, Davis. He has taught at Duke University (1980–84) and at Emory University (1984–85) and has been a visiting fellow at the Neurosciences Institute (1984) and at the Center for Interdisciplinary Studies of the University of Bielefeld (1991–92). In addition to cultural evolution, his research interests include plankton community ecology, the ecology of tropical lakes, and applied studies of polluted lakes. He has published, with Peter J. Richerson, *Culture and the Evolutionary Process* (Chicago: University of Chicago Press, 1985).

PETER J. RICHERSON is Professor of Environmental Studies at the University of California, Davis, where he received a B.S. in entomology in 1965 and a Ph.D. in zoology (ecology) in 1969. He has been a visiting professor in forestry and environmental studies at Duke University (1984) as well as a visiting fellow of the Neurosciences Institute (1984) and of the Center for Interdisciplinary Studies of the University of Bielefeld (1991–92) and director of UC Davis's Institute of Ecology (1984–90).

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Many anthropologists explain human behavior and social institutions in terms of group-level functions (Rapaport 1984, Lenski and Lenski 1982, Harris 1979, Radcliffe-Brown 1952, Aberle et al. 1950, Malinowski 1984 [1922], Spencer 1891). According to this view, beliefs, behaviors, and institutions exist because they promote the healthy functioning of social groups. Such functionalists believe that the existence of an observed behavior or institution is explained if it can be shown how the behavior or institution contributes to the health or welfare of the social group. Most functionalists in anthropology have not explained how group-beneficial beliefs and institutions arise or by what processes they are maintained (Turner and Maryanski 1979). When functionalists do provide a mechanism for the generation or maintenance of group-level adaptations, it is usually in terms of selection among social groups.<sup>2</sup> Functionalists

2. Some authors (e.g., Harris 1979) have suggested that the self-interested choices of individuals will result in group-beneficial behavior. However, this claim is not cogent—group-beneficial behavior will not result from individual choice except as a side effect of other processes or in certain limited circumstances. For example, many authors have suggested that food taboos exist because they prevent overexploitation of ecological resources. To keep things simple, let us suppose that individuals must choose to observe a particular taboo or not and that individuals who observe this taboo forgo a satisfying and nutritious food item. Choosing to ignore the taboo has a positive effect on individuals' own welfare and, by assumption, a negative effect on the welfare of the group. However, unless the group is very small, the personal effect will be much larger than the effect on the group, and thus choosing to ignore the taboo will better serve individuals' goals, even if their goals include the welfare of the group. This effect is at the heart of both rationalist and evolutionary arguments against the easy development of group-beneficial behavior. The effect is not a matter of cognitive capacity, as writers such as Harris seem to imply. Rational strategists are assumed to have unlimited cognitive capacity, whereas evolved creatures are the products of blind selective sorting, but the essential problem is the same; both rational strategists and evolved creatures are expected to act in their own self-interest.

Group-beneficial behavior may result from self-interested individual choice under certain circumstances. First, since individual and group benefit are often correlated, individual choice may often produce group-beneficial outcomes as a side effect (see Sugden 1986 for several examples). Second, markets will lead to an "efficient" allocation of economic resources if the state or some other external

believe that societies have many functional prerequisites. Social groups whose culturally transmitted values, beliefs, and institutions do not provide for these prerequisites become extinct, leaving only those societies with functional cultural attributes as survivors. We refer to this process as "cultural group selection" because it involves the differential survival and proliferation of culturally variable groups.

Cultural group selection is analogous to genetic group selection but acts on cultural rather than genetic differences between groups. This distinction is important. We will argue that cultural variation is more prone to group selection than genetic variation and that this may explain why human societies, in contrast to those of other animals, are frequently cooperative on scales far larger than kin groups. More generally, recent theoretical work on the processes of cultural evolution shows that there are many parallels between cultural and genetic evolution but also some fundamental differences (Durham 1991, Boyd and Richerson 1985, Cavalli-Sforza and Feldman 1981, Pulliam and Dunford 1980). To date, empirical investigations focused on these processes are few (but see, e.g., Cavalli-Sforza et al. 1982). In addition to conducting empirical studies specifically designed to investigate these processes, it is possible to use many of the data collected by social scientists for other purposes. Here we use a small part of the very rich ethnographic record produced by anthropologists to test the empirical plausibility of the process of cultural group selection.

As is emphasized by Campbell (1965, 1975, 1983), cultural group selection requires that (1) there be cultural differences among groups, (2) these differences affect persistence or proliferation of groups, and (3) these differences be transmitted through time. If these three conditions hold, then, other things being equal, cultural attributes which enhance the persistence or proliferation of social groups will tend to spread. There is no guarantee, however, that this process will be sufficiently powerful to overcome other social processes which act to produce other outcomes. There are two problems with cultural group selection as an explanation for the exist-

tence of group-beneficial traits: maintenance of variation among groups and rate of adaptation.

Group-functional explanations may be in conflict with the fact that human choices are at least partly self-interested. To the extent that they can evaluate alternative beliefs and attitudes, self-interested organisms should adopt only beneficial attitudes and beliefs and reject those that are individually harmful. Thus, beliefs that are costly to the individual should diminish, while beliefs that are beneficial to individuals should spread. Extensive theoretical analysis suggests that group selection can counteract this process only if groups are very small and migration among groups is very limited (Eshel 1972, Levin and Kilmer 1973, Wade 1978, Slatkin and Wade 1978, Boorman and Levitt 1980, Wilson 1983, Aoki 1982, Rogers 1990). As a result, most evolutionary biologists and social scientists influenced by them (e.g., Chagnon and Irons 1979) reject functionalist explanations.

Furthermore, Hallpike (1986) has argued that group extinction does not occur often enough to justify functionalist explanations. Group selection works by eliminating those societies that have deleterious practices or institutions. If it takes a particular number of extinctions to eliminate a deleterious ritual form, then it will take a greater number to eliminate the deleterious ritual form and a deleterious marriage practice. Still further extinctions will be required to cause other aspects of the society to become adaptive. Hallpike argues that human societies do not have high enough extinction rates for group selection to cause many different attributes to be adaptive at the group level simultaneously.

In the face of these objections, is there any justification for taking group-functional hypotheses seriously? Here we describe a theoretical model and present supporting data which show that a role for cultural group selection should not be ruled out. Boyd and Richerson (1985:chaps. 7 and 8; 1990a, b) have analyzed mathematical models of group selection acting on culturally transmitted variation and have shown that cultural group selection will work if certain key assumptions are met. Ethnographic data from Papua New Guinea and Irian Jaya give credence to some of the assumptions that underpin the group-selection model. These data also allow us to estimate an upper bound on the rate of adaptation that could result from group selection. We argue that these data suggest that group selection is too slow to be used to justify the common practice of interpreting as group-beneficial the detailed aspects of particular cultures. However, the data do not exclude the possibility that group selection may account for the gradual evolution of some group-level adaptations, such as complex social institutions, over many millennia.

## How Group Selection Can Work

We begin with the premise that individuals acquire various skills, beliefs, attitudes, and values from other individuals by social learning and that these "cultural vari-

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authority enforces contracts, external effects such as air pollution are not present, and a number of other conditions are satisfied. The allocation is efficient only in the sense that no one can be made better off without someone else's being made worse off—the distribution of wealth that results could be extremely deleterious to the survival of the society. Clearly, most aspects of culture are not regulated by markets or prices, even in contemporary societies. Third, rational planning by leaders or institutions may also lead to group-beneficial outcomes. While the extent to which political institutions can ever be modeled as acting in the common interest is debatable, it is clear that most aspects of culture are not the result of rational planning. Finally, individuals may choose group-beneficial activities if they value those activities for their own sake, not because they benefit the group (Margolis 1982, Batson 1991). For example, men may fight to defend the group if they value heroism in battle. However, one is left with explaining how men come to have such preferences—otherwise, the explanation is that people choose group-beneficial behaviors because they like to do so. Thus, we do not deny that people make group-beneficial choices. We are claiming that when such choices occur they cannot be the result of mainly self-interested choice.

ants," together with their genotypes and environments, determine their behavior. To understand why people behave as they do in a particular environment we must know the skills, beliefs, attitudes, and values that they have acquired from others by cultural inheritance. To do this we must account for the processes that affect cultural variation as individuals acquire cultural traits, use the acquired information to guide behavior, and act as models for others. What processes increase or decrease the proportion of persons in a society who hold particular ideas about how to behave? Here we will consider two kinds of processes: biased cultural transmission and selection among social groups.

Biased cultural transmission occurs when individuals preferentially adopt some variants relative to others. Individuals may be exposed to a variety of beliefs or behaviors, evaluate these alternatives according to their own goals, and preferentially imitate those variants that seem best to satisfy their goals. If many of the individuals in a population have similar goals, this process will cause the cultural variants that best satisfy these goals to spread. For example, if the two variants are more and less restrictive forms of food taboos and individuals prefer the broader diet that results from the less restrictive variant, then that variant will spread. This process, which is important in the spread of innovations (Rogers 1983), often tends to cause groups living in similar environments to have similar behaviors.

However, biased cultural transmission can also maintain differences between groups of people living in similar environments. This can occur in two ways: First, a belief or behavior may be more attractive if it is more widely used than the alternatives. Many social behaviors have this character. For example, if food taboos are used as ethnic markers, then in a group in which the more restrictive taboo predominates individuals may choose that taboo over the less restrictive one because the social benefits compensate for the nutritional costs. Game theory suggests that many kinds of social interactions, including bargaining, contests, and punishment-enforced norms, will generate an astronomical number of alternative equilibria. Second, when individuals are unable to evaluate the merits of alternative variants, they may instead use a simple rule of thumb such as adopting the most common variant. This conformist form of biased transmission causes the more common variant to increase. For example, if the majority of a group observes the more restrictive taboo, it will tend to increase.

When either common-type-advantage or conformity maintains differences among groups, group selection can be an important force. Consider a large population subdivided into many smaller, partially isolated groups. Suppose that biased cultural transmission maintains cultural differences among these groups despite frequent contact and occasional intermarriage and that these cultural differences affect the welfare of the group. For example, groups in which restrictive food taboos are common may tend to harvest game at approximately the maximum sustainable yield, while groups in which less restrictive taboos are common overexploit their game

resources and suffer significantly poorer nutritional status as a result. Further suppose that social groups are occasionally disrupted and their members dispersed to other local groups and that the rate at which this occurs depends on the overall welfare of the group. Such disruption and dispersal may be the result of population decline, social discord, or the actions of aggressive neighbors. Poor nutritional status will contribute to these risks. Thus, according to our hypothetical example, groups with less restrictive food taboos will, on average, be more likely to be broken up and dispersed. Finally, suppose that as some groups decline and disappear, other groups grow and eventually divide, forming new groups, and that the rate at which this occurs increases with the overall welfare of the group. Thus, the growing, dividing groups will tend to have more restrictive food taboos than declining ones, and restrictive food taboos will tend to spread as a result of selection among groups. Others have proposed at least implicitly similar models (e.g., Peoples 1982, Divale and Harris 1976, Irons 1975).

This model of group selection differs from those analyzed in population biology in that biased transmission maintains variation among groups. Biologists have been concerned with whether group selection could allow the evolution of altruistic behavior. In these models, natural selection acts against altruistic behavior in every group, and this selection process tends to reduce variation among groups. The only process creating variation among groups is genetic drift, a very weak force. Thus, group selection can have little effect because groups are genetically very similar. In the model outlined here, it is assumed that various forms of biased transmission, potentially very strong individual-level forces, act to *maintain* differences among groups and group selection can predominate.

The form of group selection just outlined can be a potent force even if groups are usually very large. For a favorable cultural variant to spread, it must become common in an initial subpopulation. The rate at which this will occur through random driftlike processes (Cavalli-Sforza and Feldman 1981) will be slow for sizable groups (Lande 1986). However, this need occur only once. Thus, even if groups are usually large, occasional population bottlenecks may allow group selection to get started. Similarly, environmental variation in even a few subpopulations may provide the initial impetus for group selection. Some environments may lead groups to adopt group-beneficial traits because they are also individually advantageous. These practices may then spread by group selection into environments where they have only a group advantage. For example, restrictive food taboos may arise in a very heterogeneous environment in which it is important for individuals to specialize in narrow-range food-procurement strategies and only later spread by group selection to less heterogeneous environments where they mainly function to protect resources against the tragedy of the commons.

Unlike many genetic models, this form of group selection does not require that the people who make up groups die during group extinction. All that is required

is the disruption of the group as a social unit and the dispersal of its members throughout the metapopulation. Such dispersal has the effect of cultural extinction, because dispersing individuals have little effect on the frequency of alternative behaviors in the future; in any one host subpopulation they will be too few to tip it from one equilibrium maintained by convention or conformity to another.

Cultural group selection is very sensitive to the way in which new groups are formed. If new groups are mainly formed by individuals from a single preexisting group, then the behavior with the lower rate of extinction or higher level of contribution to the pool of colonists can spread even when it is rare in the metapopulation. If, instead, new groups result from the association of individuals from many other groups, group selection cannot act to increase the frequency of rare strategies.

## Empirical Evidence

To justify using this model of cultural group selection we need data that allow us to answer three questions:

1. Do groups suffer disruption and dispersal at a rate high enough to account for the evolution of any important attributes of human societies?
2. Are new groups formed mainly by fission in groups that avoid extinction?
3. Are there transmissible cultural differences among groups that affect their growth and survival, and do these differences persist long enough for group selection to operate?

To address these questions we present data on group extinction rates, group formation, and cultural variability drawn from the ethnographic literature of Irian Jaya and Papua New Guinea. We have chosen this area because it offers high-quality ethnographic descriptions of peoples that had not been pacified by a colonial administration. Colonialism is suspected by some to increase rates of intergroup conflict in stateless societies, casting doubt on data from areas like the American Plains, where contact predated good ethnography. New Guinea is unique in the amount of good ethnography obtained within a few years of first contact with complex societies. We have focused on pre-state societies because they are characteristic of more of human history than more complex societies and the basic institutions of human societies evolved under stateless conditions.

We have made an effort to sample as many ethnographies as possible, focusing on those dealing with pre-contact warfare among indigenous peoples. We have chosen to focus on warfare only because it is a conspicuous way in which groups become extinct and is likely to be recorded. Even where defeat in war is the proximate cause of an extinction, a variety of other factors may have precipitated the event by causing the defeated group to decline in numbers. Extinction through war may be the common fate of groups which have declined for some other reason.

We define a group as a territorial population that can

conduct warfare as a unit. An extinction is said to occur when (1) all members of a group are killed or (2) members of a group are assimilated into another group either wholly or in part. When a group is routed from its territory but remains intact as a social unit (or its fate is unknown), then a forced migration, not an extinction, is said to have occurred.

## GROUP EXTINCTION

To estimate the rate of group extinction for a region, three types of information are needed: (1) the number of extinctions, (2) the number of years over which the extinctions took place, and (3) the number of groups among which the extinctions took place. We were able to assemble this information for five regions in Irian Jaya and Papua New Guinea.

*The Mae Enga.* The Mae Enga live in the Central Western Highlands, where population density averages 40 to 43 persons/km<sup>2</sup> but reaches densities of over 100 persons/km<sup>2</sup> (Meggitt 1962:158; 1977:1). The immediate causes of war (Meggitt 1977:13) are land disputes (58%), other property disputes (24%), homicide (15%), and problems related to sexual jealousy (3%). Meggitt recorded a 50-year warfare history for 14 Mae Enga clans. In the 29 conflicts for which the outcome was known, there were 5 extinctions. Extinctions did not result from the killing of all group members; routed clan members were forced to disperse and find refuge among other clans, often with kin (1977:15, 25-27). There is evidence that these immigrants became culturally assimilated into their host group, usually within a generation (Meggitt 1965:31-35). Rapid assimilation occurred because true clan members received unqualified land rights, as well as economic, ritual, and military aid. As Meggitt (1977:190) notes, "Members of defeated and dispersed groups who have gone to live elsewhere have good political and economic reasons not to draw attention to their immigrant status but instead try for relatively rapid absorption into the host clan. . . . In consequence, the identities of extinguished clans or subclans are soon lost to public knowledge and in time such groups drop out of the genealogies of their former phratries."

*The Maring.* The Maring live in the Central Highlands, an area of relatively low population densities, averaging less than 20 persons/km<sup>2</sup> (Vayda 1971:22). Wars are usually triggered by a murder or attempted murder (56% of cases). The remaining 44% are fought over land, women, or theft (1971:4). Vayda's warfare history concerns 32 clan-clusters and autonomous clans and has a depth of about 50 years (Andrew Vayda, personal communication). He mentions 14 wars in which victims were routed from their territories. Only in one case was there a clear extinction, the other groups eventually returned. However, in two of these cases routed clans reclaimed their territory only with the help of the Australian police and probably would have become extinct otherwise. Rappaport (1967:26) explains that members of vanquished groups who find refuge in another group do not maintain their autonomy: "the *de facto* member-

ship of the living in groups with which they have taken refuge is converted eventually into *de jure* membership. Sooner or later the groups with which they have taken up residence will have occasion to plant *rumbin*, thus ritually validating their connection to the new territory and their new group."

*The Mendi.* The Mendi live in the Southern Highlands, where population density is 18 persons/km<sup>2</sup> (Megitt 1965:272). Ryan (1959) describes, for a 50-year period, the history of clan degeneration, extinction, and new group formation for a group of nine clans known as the Mobera-Kunjop. In this period there were three clan extinctions. In two cases, the clans were routed by warfare and absorbed by other groups; in the third a degenerating clan was eventually absorbed by another clan.

In two cases, vanquished groups did not suffer disruption but managed to remain functioning as an intact subclan in their host group. Ryan (1959:271) suggests that such accretionary subclans eventually become assimilated into their host clan: "The refugee group, consisting of sub-clan brothers and their families, may be large enough to assume the immediate status of a sub-clan. . . . Once the people have been accepted, granted land, and have settled down, there is almost no further differentiation made between them and the original sub-clans." However, individual nonagnates suffer discrimination from members of their host clans (Ryan 1959). They are less likely to receive bridewealth support (which normally comes from fellow subclan members) than are true group members, and therefore refugees have reason to want to assimilate into their host group: "Although it is asserted that acceptance is complete . . . marriage figures indicate that non-agnatic men tend to marry later than agnatic clan members, more of them marry only once, and more of them have only one wife at a time" (p. 269).

*The Fore and Usufura.* Berndt (1962) recorded detailed descriptions of war involving groups in four adjacent linguistic regions of the Eastern Highlands—the Fore, the Usufura, the Jate, and the Kamano. Fore population density is approximately 15 persons/km<sup>2</sup> and that of the Usufura 27 persons/km<sup>2</sup> (Berndt 1962:20). No values are given for the other linguistic groups. Berndt recorded one extinction during the ten-year period preceding his research. The group was routed in warfare and dispersed into several different districts in the area. The number of groups involved is slightly ambiguous; Berndt

indicates that his warfare data are most complete for only 8 districts in the area but mentions some 24 districts in his accounts of warfare.

*The Tor.* The Tor region is located on the northern coast of Irian Jaya (Oosterwal 1961). No density figures are provided. Oosterwal recorded a 40-year history for the 26 tribal territories in the Tor region. Four tribes suffered extinction either through peaceful absorption, military defeat and dispersal, or outright extermination (Oosterwal 1961:21–26). In one of the extinctions, Oosterwal is clear about the cultural assimilation of the extinct group: "Formerly the Mander language was only spoken by the Mander, but since the Foja have lived together with the Mander, they have adopted the Mander language entirely. Save for a small number of words, these Foja do not recollect any more of their own language. Their kinship terminology is also identical with that of the Mander" (p. 23).

Table 1 summarizes extinction rates for the five regions for which there were enough data to compute such estimates. We assume that the number of groups remains constant, which means that each extinction is followed by an immediate recolonization. To the extent that this assumption is wrong, extinction rates will be higher. We found no ethnographies which yielded an extinction rate of zero. In our sample, the percentage of groups suffering extinction each generation ranges from 1.6% to 31.3%.

It seems likely that other areas in New Guinea had similar group extinction rates. There is mention of group extinction in 54% (15/28) of the societies sampled. This is no doubt an underestimate, because the failure to mention an extinction in an ethnographic account of warfare does not necessarily mean that extinctions never occurred. In 89% (25/28) of the societies sampled, there is mention of either group extinction or forced migration (see table 2). The near-ubiquity of extinction and forced migration in the ethnographic record suggests that high rates of extinction were common throughout Papua New Guinea and Irian Jaya before pacification.

#### NEW GROUP FORMATION

Group selection is most effective when new groups are made up of members of a single existing group rather than of members of many different groups. If new groups

TABLE 1  
Summary of Group Extinction Rates for Five Regions of Papua New Guinea and Irian Jaya

Region	Groups	Extinctions	Years	% Groups Extinct Every 25 Years	Source
Mae Enga	14	5	50	17.9	Megitt (1977)
Maring	32	1–3	50	1.6–4.7	Vayda (1971)
Mendi	9	3	50	16.7	Ryan (1959)
Fore/Usufura	8–24	1	10	31.3–10.4	Berndt (1962)
Tor	26	4	40	9.6	Oosterwal (1961)

TABLE 2  
Mentions of Group Extinction and Forced Migration in Papua New Guinea and Irian Jaya

People	Extinction	Migration	Source
Mae Enga	+	-	Meggitt (1977:14)
Huli	-	-	Glasse (1959)
Melpa	+	+	Strathern (1971:55-56, 67)
Raiapu Enga	+	+	Waddel (1972:37, 186, 263-65)
Wola	+	+	Sillitoe (1977:79)
Maring	+	+	Vayda (1971:11-13)
Ok	+	+	Morren (1986:266-67, 272-73, 278-79)
Kuma	+	+	Reay (1959:7, 27, 32)
Chimbu	-	+	Brown and Brookfield (1959:41, 61, 263-65)
Usufura	-	+	Berndt (1962:242)
Jate	+	+	Berndt (1962:253, 260-61)
Fore	-	+	Berndt (1962:236, 251, 257)
Auyana	+	+	Robbins (1982:213-14)
Kukukuku	-	+	Blackwood (1978:102)
Gahuku	-	+	Read (1955:253-54)
Arapesh	+	+	Tuzin (1976:63)
Abelam	-	+	Lea (1965:196, 205)
Mailu	-	+	Saville (1926)
Kiwai	+	+	Landtman (1970[1927]:148-49, 204)
Dugum Dani	+	+	Heider (1970:119-22)
Ilaga Dani	-	+	Sillitoe (1977:77)
Bokondini-Dani	-	+	Sillitoe (1977:76)
Jale	-	+	Koch (1974:79)
Kapauku	-	-	Pospisil (1966)
Tor	+	+	Oosterwal (1961:21-26, 48)
Jaqai	-	-	Boelaars (1981)
Marind-Anim	+	-	Ernst (1979:36)
Bena Bena	+	-	Langness (1964:174)

are formed when a single group generates a daughter group from among its own members, then the daughter group will preserve the cultural variants common in the mother group. Cultural variants which facilitate daughter-group formation will become more common in the region as a whole.

Societies in Irian Jaya and Papua New Guinea are characterized by a segmentary social system (Langness 1964). When members of a social group become too numerous, the group may split into two similar groups. Conversely, when members of a social group become too few, they may be absorbed by another group at a lower segmentary level (Brown 1978:184-85, 187-88). There are numerous anecdotal accounts of new group formation (e.g., Brown and Brookfield 1959:57; Sillitoe 1977:79; Vayda 1971:17; Morren 1986:269-70), but Meggitt (1962, 1965) and Ryan (1959) provide the most detailed descriptions of new group formation in two highland societies.

The Enga have a nested hierarchy of patrilineal descent groups. The phratry is the most inclusive, followed by the clan, the subclan, the patrilineage, and the family. Groups everywhere in the hierarchy may grow or decline over time, generate daughter groups, or become absorbed by other groups: "Groups may emerge, increase in size and take over different functions, and in doing so achieve higher status by becoming co-ordinate with groups that previously included them. In absorption,

groups that are decreasing in numbers have to relinquish particular functions and descend to a lower level in the hierarchy. . . . If the decline continues, the groups eventually vanish" (Meggitt 1965:79). For a group to achieve or retain a particular position in the hierarchy, it must contain enough members to perform the functions appropriate to that position. For example, from 1900 onward, the population of one Enga clan began increasing noticeably until one of its two subclans could no longer support itself on its share of land and began encroaching on a neighboring clan's territory (Meggitt 1965:62-63). In skirmishes with the neighboring clan, the subclan functioned as if it were a sovereign clan, fighting and negotiating homicide payments independently of the second subclan, which was itself trying to expand in another direction. Eventually members of the two subclans settled at opposite ends of the clan territory and behaved as members of separate clans by intermarrying.

Meggitt (1965:78-79) gives an account of two Laiapu Enga phratries demonstrating extinction and new group formation. Each phratry was initially made up of four territorial clans. One expanding clan of phratry A attacked and killed many members of two clans of phratry B. The survivors of the two clans fled to other clans, and the victorious clan occupied the abandoned territory. This successful clan was becoming so large as to achieve subphratry status (Meggitt 1965:79). Ryan (1959) gives similar accounts of group extinction and new group for-

mation in the Mendi Valley. When clans become too populous, they expand into new territory and an offshoot subclan occupies it. The breakaway subclan attains clan status as it takes on more and more functions appropriate to a clan.

#### CULTURAL VARIATION AMONG GROUPS

Group extinction and group fission will lead to cultural change only if there are transmissible cultural differences that affect the extinction rate or the proliferation rate. Unfortunately, there is little evidence about the amount of cultural variation among local groups because so few ethnographers study more than one local group. Furthermore, there is even less evidence about how differences between local groups are related to individual and group fitness in New Guinea ethnography, although there is quite good evidence from other areas that such variation exists (e.g., Kelly's [1985] study of the causes of Nuer expansion at the expense of the Dinka). Nor is there evidence about how long such differences can persist in New Guinea groups. Archaeological and linguistic data from small-scale societies elsewhere document many examples of group expansion by cultures with more effective social organization in which the differences persisted for many generations during the expansionary phase (e.g., Bettinger and Baumhoff's [1982] study of the Numic expansion from southeastern California across the Great Basin).

Here we review three detailed studies of cultural variation among local groups in New Guinea. Two of these studies focus on the Mountain Ok of Papua New Guinea, while the third covers the lowland Tor region of northern Irian Jaya. Each of these studies suggests that there is substantial cultural variation among local groups.

*The Mountain Ok.* The Mountain Ok occupy the center of New Guinea and are made up of nine "tribes" based on ethnolinguistic affinities (Morren 1984:180–81). Within these tribes are endogamous "communities," sometimes composed of several exogamous clans. Only 15% of marriages take place between members of different communities (Barth 1971:176).

Ritual practice and belief vary considerably from community to community. Ritual knowledge, surrounded by secrecy, is fully shared by only a few elders in each community. It is transmitted at male initiations, where it is rationed out to initiates in steps. Barth argues that the ritual knowledge of different communities diverges because of error and innovation on the part of the few persons who control it. This produces intergroup variation in such things as the interpretation of important ritual symbols, the use of myths in ritual contexts, theories of conception, and the emphasis on symbolic constructions of human sexuality in ritual (Barth 1987).

Sacred objects used in the initiation ritual take on different symbolic meaning in different communities (Barth 1987:4–5). For example, fat from a wild male boar is emphatically "male" among both the Bimin-Kuskusmin and Baktaman of the Faiwolmin tribe. The pig's fat is mixed with various substances to form a red

paint which is applied to the bodies of novices, except for their "female" parts. In communities of the Telefomin tribe, however, the red paint signifies female menstrual blood. In fact, menstrual blood is sometimes added to the concoction, a practice which would be "completely destructive" to the integrity of the Faiwolmin rituals.

Modes in which cosmological ideas are communicated also differ among Ok communities. The Baktaman know almost no myths at all. A peripheral Ok community, the Mianmin, has a larger corpus of myths, but these are not central to their ritual events. The Bimin-Kuskusmin, in contrast, have an abundance of myths which are integrated into ritual (Barth 1987:5–6).

Theories of conception differ among communities (Barth 1987:13–15). Members of the Baktaman and neighboring communities believe that children spring from male semen which is nourished in the mother. Telefomin males believe that children are created from a fusion of male and female substances; females believe that a fusion of male and female substances creates only the flesh and blood of a child, while the female's menstrual blood alone forms the bones. Other communities are characterized by still different theories of conception.

*The Faiwolmin.* Variation among communities within the Faiwolmin tribal area of the Ok region may provide an example of cultural variation that is linked to group survival. Barth (1971; cf. Morren 1984) argues that more elaborate, communal rituals and specialized cult houses lead to more centralized community organization which increases the survivability of the communities embracing them and that communities with less elaborate cultural forms and more dispersed settlement patterns are more likely to become extinct. Within the Faiwolmin tribal area, ritual organization and specialization find their most elaborate expression in the centralized communities (Barth 1971:179–81). Male initiation is organized in seven grades through which males pass as age-sets. In western communities there are four such grades, and in the southeastern communities they range from four to one (p. 185). Different rituals take place in specialized cult houses. Most Faiwolmin communities contain three permanent cult houses as well as a communal men's house. As one moves east and southward from central Faiwolmin, the number of cult houses declines. Most of the southeastern communities contain only one permanent cult house, and some perform initiations in temporary structures.

There is also variation in social organization among Faiwolmin communities, following a similar west-to-east pattern of decreasing centralization (Barth 1971:184–86). The centralized communities of the Faiwolmin form compact villages around several types of semipermanent cult houses, and several exogamous clans make up an isolated, largely endogamous political unit. In the east the population is dispersed within the community territory, shifting household locations at intervals because of soil depletion or fear of sorcery.

According to Barth, "The dispersed pattern without

the cult houses . . . clearly organizes a smaller population for defense; and their history of displacement would seem to demonstrate this disadvantage" (p. 189); "the greater centralization clearly also offers military advantages and has resulted in conquest and territorial expansion of the more highly centralized groups in a general south-eastward direction" (p. 186). He argues that the elaborate rituals and the concomitant communal centralization were first introduced to the Faiwolmin communities from the northwest, and the diffusion of these cultural forms created cultural variation among them. Finally, selection among groups increased the frequency of those cultural forms conferring the highest fitness on groups (p. 188):

The distribution of [cultural] forms is thus generated by a number of simultaneously partly independent processes. A process of diffusion from an innovation centre . . . seems to be taking place. Simultaneously, the organization of local cultural transmission is such that both loss and improvisation occur and new local variants emerge. Different ritual forms imply different community types; these again confront each other in warfare and compete and replace each other on the basis of their unequal defensive and offensive capacities.

If Barth is correct, this is an example of group selection increasing the cultural variants which enhance group survival. He considers the alternative hypothesis that ecological processes explain the smaller scale of social organization. Although he cannot completely rule out an ecological explanation, he clearly suggests that a ritual system that organizes more people and thus leads to a greater frequency of victory in violent conflicts is leading to the spread of more complex ritual (pp. 188–89).

*The Tor.* Significant cultural variation also existed between tribal territories of the Tor region (Oosterwal 1961). The Tor region is divided into 26 tribal territories, but it has 8 separate languages (Oosterwal 1961: appendix). Thus, many adjacent tribes speak different languages, although the most common language, that of the Berrick, is known by members of all tribes (Oosterwal 1961:18). Oosterwal also notes these differences: "the three culture areas in the Tor district are very distinct. . . . [There are] differences in . . . kinship terminology, the kinship structure, the socio-religious aspect of culture, the way of counting, language-(dialect)-differentiations, and some aspects of material culture" (p. 46). These three "cultural areas," with associated kinship terminologies, are the Berrick, the Ittik and Mander, and the Segar and Naidjbeedj. Tribes in "transitional zones" have elements of all three cultural areas, and there is variation within each area (pp. 149–74). The terminology of the Berrick tribe emphasizes the age criterion (e.g., MoElSi is terminologically distinguished from MoYoSi) but often ignores the generational criterion (e.g., MoBr and SiSo call each other by the same term). The terminology of the second cultural area ig-

nores the generational criterion to a far greater extent. In contrast to those of the previous two areas, cultures in the third region have a strong generational aspect in their terminology. There is also variation within each of these three broad areas. For example, the cousin terminology of the Berrick is of the Hawaiian type (all cross and parallel cousins called by the same terms as those for sisters), while the Waf and Goeammer (of the same culture area) use the Iroquois type (FaSiDa and MoBrDa called by the same terms but terminologically differentiated from parallel cousins and from sisters, parallel cousins commonly but not always classified with sisters).

Although it is difficult to show that the particular group extinctions that we have counted for the five regions are due to persistent cultural differences, there is abundant evidence in New Guinea and elsewhere that cultural differences do lead to the success of some groups and the decline of others. For example, among the Fore the practice of mortuary cannibalism caused the spread of the deadly disease kuru. According to Durham's (1991:411–13) account of this episode, ritual cannibalism was originally adopted by Fore women as a response to a shortage of game. Nevertheless, the spread of the disease as a by-product of this ritual innovation threatened Fore groups with extinction until modern medical teams intervened. This case points up the ambiguous role of rational choice in the group-selection process. Individual calculation of advantage may often run counter to group advantage, especially when acts of cooperation are involved. Rappaport (1979:100) called attention to the role of the sacred in concealing group-advantageous traits from ready attack by selfish reason. As the Fore experience with kuru illustrates, traits disadvantageous to groups (and to individuals in this case) may sometimes be concealed in the same way.

Knauft (1985) gives an example of an apparent group extinction in progress. The completely acephalous Gebusi were a small and declining group at the time of his study. The better-organized Bedamini, making use of the big-man style of political organization, were able to raid Gebusi villages, but the Gebusi were unable to organize an effective defense or a retaliatory response. The boundary Gebusi villages most exposed to Bedamini raids were in the process of assimilating to Bedamini customs.

Knauft (1993a) also provides examples of cultural differences among seven culture areas along New Guinea's south coast. He describes how the Marind-Anim system of mythico-religious affiliation supports intragroup peace and the organization of large-scale head-hunting raids against distant enemies. By contrast, the Purari head-hunt among themselves and are declining relative to their neighbors. The existence of considerable variation at the scale of language groups suggests a considerable time depth for these differences. Although this variation occurs among larger groups than we are concerned with here, it does show that variation in sociopolitical organization encoded in myth and religion has a strong effect on group success.

It is also important that cultural differences between



groups persist on time scales sufficient for the operation of group selection. Although there is variation among local groups in New Guinea, there are no data bearing on the question of how long that variation persists. However, there is ample evidence for the long-term persistence of cultural differences among larger groups in other culture areas. For example, concepts such as *mana* and *tabu* typify political culture throughout Polynesia despite the fact that these societies have been isolated from each other for more than 1,000 years (Kirch 1984). Egerton (1971) documents the existence of important differences among four tribal groups living in two different types of environment, including two tribes belonging to the Bantu and two to the Kalenjin language groups, which have been separated for thousands of years. He notes that tribal history is more important than contemporary environmental circumstances in explaining most of the variation in attitudes and values measured in his data. The roots of the 38 languages of Western American Indians go back 6,500 years, and cultural differences among close neighbors with different cultural history have persisted for long periods (Jorgensen 1980:109). Belgium is divided by a stable linguistic boundary, with a Flemish North and a Walloon South (van den Berghe 1981); despite the fact that there is no topographical separation, the linguistic frontier has persisted for 2,000 years. Such examples from archaeology and history can be multiplied at will. While they do not prove that cultural differences can persist at smaller scales as required by the model, they indicate that this assumption is plausible.

## Discussion

Cultural group selection can explain the evolution of group-functional behaviors and institutions in human societies if two conditions are met: First, there must be some mechanism that preserves between-group variation so that group selection can operate. The model described above provides one such mechanism, and we have here tested several of the model's basic assumptions against the ethnographic record to determine if those assumptions are empirically realistic. Second, group selection must be sufficiently rapid to explain observed patterns of cultural change. The data from Papua New Guinea and Irian Jaya allow us to estimate the maximum rate of adaptation through group selection. Thus, we can estimate a minimum time period in which the group-selection process can give rise to group-level adaptations. Cultural changes which have occurred on a longer time scale are possibly the result of group selection; cultural changes which have occurred on a shorter time scale are unlikely to have resulted directly from group selection, but they may be its indirect result. For example, cultural group selection may lead to the evolution of property rights, which lead to efficient allocations of resources, or of political institutions that lead to group-beneficial decisions.

## MODEL ASSUMPTIONS

The data from New Guinea provide some qualified support for the model of group selection described above.

1. Group disruption and dispersal are common. Extinction rates per generation range from 2% to 31%, with a median of 10.4% in the five areas for which quantitative data are available, and the frequent mention of extinction elsewhere suggests that these rates are representative.

2. New groups are usually formed by fission of existing groups. The detailed picture from the Mae Enga and the Mendi is supported by anecdotal evidence from other ethnographies. We are not aware of any ethnographic report from New Guinea in which colonists of new land are drawn from multiple groups.

3. There is variation among local groups, but it is unknown whether this variation persists long enough to be subject to group selection and whether this variation is responsible for the differential extinction or proliferation of groups.

## RATES OF CHANGE

The New Guinea data on extinction rates allow us to estimate the maximum rate of cultural change that can result from cultural group selection. For a given group extinction rate, the rate of cultural change depends on the fraction of group extinctions that are the result of heritable cultural differences among groups. If most extinctions are due to nonheritable environmental differences (e.g., some groups have poor land) or bad luck (e.g., some groups are decimated by natural disasters), then group selection will lead to relatively slow change. If most extinctions are due to heritable differences (e.g., some groups have a more effective system of resolving internal disputes), then group selection can cause rapid cultural change. The rate of cultural change will also depend on the number of different, independent cultural characteristics affecting group extinction rates. The more different attributes, the more slowly will any single attribute respond to selection among groups. By assuming that all extinctions result from a single heritable cultural difference (or tightly linked complex of differences) between groups, we can calculate the maximum rate of cultural change.

Such an estimate suggests that group selection is unlikely to lead to significant cultural change in less than 500 to 1,000 years. The length of time it takes a rare cultural attribute to replace a common cultural attribute is one useful measure of the rate of cultural change. Suppose that initially a favorable trait is common in a fraction  $q_0$  of the groups in a region. Then the number of generations ( $t$ ) necessary for it to become common in a fraction  $q_t$  of the groups can be estimated (see appendix). The time necessary for different parameters is given in table 3. If we take the median extinction rate as representative, these results suggest that group selection could cause the replacement of one cultural variant by

TABLE 3  
*Minimum Number of Generations Necessary to Change the Fraction of Groups in Which a Favorable Trait Is Common Assuming a Particular Extinction Rate*

Initial Fraction Favorable Trait	Final Fraction Favorable Trait	Extinction Rate			
		1.6%	10.4%	17.9%	31%
0.1	0.9	192	40.0	22.3	11.8
0.01	0.99	570	83.7	46.6	24.8

NOTE: Extinction rates were chosen as follows: 1.6% (for the Maring) is the lowest estimate, 10.4% is the median extinction rate, 17.9% (for the Mae Enga) is the estimate based on the best data, and 31% (for the Fore/Usufura) is the highest estimate.

a second, more favorable variant in about 40 generations, or roughly 1,000 years. If we take the extinction rate calculated using the best data, those from the Mae Enga, this time is cut roughly in half. These calculations assume that colonizing groups are selected at random from the population. If group proliferation is as selective as group extinction, then the time is again cut in half, reducing the substitution time (based on the median extinction rate), once again, from 1,000 to 500 years. Not all extinctions and new group formations result from heritable cultural differences. Since the New Guinea ethnographic data are not sufficient to estimate the extent to which cultural variation influences group extinctions, it is not possible to make an estimate of the actual strength of group selection in New Guinea. If such estimates were possible, we expect that they would show that actual rates are considerably below the maximum. The maximum rate is nevertheless useful as an upper bound on the kinds of evolutionary events that cultural group selection might explain.

Our estimate of the maximum rate of adaptation suggests that group selection is too slow to account for the many cases of cultural change which occur in less than 500 to 1,000 years. For example, according to Feil (1987) the arrival of the sweet potato in the highlands of New Guinea sometime in the 18th century led to many important cultural changes. The introduction of the horse to the Great Plains of North America in the 1500s led to the evolution of the culture complex of the Plains Indians in less than 300 years. If the rates of group extinction estimated for New Guinea are representative of small-scale societies, cultural changes such as these cannot be explained in group-functional terms. There has not been enough time for group selection to have driven a single cultural attribute to fixation, even if that attribute had a strong effect on group survival. Processes based on individual decisions are likely to account for such episodes of rapid evolution (see Smith and Win-

terhalder 1992, Boyd and Richerson 1985). Such processes will not lead to group-functional outcomes except in certain special circumstances (see n. 2). It is possible that situations in which a trait or trait complex that increases the scale of cooperation is spreading such as the one Barth posits for the Faiwolmin do show rapid cultural group selection in progress. If the arrival of the sweet potato a few centuries ago did provide the subsistence basis for larger and more complex societies, we might expect to observe group selection in the early to middle stages of the spread of newly advantageous forms of social organization (Golson and Gardner 1990, Feil 1987).

These results also suggest that group selection cannot justify the practice of interpreting many different aspects of a culture as group-beneficial. A given extinction rate will lead to slower change if many different, unrelated aspects of the culture affect group survival. Suppose that both beliefs about food consumption and beliefs about spatial organization affect group survival. Then, unless each extinction occurs in a group in which both deleterious beliefs about food consumption and deleterious beliefs about spatial organization are common, some extinctions have no effect on the fraction of groups with deleterious beliefs about food, and some extinctions have no effect on the fraction of groups with deleterious beliefs about spatial organization. Thus a given number of extinctions must lead to slower evolution of each character than would be the case if only one of the characters affected group survival. If group selection can cause the substitution of a single trait in 500 to 1,000 years, the rate for many traits will be substantially longer. We know from linguistic and archaeological evidence that related cultural groups which differ in many cultural attributes have often diverged from a single ancestral group in the past few thousand years. Thus, there has not been enough time for group selection to have produced the many attributes that distinguish one culture from another.

It is important to understand that slow does not necessarily mean weak. When individual decision making is in opposition to group function in every group, then the relatively slow group-selection process will be too weak to favor group-functional behaviors. But when social interaction results in many alternative stable social arrangements, then individual decision making maintains differences among groups. If the resulting variation is linked to group fitness, then group selection will proceed. For example, consider the response to an environmental change such as the opening of New Guinea to trade with Europeans. Initially, changes in the costs and benefits of alternative beliefs and values will cause rapid cultural change, soon leading to a new sociopolitical equilibrium in each culture. But if there are many alternative equilibria, the nature of each new equilibrium may depend on existing norms and values. As long as the resulting differences affect group survival, selection among groups will continue. Over a millennium or so, New Guinea societies with a better political adaptation

to world contact will replace those with a poorer adaptation.

Thus it follows that these results do not preclude interpreting *some* aspects of contemporary cultures in terms of their benefit to the group. The model demonstrates that under the right conditions group selection can be an important process, and the data from New Guinea suggest that some of these conditions are empirically realistic. The data also suggest that the rates of group extinction are high enough to cause a small number of traits with substantial effects on group welfare to evolve on time scales that characterize some aspects of cultural change. Group selection cannot explain why the many details of Enga culture differ from the many details of Maring culture. It *might* explain the existence of geographically widespread practices that allow large-scale social organization in the New Guinea highlands, practices that evolved along with, and perhaps allowed, the transition from band-scale societies to the larger-scale societies that exist today.

Cultural group selection provides a potentially acceptable explanation for the increase in scale of sociopolitical organization in human prehistory and history precisely because it is so slow. Scholars convinced of the overwhelming power of individual-level processes have real difficulty in explaining slow, long-term historical change. Anatomically modern humans appear in the fossil record about 90,000 years ago, yet there is no evidence for symbolically marked boundaries (perhaps indicative of a significant sociopolitical unit encompassing an "ethnic" group of some hundreds to a few thousand individuals) before about 35,000 years ago (Mellars and Stringer 1989). The evolution of simple states from food-producing tribal societies took about 5,000 years, and that of the modern industrial state took another 5,000. Evolutionary processes which lead to change on 10- or 100-year time scales cannot explain such slow change unless they are driven by some environmental factor which changes on longer time scales. In contrast, the more or less steadily progressive trajectory of increasing scale of sociopolitical complexity over the past few tens of thousands of years indeed is consistent with adaptation by a relatively slow process of group selection.

These results should be interpreted with caution. It is important to remember that we have estimated a maximum rate of change for group selection on the basis of the assumptions that observed differences among local groups are heritable and that they are persistent. Unless both assumptions are satisfied, group selection will be less important than our results indicate. It is also important to keep in mind that we have studied only one form of group selection—competition among small, culturally heterogeneous groups. Other plausible group-selection processes might lead to more rapid change. For example, one cultural region may encroach upon another along a frontier, constantly capturing additional land and gradually expanding its domain. The Nuer and Dinka formed such a system before they were both over-

taken by European colonists (Kelly 1985). In state-level societies, we have to allow for internal group selection via the extinction and proliferation of subgroups, such as ruling classes, interest groups, firms, and the like, as well as selection among states themselves (Hannan and Freeman 1989). Some economists have considered business failure and proliferation rates sufficient to drive group selection of these units (Alchian 1950, Nelson and Winter 1982). The development of collective decision-making institutions like bureaucracies and legislatures may permit group-functional behaviors to be deliberately adopted by state-level societies. These processes might act at a much faster rate than we have estimated on the basis of tribal institutions.

In conclusion, these data suggest that group selection cannot explain rapid cultural change or the many differences between related cultures. However, they also show that group selection, perhaps in concert with other processes, is a plausible mechanism for the evolution of widespread attributes of human societies over the long run.

## Appendix: Time for Trait Substitution

Assume that there are two cultural variants—deleterious and advantageous. Each is at a local equilibrium under the influence of within-group processes. Groups are connected by the mixing of individuals, and there are many such groups. Groups in which the advantageous variant is common never go extinct. A fraction  $e$  of the groups in which the deleterious variant is common suffer an extinction each generation. The dynamics of this system are quite complicated because the frequency of advantageous variants within subpopulations in which that variant is common depends, to a small degree, on the frequencies of both variants in the population as a whole. However, if both variants are in local equilibrium, even when there is only a single population in which they are common, then it is roughly correct to regard the subpopulations as individuals and use formulas from population genetics (see Boyd and Richerson 1990a for a fuller treatment). Then, if the advantageous trait is common in a fraction  $q$  of the groups in the region, after one generation

$$q' = \frac{q}{(1-q)(1-e) + q}$$

and the frequency after  $t$  generation is

$$q_t = \frac{q_0}{(1-q_0)(1-e)^t + q_0}$$

Solving this for  $t$  yields

$$t = \frac{\ln\left(\frac{q_0(1-q_t)}{(1-q_0)q_t}\right)}{\ln(1-e)},$$

which was used to generate table 3.

## Comments

C. R. HALLPIKE

*Department of Anthropology, McMaster University,  
Hamilton, Ont., Canada L8S 4L9. 2 XII 94*

Soltis, Boyd, and Richerson are to be congratulated on providing, for the first time, a solid empirical test of the belief that functional/adaptive social traits are the result of some process of group selection. Their demonstration of the extreme slowness of such a process effectively places it on the margin of any evolutionary theory of human society. Endogenous processes (such as changes in the resource base) and diffusion are obviously far more powerful explanations, for which there is also abundant evidence.

It is worth noting, however, that this is yet another demonstration of the basic implausibility of the whole functionalist/adaptationist style of explaining social evolution, because some model of group selection is the *only* possible theory that has ever been produced to explain why we should expect functional/adaptive traits as the norm in human society. (I am excluding, of course, those traits which are conscious responses to obvious problems, such as bandages for wounds.)

Once this selectionist model has been rejected, the only solution to the functionalist dilemma is the one that I have advocated (Hallpike 1986:86–122), which is that there never was such a problem in the first place. This is because in small-scale societies with simple technologies there are many ways of organizing social relations and of adapting to the environment, and within very broad limits they will all work. This being so, it is futile to try to explain any of them as some kind of optimal strategy for anything, and the reason they exist will be a matter of historical contingencies. To call some cultural feature adaptive will only mean that it must meet some minimal criteria of practical adequacy. Functionalist/adaptive “explanations” always depend on the *post hoc* fallacy that because something is beneficial to someone in some way (which is never hard to prove) this must be why it has survived.

One cannot agree, however, with the authors’ attempt to salvage something of the group selection theory when they say, “Cultural group selection provides a potentially acceptable explanation for the increase in scale of sociopolitical organization in human prehistory and history precisely because it is so slow.” In the first place, endogenous processes and diffusion are quite adequate explanations for the slow increase in sociopolitical complexity to which they refer and therefore preclude any need to call upon group selection. But some of the most obvious examples of increase in social scale, such as the Roman Empire or the Industrial Revolution, have been extremely rapid, and these cases obviously cannot be explained by group selection. To move to the level of subgroups, such as interest groups or business firms, as the authors contemplate doing, is no solution because

such groups are themselves only components of wider social processes. If the demise of subgroups is to be taken as a valid instance of group selection, why should it be limited to firms that go bankrupt and not also include couples who divorce? The obvious absurdity of this example demonstrates that when we are discussing group selection we must confine ourselves to groups which are self-sufficient communities.

MASAKADO KAWATA

*Department of Biology, Faculty of Education,  
Shizuoka University, Ohya 836, Shizuoka 422, Japan  
(kawata@ed.shizuoka.ac.jp). 9 XII 94*

Soltis, Boyd, and Richerson’s article is an important analysis that shows when and to what extent cultural group selection plays a role in cultural evolution. It is a significant contribution to the fields of both anthropology and evolutionary biology. Although they do not deny a role for group selection over a long time period, they suggest that it cannot explain cultural change over a shorter period. I do not object to the main framework of their analysis, but I would like to add some points to their discussion.

The most important assumption of group selection may be that a difference in group properties causes differences in group survival and extinction. Soltis et al. recognize this assumption and discuss how cultural differences in groups relate to differences in group fitness. It is important, however, to distinguish group selection from group drift. If there is cultural variation among groups, some cultural traits may change in their frequency by group extinction or by new group formation even if the traits do not relate to the causes of extinction and formation of the group (i.e., are neutral). This process is similar to random genetic drift and therefore can be called group drift (Turner 1988). Both processes are potential causes of change in the frequencies of cultural traits.

Another important point that Soltis et al. do not discuss is the distinction between group properties and individual properties. Political organization, spatial distribution within tribes, and ritual practices are examples of group properties. In contrast, food habits adopted by individuals are examples of individual properties. If individuals can choose a food habit irrespective of group cultural forces such as the religious preference of the group, an increase in the number of individuals adopting the food habit may cause the extinction of the group. But in this case the group extinction is caused merely by the sum of individual deaths caused by the properties of individuals—individual food habits. Thus, this is an example not of group selection but of individual selection.

Soltis et al. suggest that cultural evolution by group selection may be a slow process on the basis of their low estimates of extinction rates. But there is another type of group selection that does not require group extinction. In evolutionary biology, group selection has sometimes been classified into two types: interdemetic and intra-

demic (Wilson 1983). The group selection that Soltis et al. discuss is analogous to interdemic group selection (or intergroup selection). In intrademic group selection, also called trait group selection, a difference in the growth rates of groups causes changes in gene frequencies (Wilson 1980). In this type of group selection, group properties should affect differential growth rates among groups. After the dispersal of individuals, individual properties that produce the group properties affecting growth rates increase in frequency in a global population. An analogous process may occur in cultural evolution (here this is called cultural trait group selection). For instance, a group property such as a political organization may cause an increase in the size of the group. Consequently, the group will produce more emigrants to, or will increase the chance of contact with, other groups. This, in turn, will increase the probability of cultural transmission to those groups.

Sober (1984) distinguished two concepts in natural selection: properties for selection (i.e., properties causing selection) and objects of selection (i.e., objects that can reproduce and die). For intergroup selection, properties for selection are group properties and the objects of selection are the groups. For trait group selection, in contrast, properties for selection are group properties but the objects of selection are individuals. Accordingly, for cultural trait group selection as for trait group selection, properties for selection are group cultural traits and objects of selection are individuals. Cultural trait group selection does not require the extinction of groups, as does intergroup cultural selection, and thus cultural change by this process may be more rapid. In addition, this process can be examined by using contextual analysis (Heisler and Damuth 1987) of present-day social groups. Intergroup selection and cultural trait group selection may affect the maintenance and change in frequency of cultural traits over a short time period, although the replacement of one cultural trait by another over such a short period cannot be explained by these group selections, as Soltis et al. have suggested.

BRUCE M. KNAUFT

*Department of Anthropology, Emory University,  
Atlanta, Ga. 30322, U.S.A. 28 XI 94*

Units of selection above the individual (and below the gene) are receiving increasing scholarly attention (see Wilson and Sober 1994); it is appropriate that group selection be seriously reconsidered in human cultural evolution. The rate of group extinction that Soltis, Boyd, and Richerson assess for precolonial interior New Guinea seems appropriate. A substantial review indicates that the rate of indigenous warfare, local killing, and group turnover was high in many areas of interior New Guinea (Knauft 1990, 1992; see also Healey 1985: 11–14 with more detailed information on Maring). Gebusi can be added to Soltis et al.'s specific cases (Knauft 1985, 1987); 1 of the 22 clans has become extinct in the past 40 years, and a second has no remaining male

members and will be extinct within a few years (Gebusi do not admit changes in clan affiliation such as cumulative patrilineality). Two other Gebusi clans may have become extinct since 1940 (no survivors are known, though it is possible that some survived outside my survey of clan genealogies), and several other clans are in danger of extinction. I estimate the Gebusi extinction rate to have been equivalent to 3–4 per 22 clans per 50 years, yielding a 25-year group extinction rate of between 6.8% and 9.1%. Gebusi clan extinction is due to natural demise and the killing of suspected sorcerers rather than the impact of introduced diseases.

Another case not cited by Soltis et al. is population replacement in the Ilaga Valley of Irian Jaya documented in detail by Larson (1986). From about 1910 to 1961, the indigenous Damal population was subjected to a series of 14 major wars; it declined approximately 15%, from 1,300 to 1,100. Over this time period, the intrusive Ilaga Dani population increased at least sixfold, from 600–700 to 4,100. However, significant Damal groups were displaced outside the Ilaga Valley and formed bitribal communities and political confederacies with Dani. This raises a long-standing problem that Soltis et al. skirt: What is a "group"? Presidential groups, political groups, culturally ascribed kinship groups, and groups of biogenetic kin are nonisomorphic. Under certain conditions, cultural groups can change their identity and their composition incrementally rather than simply "surviving" or "becoming extinct." This is theoretically important because, like most evolutionary modeling analyses, Soltis et al.'s is highly dependent upon its initial assumptions and definitions; a small change in the definition of "group" can produce a substantially different outcome.

The kinds of sedentary and relatively discrete residential kin groups that Soltis et al.'s analysis seems to assume for New Guinea are relatively late in evolutionary terms and not a good model for assessing the full potential of group selection over the longer course of human development (see Knauft 1989, 1991, 1993*b*, 1994, n.d.). Most dispersed foragers exhibited fluid residential composition facilitated by numerous fictive kin, classificatory clan, totemic, and affinal relationships. These arrangements were consistent with the social and residential flexibility needed for the full exploitation of resources that were dispersed, patchy, and hard to defend. Given the small population size and low density of such bands, this flexibility would not appear to lessen the importance of collective selection (e.g., see Rogers's [1990:408] suggestion that group selection via selective emigration is facilitated by mobility rather than by isolation of local groups). Important for Soltis et al.'s model, dispersed foragers from two geographically distant regions seldom fuse or interpenetrate to inhabit a new locale.

Concerning the maintenance of variation, Soltis et al.'s notion of group selection appears to adopt the conservative assumption that all traits will spontaneously diffuse between groups under conditions of social contact. While this may be the case for mating behavior and

gene pool dispersion among nonhuman populations, it is far from uniform for traits influenced by human culture—even among flexibly intertwined groups. Diversity in behavior and belief can be preserved in the face of social contact and in the absence of ethnic polarization between “groups.” Among Gebusi subgroups, for instance, chains of divergence in a number of residential, bodily, aesthetic, and discursive practices were evident despite highly prosocial affiliations and common tribal identity across the gradients. The strong need to preserve variation in order for selection to operate (Darwin’s dilemma in ignorance of Mendelian genetics) does not seem to be as much of a problem for group selection in human populations as Soltis et al.’s conservative assumptions imply. The complement to this microdifferentiation of culture is the distinctive cultural propensity constantly to generate and produce new variation. The great curiosity, neoteny, and cognitive development of humans provide the infrastructure upon which spontaneous cultural elaboration of human ideas and behaviors takes place on a continuing basis.

These comments suggest that group selection among humans may have been more important than Soltis et al.’s assumptions allow. More ethnographically realistic assumptions about human groups and about the spontaneous generation and maintenance of cultural variation are likely to increase the importance of collective adaptations in the consideration of human evolution.

KEVIN N. LALAND

*Sub-Department of Animal Behavior, University of Cambridge, Madingley, Cambridge CB3 8AA, United Kingdom. 7 XII 94*

Gene-culture coevolutionary theory is undoubtedly a valuable set of tools with which human scientists can explore the interaction between genetic and cultural processes. Over the past two decades, Boyd and Richerson have been at the forefront of the development of this theory. I consider their theoretical investigation of the feasibility and consequences of cultural group selection to be one of the most important achievements of the field in recent years. The significance of this paper is that, together with Soltis, they have set out to test this body of mathematical theory, using data from societies in New Guinea. The authors are to be commended for their efforts to integrate theoretical and empirical findings and illustrate how theory can spawn empirical investigation. I hope that this paper will act as a bridge to assist those motivated to tackle Boyd and Richerson’s more technical papers and will stimulate interest in the work of other practitioners in the field, notably Cavalli-Sforza and Feldman. At the very least, it has informed the debate on the feasibility of cultural group selection.

Now that Soltis, Boyd, and Richerson have established that cultural group selection is not implausible, perhaps they could reconsider whether cultural group selection can really explain self-sacrificial behaviour. The mechanism of group selection was of interest to evolutionary

biologists because of the possibility, now thought to be small, that it might lead to the evolution of altruistic behaviour. It seems to be a common assumption that cultural group selection could explain self-sacrificial traits (Campbell 1975). Yet even if cultural group selection is plausible, there are at least two good reasons to be suspicious of this assumption. First, how many traits are likely to impose a fitness cost at an individual level and still be able to increase the persistence or proliferation of groups? For a population to bud off into a new group requires sufficient individuals to people it, but self-sacrificial traits by definition reduce individual viability. Clearly the rate of group proliferation is not independent of natural selection. Does this mean that the only stable group-functional traits will be those also favored by natural selection? Can cultural group selection only operate in conjunction with natural selection? Second, unless the pressure to conform is intense, individual learning will reduce the frequency of maladaptive cultural traits. The authors mention the cannibalistic behaviour of the Fore, which facilitated the spread of kuru and almost certainly increased the chances of group extinction. It is interesting that the Fore did not eat people who died of dysentery or leprosy, since they had learned that these conditions were infectious, but other causes of death did not deter this practice (Lindenbaum 1979). This suggests a role for individual learning in the dynamic, eroding cultural variants which are obviously maladaptive. We might hypothesize that the only maladaptive variants that can be stably transmitted across generations will be those that pass the selective filter of individual experience. Perhaps the authors could clarify the conditions under which they would expect self-sacrificial behaviour to evolve by this means.

I wonder whether Soltis et al. may be underestimating the role of cultural group selection in other respects. They focus exclusively on extinctions as the elimination of populations of individuals rather than populations of cultural variants. If some cultural variants become extinct simply because the idea dies out or individuals choose not to propagate it, then the frequency of groups with the cultural variant will have been reduced just the same as if the population had been destroyed. Consideration of both types of extinction will increase the rates of change of cultural variants by group selection. Secondly, a cultural trait clearly does not have to affect the probability of group propagation or extinction to spread by group selection, although group selection is a weaker force when this is the case. Nonetheless, the extinction of a population is a very dramatic event compared with the death of an individual, the loss of an allele, or the extermination of an idea, since the frequency of a large number of traits in a large number of individuals is affected. Consider the fate of “neutral” cultural variants that do not affect individual viability: While natural selection does not change the frequency of neutral traits unless they are strongly associated with selected variation, in contrast group selection will change the frequency of all neutral variants. This raises the possibility that if the authors were simultaneously

to consider the dynamics of a number of traits (i.e., multilocus models at a cultural level), group selection could be found to be a more significant agent.

JAMES G. PEOPLES

*Department of Sociology/Anthropology, Ohio Wesleyan University, Delaware, Ohio 43015, U.S.A.*  
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Soltis, Boyd, and Richerson have given us another paper that extends and applies some of the evolutionary models formulated in the past fifteen years by Boyd and Richerson. In their pioneering approach, the frequency of a given cultural feature in a human group results from the operation of certain evolutionary forces that affect rates of intergenerational transmission (discussed and modeled in Boyd and Richerson 1985). The fact that the mechanism of cultural transmission is social learning rather than biological reproduction imbues culture with properties that make humans unique. Two of the most important of these properties are that (1) humans cooperate on a much larger scale than other organisms and (2) group selection is potentially a more powerful evolutionary force in human behavior than in other organisms (Boyd and Richerson 1982, 1987, 1990b).

The present paper attempts to determine whether estimated rates of group extinction among well-studied New Guinea peoples are sufficiently high for cooperation in warfare to be fixed by a process of group selection. A more general suggestion is that group selection is more likely to be responsible for changes over very long time spans than over short periods.

The authors perform a valuable service in pulling together available data on group extinction rates for pre-contact New Guinea. I agree with the essentials of their model of how group selection might work in human populations, and I applaud their effort to determine whether the conditions for the model are met by real human groups. My main reservations have to do with (1) the implications of their findings on group extinction rates and (2) the conclusion that group selection can explain only very long-term cultural changes.

1. The data presented on extinction rates are critical because group selection requires relatively high rates of biological or social extinction. In New Guinea, the authors doubt that group extinction rates are high enough for cooperation in warfare to have been fixed by group selection. Their skepticism arises from their unspoken assumption that observed extinction rates apply to the past as well as the present—that is, that rates have been roughly constant over long time periods. But if extinction rates were higher during previous historical periods, then past group selection could have fixed high levels of cooperation among present-day groups such that they seldom go extinct—that is, over long time spans groups approached equilibrium with one another, resulting in low extinction in the present. Indeed, under conditions of organized intergroup conflict, intuition as well as the New Guinea ethnographic record suggests that short pe-

riods of violent warfare alternate with longer periods of uneasy peace. To determine whether extinction rates are sufficiently high we need data collected during times of great hostility, not data gathered during peaceful intervals and not data collected after the group selection process may have run its course. Such data are difficult to find and collect. My first comment, then, is that information about recent extinction rates is an inadequate basis on which to judge whether cooperation could have been fixed by historical group selection.

2. The article's conclusion suggests that, under real-world conditions, group selection operates so slowly relative to other processes that it cannot explain most short-term cultural changes. However, this suggestion is not compelling, for the authors overgeneralize their findings: one cannot use data on extinction rates from one part of the world to conclude that group selection is unimportant elsewhere. We just do not know whether group extinction rates in other places and times are comparable to those given for New Guinea. Lacking such information, we cannot conclude (although certainly we can "suggest") that group selection is a weak force.

In my view, group selection can be a powerful evolutionary force to explain a given cultural feature(s) X when all of the following conditions exist: (1) coequal groups compete over resources, with the losers becoming socially or biologically extinct; (2) competitive success against other groups increases with increased cooperation; (3) the benefits of cooperation are public goods; (4) the willingness to cooperate depends upon cultural feature X, but actors are unaware of the connection between feature X and their cooperative behavior; and (5) competitive success leads either to territorial expansion through subdivision or to growth of the successful population(s), which replicates its cultural features over long time spans. "Coequal" in condition 1 means that no group has such a strong competitive advantage that it can reliably and regularly overwhelm its competitors. "Socially extinct" means that the group disintegrates as an organization and the members disperse. Condition 2 simply says that success varies with the ability of a group to induce its members to cooperate (all else equal). Condition 3 is necessary because if noncooperators can be excluded from acquiring benefits, then selfish rationality or tit-for-tat may be sufficient to lead to sufficient cooperation and selection between groups will not operate. Condition 4 requires that group members not recognize that their willingness to cooperate is partly due to the existence of feature X but believe that feature X exists for some other reason (i.e., the functionalist assumption). This condition is necessary because otherwise the characteristic to be explained (feature X) is more likely to be explained by planning or some other form of group decision making than by group selection. Condition 5 is necessary for feature X to spread among the metapopulation, as the article points out.

These five conditions may appear restrictive and group selection therefore rare. However, it is reasonable to believe that these conditions will often apply to many horticultural and pastoral peoples engaged in organized

intergroup warfare, to firms in a competitive marketplace, to political parties, to athletic teams, and to business associations. I suspect that feature X will commonly take the form of group-enacted rituals and ceremonies, ethnic and other emblematic symbols, abstract ethical principles, and values of loyalty.

ANDREW P. VAYDA

*Department of Human Ecology, Cook College,  
Rutgers University, New Brunswick, N.J. 08903,  
U.S.A. 21 XI 94*

Although generally an admirer of Boyd and Richerson's work on processes and mechanisms of cultural evolution (see Vayda 1995), I must question whether they and coauthor Soltis have been able to find in New Guinea data the evidence they need for a meaningful test of their model of group selection. Thus, for their crucial assumption that biased cultural transmission is a mechanism whereby cultural differences among small local groups are maintained despite contacts and intermarriage, there is no evidence at all. Consistent with this, there also is, as the three authors concede, no evidence from New Guinea that cultural variation among local groups "persists long enough to be subject to group selection and . . . is responsible for differential extinction or proliferation." And there *is* evidence of trading and marriage contacts, as well as other mechanisms, which would have—or, at least, could have—worked *against* the long persistence of particular cultural differences. As I noted long ago (Vayda 1966:294), the widespread cultural uniformity which has impressed some anthropologists in New Guinea (e.g., Pouwer 1961:1–2; Read 1954:6) may well have resulted from the trading and intermarriage which joined local groups in diffusion chains extending sometimes for distances of more than 100 miles (Pospisil 1963:337–38; Salisbury 1956:562; Vayda, Leeds, and Smith 1961:73 n. 10). I further noted in the same article that my own studies in the Bismarck Mountains on the fringe of New Guinea's central highlands indicated that even when wives coming from other groups were native speakers of different languages and made no substantial *direct* contributions to the culture of their husbands' groups, a result of marriage with such women was affinal connections serving as channels for cultural importations. Informants cited not only certain new crops and tools but also certain new rituals as having been obtained by virtue of such connections (Vayda 1966:295).

Other New Guinea ethnographers have described other mechanisms that would have worked against long persistence of particular cultural differences. Barth's Mountain Ok case (1987) is noteworthy because of the several paragraphs devoted to it by Soltis et al. To explain the differences that he found among Mountain Ok groups in rites and associated cosmological ideas which had evidently come from a common source, Barth referred to guesswork and improvisation by the elderly ritual experts who, with imperfect mnemonic capabilities,

were responsible for maintaining knowledge of the rites in secrecy between times of their performance every ten years or so. This explanation is cited and presumably accepted by Soltis et al., but they fail to mention that Barth (1987:24, 26, 27) referred also to borrowing from other communities as a means of filling the gaps in ritual specialists' memories. As variable combinations of what is remembered, what is improvised, and what is borrowed, ritual practices and beliefs may still differ among Mountain Ok groups at any one point in time, but the differences can hardly be taken as evidence of the kind of intergenerationally persisting cultural variations called for by Soltis, Boyd, and Richerson's model of cultural group selection.

As for evidence of local-group extinctions, I must question the decision by Soltis et al. to consider extinction only through warfare and their justification of this decision on the grounds that such extinction may be the common fate of declining groups. Among Maring there were, as indicated by my unpublished data on changes in local groups, considerably more local-group extinctions than the single one cited by Soltis et al. from my article on Maring warfare (Vayda 1971). These extinctions were not necessarily connected proximately with warfare; they occurred exclusively at the lower altitudes where Maring local groups were, because of environmental factors, much smaller and much more subject to deaths from malaria than in the higher, core areas of Maring settlement (cf. Lowman 1980 and the summary of it in Foin and Davis 1987:13).

My reason for referring here to these extinctions is merely to set the record straight rather than either to support or to oppose the Soltis-Boyd-Richerson model. In line with what I have said at the beginning of this comment, I regard evidence of local-group extinctions as having little relevance to their model in the absence of evidence of long-persistent cultural differences between those groups which become extinct and those which do not.

DAVID SLOAN WILSON

*Department of Biological Sciences, Binghamton  
University, State University of New York,  
Binghamton, N.Y. 13902-6000, U.S.A. 17 XII 94*

Soltis et al. make a valuable and judicious effort to measure rates of cultural change that can be expected to occur at the group level. The very fact that they are attempting to provide data for a subject that is dominated by speculation deserves praise. I think that their estimate of 500–1,000 years is reasonable for some kinds of cultural group selection but that other kinds can occur more rapidly. Thus, their suggestion that "group selection cannot justify the practice of interpreting many different aspects of a culture as group-beneficial" is not warranted by their analysis.

It is important to distinguish between two kinds of cultural evolution. Some cultural transmission rules perpetuate behaviors but do not automatically cause



them to spread through the population. For example, the rule "Do what your parents do" will simply cause traits to be passed from parents to offspring in the same fashion as genetic traits. Whether a particular trait increases in frequency will depend on differential births and deaths and therefore will have a time scale similar to genetic evolution. Other cultural transmission rules actually cause traits to spread of their own accord, sometimes very rapidly. For example, rats are normally reluctant to accept novel foods (which may be poisonous) but will readily do so if they smell the odor of the food on another rat. The transmission rule "Accept a novel food if you smell it on another rat" can cause the acceptance of a novel food to spread rapidly through a population without a differential birth-and-death process.

To understand the second kind of transmission rule, we must ask how it evolved. In the rat example, it is fairly obvious that the transmission rule is biologically adaptive because the novel food will not be poisonous if another rat has been eating it. Furthermore, it is adaptive at the individual level. Rats that follow the decision rule will have more offspring than rats in the same population that do not. Thus, the decision rule probably evolved by individual selection.

It is conceivable that the second kind of transmission rule can also evolve by group selection (see Wilson and Sober 1994 for a review of group selection as it relates to human behavior). For example, imagine that rats have a special alarm call that they give when their group is challenged by another, hostile group of rats. The alarm call is repeated by any rat that hears it before rushing to the source of the disturbance. The transmission rule "Call if you hear a call" does not increase the fitness of callers relative to noncallers in the same group but rather causes the whole group to mobilize quickly, increasing its fitness relative to other groups (at least as the example is constructed).

When we observe the cultural transmission of alarm calls, do we say that it evolves by cultural group selection? Obviously not, if we are looking at the here-and-now process of cultural transmission, because it spreads within the group in a matter of seconds. In a more ultimate sense, however, we are justified in saying that the behavior evolved by group selection, since the cultural transmission rule that promotes it evolved by group selection. We are also justified in interpreting this aspect of culture as group-beneficial.

To state the argument more generally, transmission rules that cause traits to spread through the population can evolve by within- or between-group selection. The role of group selection can be evaluated only by examining the fitness consequences of the traits. If the transmission rule consistently promotes traits that increase the fitness of groups relative to other groups, it probably evolved by group selection (as in the alarm-call example). If it consistently promotes traits that increase the relative fitness of individuals within groups (as in the food-acceptance example) it probably evolved by within-group selection.

The transmission rules that Soltis et al. consider are

an interesting mix of the two kinds of cultural evolution discussed above. The majority rule makes the most frequent traits actively spread to fixation within groups, but then a differential birth-and-death process at the group level is required for additional spread. Five hundred years is remarkably *short* as differential birth-and-death processes go. How long would it take a trait that is culturally transmitted from parents to offspring to spread by a differential birth-and-death process at the individual level? It is extremely important for us to know the probable rates of ongoing cultural group selection, and no more should be expected of the target article. However, for a complete understanding of group selection and cultural evolution we must examine the evolution of transmission rules that actively propel traits through populations. To the extent that they promote group-level functional organization, they may well have evolved by group selection.

## Reply

JOSEPH SOLTIS, ROBERT BOYD,  
AND PETER J. RICHERSON  
*Los Angeles, Calif., U.S.A. 20195*

We are grateful to the several commentators who have suggested useful amendments to our paper. Knauff provides an additional extinction-rate estimate from his work among the Gebusi. This estimate (between 6.8% and 9.1%) provides a 20% increase in the size of our sample! Knauff also makes a good point about the importance of how groups are defined. The size of groups, the degree to which they are bounded, and their internal structure are important empirical questions. Our simple model seems to be an adequate first approximation for precolonial New Guinea, but undoubtedly things are more complex elsewhere. As we note, the specific form of group selection that we modeled is only one of many possible forms.

Kawata makes two useful theoretical suggestions. As he notes, we neglected the effect of drift at the group level. Such a process will act whenever extinction and recolonization are random processes and the number of groups is small. Group drift has two effects: it reduces variation among groups in the same way that genetic drift reduces variation among individuals, and it introduces a random group-level process that may often oppose group selection. As a result, group drift will reduce the likelihood that group-functional behavior will evolve. Group drift is likely to be relatively more important than individual drift because the number of competing groups will typically be small. Kawata suggests that it is important to distinguish group and individual properties. We agree. Because we focus on selection among groups at different local equilibria, all selection discussed in this paper is selection for group properties. We also concur with Peoples's suggestion that group-

beneficial beliefs, if they do occur, are most likely to be involved in ritual and religion because such beliefs are most resistant to the corrosive effects of rational calculation.

Hallpike offers two reasons that group selection is even less important than our results suggest. First, he argues that group selection cannot account for the long-term increase in social complexity seen in the archaeological record because there are examples of rapid increase in scale and social complexity such as the expansion of the Roman state and the industrial revolution. There is no doubt that particular polities have vastly increased in size in short periods of time. One could add the Inca, Aztec, and Mongol empires to Hallpike's list, along with many other examples. However, the expansion of a particular political unit need not correspond to the evolution of beliefs, norms, and institutions that *permit* the increase in scale. It is likely that the cultural changes that allowed Rome to expand at their neighbors' expense were under way long before the Roman expansion and were part of a long tradition of city-state polities in the Mediterranean basin. Moreover, many norms and institutions that spread with Roman military and economic success did not disappear when the Roman state collapsed. Instead, they were adopted by other groups in Europe and the Middle East and, recombined with local concepts, may have provided the basis for Arab and later European states.

Second, Hallpike argues that selection among subunits of societies such as lineages or firms is not group selection because they are embedded in and dependent on a larger social system. He argues that we should limit the term "group selection" to self-sufficient communities. He attempts to demonstrate this by the *reductio ad absurdum*—if group selection can apply to firms, why not to married couples? We don't care very much what gets labeled group selection. However, Hallpike is wrong if he thinks that only selection among self-sufficient communities can lead to the spread of group-beneficial practices. Mae Enga clans are embedded in phratries, which, in turn, are embedded in the Mae Enga ethnic group. At lower levels there are subclans, families, and so on. If there are cultural differences between groups at any level in this hierarchy, and if these differences are heritable so that daughter groups are like their parents, and if these differences affect the probability of survival or production of daughter groups, there will be a selective process that leads to the spread of cultural beliefs or practices that enhance the survival or reproduction of groups at that level—that is, cultural attributes that benefit groups not individuals. The degree to which groups are self-sufficient is relevant only to the extent that it affects the necessary conditions for group survival or reproduction. Competition between firms can occur only in a particular cultural and institutional environment, and as a result business firms are not, in any sense, self-sufficient. They must recruit employees, import resources, and export goods or services. Nonetheless, there is much evidence that practices that enhance the ability of firms to survive and grow spread because

unsuccessful firms go bankrupt (Nelson and Winter 1982, Hannan and Freeman 1989). In principle, there is nothing absurd about selection among married couples. If married couples varied culturally, if these variations affected the divorce rate, and if these variations were transmitted to the next generation of married couples, then selection at that level would increase the frequency of beliefs that inhibited divorce. In fact, however, married couples probably do not transmit their particular social arrangements intact to other married couples, at least not very often.

We partially endorse Hallpike's claim that there are many solutions to group-functional problems. Such variation is consistent with the action of a slow, awkward, historically contingent process like group selection. However, his blanket dismissal of group functionalism on the basis of such evidence very plainly goes too far. It is easy to cite a vast number of well-described cases in which social-organizational differences influence the outcome of intergroup conflicts. Barth's (1981) classic study of Swat is a typical example. The feudal Pathan system could expand at the expense of Kohistani village-level polities, but only to where environmental limits permitted enough farm productivity to support Pathan warrior elites. Beyond that frontier, the Kohistanis had an advantage, and the intercommunity boundary has remained stable for hundreds of years. More generally, we take it that there are three features of human social groups that have to be explained: (1) Large-scale human societies work well enough to have made us the earth's dominant animal species in the past 10,000 years. (2) Human cooperative institutions are highly variable from place to place and time to time. (3) These institutions—even the best of them—are today very far from exhibiting adaptive perfection. Hallpike leans on evidence for 2 and 3 in order to discount 1, but 1 is, it would seem to us, empirically true. A relatively slow group-selection process, gradually culling through a myriad of complex alternative social arrangements against a background of ongoing technical change, can produce steady improvements in cooperative capabilities without reaching adaptive perfection for a very long time. Any mechanism which purports to explain human social evolution over the past 35,000 years or more must account for all three bodies of evidence. In general it is a mistake to think that adaptive and historical explanations are antithetical (Boyd and Richerson 1992). This mistake leads to the absurd dilemma that Hallpike erects.

Laland argues that cultural group selection is unlikely to lead to the evolution of self-sacrificial behavior because (1) most individually deleterious behaviors are also deleterious to the group and (2) when behaviors are individually deleterious they will be rapidly eliminated by individual learning unless the conformist effect is unrealistically strong. We disagree. There are many behaviors that are individually costly but group-beneficial. Such a payoff structure (called an *n*-person prisoner's dilemma by game theorists, a public good by economists, and the tragedy of the commons by human ecologists) arises in a wide variety of social contexts, includ-

ing environmental pollution, overexploitation of game and other common-property resources, warfare, collective political action, and many, many others. We also believe that a weak conformist effect can stabilize individually costly behaviors against the effects of individual calculation whenever it is difficult for individuals to discern the relative costs of alternative behaviors. Religious beliefs provide many examples. Religious ideologies create elaborately rationalized, difficult-to-doubt beliefs such as that there is an afterlife in which heroes are rewarded and cowards are punished. Dramatic ceremonies and effective systems of indoctrination generate great emotional salience for such beliefs. As a consequence, individual learning may have little effect on their spread. A group in which most people fervently believe that heroes will live forever in paradise may have an advantage in conflicts with more rational groups (Rappaport 1979).

Several commentators suggest that our data are biased in a way that underestimates the strength of group selection. Peoples cautions that New Guinea may not be representative, Vayda suggests that many extinctions may occur without warfare, and Knauff notes that the hunter-gatherers live in much more flexible, fluid population structures that may potentiate group selection. All of these objections are well taken. We have provided a single, rough upper-bound estimate on the rate of group selection for a particular form which seems to have characterized New Guinea societies in the first half of this century. It would clearly be very desirable to derive estimates for people living in other environments using different subsistence techniques. Our estimate may be robust, or it may be that changes in the details of how the process works will turn out to be very important. As does Knauff, we think that estimating group-selection rates for hunter-gatherer populations is of particular importance because it is plausible that cultural group selection occurring over much of the Pleistocene may have created social environments which favored genetic altruism. When we began this project we attempted to find comparable data for several other areas but were unsuccessful. We hope that this paper may stimulate others who are more knowledgeable than we are to publish additional estimates.

Kawata suggests that intrademic group selection may be faster than the interdemographic group selection considered here. While we agree that there may be other forms of group selection that could lead to more rapid social evolution, we do not think it is likely that intrademic selection could have this effect. Biologists distinguish between interdemographic group selection, in which long-lived, partly isolated groups compete, and intrademic group selection, in which competition is among ephemeral groups that are formed anew each generation. The central problem with both mechanisms is the generation of variation among groups. Many biologists believe that kinship is the only mechanism that can generate substantial genetic variation among the ephemeral groups posited in intrademic models. Elsewhere, Boyd and Richerson (unpublished) have modeled intrademic group

selection among alternative stable equilibria and found that it cannot generate the variation necessary for group selection to work. The reason is that rare beneficial equilibria cannot reproduce themselves and therefore such traits are eliminated by within-group processes.

Two commentators believe that the model of group selection we have outlined requires that groups be isolated from each other. Vayda argues that variation among groups cannot persist over long time periods because there is frequent contact and intermarriage among groups and such contact would rapidly destroy between-group variation. Knauff, in contrast, chides us for being unnecessarily conservative—group differences can persist, he argues, despite frequent contact and intermarriage—and as a consequence underestimating the importance of group selection. In fact, the model does not assume that frequent contact will necessarily erode variation among groups. Rather, it assumes that this tendency may be counteracted by the tendency of people to adapt their beliefs and values to local circumstances. If these adaptive processes, which we have labeled biased cultural transmission and guided variation, are strong, they can maintain differences among groups despite extensive mixing. Consider the following hypothetical example: There is a population subdivided into a number of groups with frequent contact and intermarriage. In most groups most people believe that nepotism is morally correct. However, there are a few groups in which most people believe that nepotism is wrong and should be punished. If adaptive processes are strong, they can maintain this situation indefinitely. New nepotistic immigrants who arrive in a group in which nepotism is thought to be wrong rapidly learn that nepotism is a bad idea, so that when yet more nepotistic immigrants arrive they find themselves to be in the minority and rapidly learn to avoid nepotistic behavior, thus maintaining the strategy that originally arose merely by chance. If, in contrast, adaptive processes are weak, then in a nonnepotistic group most of the immigrants will believe in nepotism and only a few immigrants will have rejected their previous beliefs by the time more immigrants arrive. This reduces the cost of behaving nepotistically, and thus even fewer of these new immigrants reject nepotism, nepotism eventually becoming the norm and the subpopulation coming to resemble the global population.

We believe that there is ample evidence that cultural differences among neighboring groups can persist for long periods of time. However, we also believe that it is important to understand the processes that maintain cultural variation because they may have important consequences. In the present context, that extinction results from the disruption of the group and that group selection requires that new groups be formed by fission both follow from the nature of the processes that are assumed to maintain differences among groups. If some other processes were important in maintaining differences between groups, as is the case in most genetic models, then group selection would work quite differently.

That two specialists who have worked in the same region can disagree so fundamentally about the nature of the persistence of cultural differences points up how much more we need to know about cultural variation. We have tried to show here how ethnographic data can be used to make rough estimates of most parameters in a theoretically significant model of cultural evolution. Such an estimate is better than nothing, but it is also not the last word on the importance of group selection. We hope that it will inspire others to do more and do it better.

Laland and Wilson suggest that group-beneficial traits may evolve more rapidly if they spread by individual choices rather than the differential extinction of groups. There is no doubt that this suggestion is correct if people make group-interested, rather than self-interested, choices. Moreover, there are experiments which suggest that people do just that under controlled conditions (Batson 1991), as well as when observed under "natural" conditions (e.g., voters and legislators are far less self-serving than cynical individualists allow [Mansbridge 1990]). The problem is accounting for people's preferential adoption of beliefs that are not in their own self-interest. Both theory and observation in evolutionary biology suggest that cooperative and altruistic behavior in large groups will be limited to close kin. Thus there must be something special about the human case. One way to solve this problem is to imagine that cultural group selection acting over the very long run led to the cultural evolution of cooperative norms among Pleistocene humans. In such a social environment, selection might then have favored *genetic* traits that predisposed people to further cooperation because such genotypes would avoid sanctions that result from noncooperation—an example of the Baldwin effect. It is also possible that the basic cultural values which structure human motivations have been subject to group selection, so that socialized individuals are inclined to make group-favoring choices (Richerson and Boyd 1989). If human individual and collective choice making is guided by at least partly unselfish motives, then effective arrangements for cooperation may evolve much faster than would be consistent with the action of group selection. Indeed, in a world where intergroup rivalries are important, it would be quite useful to have collective institutions that anticipate the eventual results of group selection in many contexts and get there first. However, the facts alluded to by Hallpike make us doubtful that human political evolution has been governed by any process that allows the rapid achievement of perfection.

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