

Chapter 13. EVOLUTION OF SOCIAL ORGANIZATION

“Honor, duty, country”

West Point Motto

“To us at the time, a suicide air force was a very natural thing, nothing more than a means of self-defense toward the end of the war. True, the war ended and saved me 28 years ago, but if I had to be a Kamikaze pilot again, I would.”

Sei Watanabe

Lt. Gen. Japanese Defense Forces, ret.

I. The Problem of Cooperation

A. *Three Unusual Features of Human Societies*

Human societies exhibit cooperation, coordination, and division of labor, three features that place them at striking variance with most animals. Cooperation involves individuals doing something for the common benefit of everyone in a social group, as when soldiers defend a whole nation against its enemies. *Coordination* involves everyone doing things one way instead of another so that social activity can proceed efficiently (Susden, 1986). For example, we all agree to drive on the same side of the road and to pronounce words in the same way to avoid the chaos that would result if everyone ‘did their own thing’ (as we children of the 60s once imagined possible). The *division of labor* results when different individuals undertake specialized tasks, and then exchange the products of their labor. The sexual division of labor is the most ancient example in human societies. Historically, men’s and women’s activities have differed fairly radically, but within the household each sex’s products are contributed to a common pot that family members draw upon.

Highly social animals are rare, and basic Darwinian analysis shows why (Alexander, 1974). An animal’s *conspicifics*, members of its own species, are its closest competitors for food, mates, shelter, and so forth. Groups are likely to be easier for predators to spot, and group living ought to favor the spread of diseases. The theoretically most interesting problem is competition. Why should any animal help its competitors? It will cost me some resources, ultimately fitness, to help you, and selection should favor me increasing my fitness, not yours. If one individual helps another, isn’t the smart thing to take advantage of the help, but never reciprocate? Animals are thus usually solitary, staying as far away from their fellows as is practically possible. In most mammals, the contact between the sexes is limited to mating, and “society” consists of the minimum coordination between adults

necessary for fertilization, mothers' contribution of resources to juveniles to the point of independence, and no division of labor at all. Bears are a good example. Except for mothers taking care of cubs, and brief mating episodes, they are belligerently antisocial.

Even in the case where animals do live in groups, the degree of cooperation, coordination and division of labor within groups is usually very modest. For example, in herds of grazing animals or in schools of fish, there is virtually no cooperation, or division of labor. There is just a system of coordinating movements. The evolutionary explanation here is that in very open environments with no place to hide, big groups of animals are a passive form of predator protection. Predators have to discover the herd in a vast, otherwise empty landscape. Once the herd is discovered, only a few can be eaten before the rest run away. Then the search for the herd must begin again. Life would be much easier for the lion and the tuna if wildebeest and sardines were evenly distributed. Individual victims would almost always be in sight, and there would be little chance of starving between finding them. The clumping of herds forces a feast-or-famine regime on the predator. The benefit to members of such herds is simply that when a predator does find a group, the bigger it is, the less chance you personally will be the lunch. Biologists call this sort of coordinated group a "selfish herd" because there is no cooperation, for example individuals actively guarding the herd or attacking predators. In essence, in a selfish herd animals are hiding behind each other; nothing more sophisticated is involved. In a dense forest, where hiding is easy, selfish herds are not found. Sometimes animals collect around a scarce resource, and are forced to be minimally social. Bears sometimes collect at prime fishing spots for example. In such circumstances, each animal defends the largest territory it can, though the rich resource often means this as small as a vicious paw-swipe or peck can reach.

When cooperation does exist, the groups are typically very small. Many birds form mated pairs that cooperate to raise a nest of young, but bird flocks, when they exist, are selfish herds. A division of labor is even rarer, aside from those differences directly enforced by the biology of sex. Even in the case of sex, the commonest form of "division" of labor is that males contribute less or nothing to the rearing of offspring compared to females. The discovery by ethologists that cooperation and complex societies are rare in the animal world was an important advance over the anthropomorphic ideas of early naturalists. Small societies are fairly easy to imagine through the mechanisms of *kin selection* and *reciprocal altruism*, as we'll see below.

There are three conspicuous groups of animals that are eusocial and have complex societies (Wilson, 1975). One set of social species occurs in the "lower" invertebrates. The Portuguese Man-O-War is an example (see figure 15-1) . It is actually a communal organ-

Figure 13-1. The Portuguese Man-O-War is an example of a collective organism where specialized individuals cooperate, coordinate, and specialize.



ism whose gas-filled float, digestive apparatus, and tentacles are all specialized individuals that cooperate, coordinate, and specialize to make this spectacular “jellyfish.” The second set of species occurs in the “higher” invertebrates, the social insects. Bees, wasps, ants, and termites also have societies with all three attributes well developed. Finally there are humans. Since Wilson wrote, one other eusocial mammal has been discovered, the African naked mole rat. *All cases of eusociality except humans turn out to be cases of kin selection*(see Section III below) *writ large, leaving us a unique problem for Darwinian explanation.*

The problem of complex societies did not escape Darwin. He realized that his mechanism of natural selection favored selfishness, and exceptions like bees and humans worried him. The sharpest theoretical problem is cooperation.

II. The Evolutionary Dilemma of Cooperation

A. Theoretical Advantages of Cooperation

The theoretical problem is especially acute because cooperation often seems to have huge benefits that natural selection usually can achieve. Ants, termites, bees, and wasps are very abundant. In the human case, we’ve argued that pastoralists live in groups to defend

their herds from human and animal predators (and to make effective raiding parties to seize animals from other groups). Two-against-one is very tough to beat; cooperation in defense and offense has very decided advantages if it can be organized. Similarly, cooperative hunting, such as humans practice, means that much larger game can be taken. Moreover, food sharing provides an insurance function that seems to be a general advantage for predators. In complex societies we've seen how a division of labor and exchange can increase human welfare. Humans seem to be very successful due to cooperation. Similarly, despite having evolved eusociality only once, ants are a hugely successful group. Other animals, such as our close relatives baboons and chimps, whose ecological niche is rather similar to that of hunters and gatherers, have not evolved cooperative hunting and division of labor. Recall that both chimps and baboons hunt, but without much cooperation and sharing; the dominant animal tends to monopolize the carcass regardless of who killed it.

B. Evolutionary Advantages and Disadvantages of Selfishness

Why is it so hard for cooperation to evolve, if it is so successful when it does evolve? This is a classical problem. Economists have analyzed the problem under the heading of the "public goods problem". Game theorists have dealt with the same problem in their research into the perverse logic of the "prisoners' dilemma game". Similarly, evolutionary biologists have addressed the tendency of selection to favor those traits that are advantageous to individuals rather than the group. In all of these manifestations, the problem is that the altruistic self-sacrifice of individuals for the common good is hard to explain.

The precise evolutionary reason for being selfish is straightforward: Suppose I sacrifice my selfish personal interests, fitness, or payoffs in a game so that everyone will be a little better off. If everyone does this, we'll all be better off, perhaps much better off if there are big rewards to cooperation and collective action. But what if there are individuals who cheat, taking advantage of others' altruism¹, but act selfishly themselves? When altruists are common, cheaters will have a big advantage, and when cheaters are common they suffer no penalty relative to other cheaters. Theorists have found it easy to imagine situations in which neither rational calculation nor natural selection will lead to much cooperation, and correspondingly it is much harder to produce situations where cooperation ought to arise. Perhaps this result is quite reasonable; cooperation is relatively rare in nature. But we also have to account for the conspicuous exceptions like humans that do live in large cooperative societies.

To pose the problem in a more formal way, let us adopt the economists' approach.

1. *Altruism* is defined as behavior by an individual organism that is either not beneficial or is harmful to itself, but that benefits the survival of others.

Public goods are those goods or services which are not depleted by an additional user, and for which it is difficult or impossible to exclude users. A typical example is national defense. Adding more people to a country does not make its borders any more expensive to defend, and every citizen is protected by whatever level of defense is provided. The defense of one is the defense of all, more or less. Economists argue that people will not ordinarily provide public goods in optimal amounts because rational individuals will find the private costs of providing their share of the public good exceeds the incremental benefit to themselves—even though the total benefit to society greatly exceeds this private cost. For example, economists find it hard to imagine why people vote. It costs each of us only a little time and effort to vote but it costs us *something*. The chance that our one vote will influence the outcome of even a local election is very small. Democratic government is good for us all, but why shouldn't I let you pay that cost, and save myself the time and trouble, given the tiny difference my one vote makes? According to this logic, we should all think this through, and not vote. Democracy will collapse, even though we were all better off when we had it.

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C. A Game Theory Example

One of the most common ways to illustrate the dilemmas of cooperation is to use simple game theory models. The philosophy is now familiar to you. We want to boil the essence of a problem down to a simple understandable model that schools our intuition about a whole class of problems. Game theory imagines that there are individuals interacting in the framework of a game with rules and strategies that can be played. The essential thing about games is that my payoff in general depends upon both my strategy and your strategy. Given a set of rules, and a specified set of strategies, the theorist asks “what is the right strategy to play?” “Right strategy” is often defined as the strategy that is individually “rational” (maximizes the payoff to individuals) or the one that is an “Evolutionarily Stable Strategy (ESS).” An ESS is one that selection can favor. If the ESS is common, no rare mutant strategy can increase. In other words, if a new strategy arises due to mutation from an existing strategy or migrates into a population, selective pressures cannot cause it to grow and replace an ESS. *One of the most famous results of game theory is that cooperative be-*

havior is not, in general, either rational or an ESS.

Let's use pastoralists collectively guarding their herds as an example to see what is the problem with public-goods-producing or altruist strategies. Imagine two herders, Genghis and Attila. We assume that each individual's animals are mixed in a common herd, so that any effort spent guarding benefits both men equally. Suppose that the average loss reduction (benefit) gained by an individual herder who guards is B and the cost he pays for guarding is C . The calculation that each herder should make is as follows:

Attila's Payoff Matrix With One Other Pastoralist:

Attila's behavior	Genghis's behavior	
	<i>don't guard</i>	<i>guard</i>
<i>don't guard</i>	0	$B/2$
<i>guard</i>	$B/2 - C$	$B - C$

If Attila doesn't guard and Genghis doesn't guard either, neither of them gains any benefit (B) nor pays a cost for guarding (C). Put your finger on the cell in which each player's 'don't guard' behavior intersects with the other's. You should have selected the cell with the lightest shading. What is the value given in that cell? If Attila guards and Genghis doesn't guard, what is Attila's payoff? Put your finger on the cell in which these two behaviors intersect. You should have selected the cell with the next-to-the-darkest shading; Attila's payoff is half the benefit ($B/2$)² minus the cost of guarding (C).

For simplicity sake, we'll assume Genghis's payoff matrix is identical. There is no problem here if $B/2 > C$; both will be selfishly motivated to guard. But suppose $B/2 < C$, but $B > C$. Now, both Genghis and Attila will be better off if both guard, but if both are "rational", neither will guard. Notice that no matter what Genghis does, Attila is better off if he does not guard (when $B/2 < C$ but $B > C$). If Genghis doesn't guard, Attila will be better off if he doesn't and if Genghis is so foolish as to guard, Attila is better off if he takes advantage of him. Under this system of payoffs, it is irrational to guard; neither herder will guard, the public good of herd protection is not furnished, and both will get 0 payoff. If we imagine that payoff means Darwinian fitness, Don't Guard is an ESS. When common, it cannot be invaded by Guard, but when Guard is common, rare Don't Guard individuals will have the parasite's field day taking advantage of all the guarding while avoiding the cost.

2. because he share's the benefit equally with Genghis

If this common analysis is correct, people will be better off if everyone cooperates, but everyone will be motivated to cheat, to save the private cost of producing the public good, hoping someone else will do it. But everyone has the same motivation to cheat. Therefore, cooperation is neither rational nor an ESS. Cooperation doesn't evolve.

The problem gets much worse as groups get larger. Consider Attila's payoff matrix if he is in a group of N pastoralists, M of whom guard and the rest don't:

Attila's Payoff Matrix With 'N' Other Pastoralists:

Attila's behavior	
	His payoff if M others guard
<i>don't guard</i>	B(M/N)
<i>guard</i>	[B(M+1)/N] - C

Now, in a big camp, Attila is even less motivated to guard. If N is at all large, his help guarding the herd provides only a small incremental benefit (+B/N) to himself, but his cost remains the same, C. A great deal of theoretical attention has been paid to this problem, and it is not an easy one to solve. Selection will not favor guarding in this circumstance. Suppose that B and C are measured in units of fitness. Unless B is very large, or N quite small, or C quite small, the fitness of altruistic guarders will be less than selfish non-guarders.

It might be supposed that the possibility of punishment will cause people to do their fair share, but punishment is itself a public good. Attila is a tough brute, and it is likely to cost Genghis something to punish him. But in a large group, everyone will benefit if Attila is punished if he does not guard. Genghis is liable to figure it is not worth his private cost to punish Attila, though everyone would be better off if he did. This is the same problem as guarding the herd in a new guise. The dilemma of punishment is familiar to you as the problem of reporting small property crimes. We'd all be better off if we reported every crime because it would help the cops catch the bad guys. But if it is more trouble to me personally to report a small crime, why should I bother? (Actually, games with punishment are just now being studied, so the consequences of punishment are not yet clear.)

The problem is that people, unlike bears, don't behave according to theory! Any modern infantry's junior officers are an extreme, but very common, example. To provide national defense they engage in acts that are very frequently fatal. The deliberate, premed-

itated suicide of the kamikaze a bit more than West Point expects, but West Point expects much more from a 2nd Lieutenant than you could expect of a bear. The common voter is, in his and her own small way, just as *baka* (Japanese for crazy) as a Kamikaze pilot according to the game theory analysis.

There must be something wrong with this simple calculation in the special case of humans and the other cooperative animals. Just what is wrong, however, is the center of long-standing debate. (Incidentally, psychologists often ask people to play cooperation games in the laboratory. Most people cooperate when the theory says they should cheat. An exception is economics students; they have been taught about selfish rationality and that it is OK, if not a virtue. Having learned the theory, they obey it!)

This brings us to the problem that will occupy the remainder of this chapter: Given that we can explain the fairly common cases of small-scale cooperation, we want to ask if any of the standard animal mechanisms of cooperation are sufficient to account for the extremely high levels of cooperation found in humans compared to other mammal societies. How do we do what otherwise only jellyfish and bugs can do?

KEY QUESTION:
Are any of the standard animal mechanisms of cooperation sufficient to account for the extremely high levels of cooperation found in humans compared to other mammal societies?

III. Kin Selection Theory

A. Darwin's Worry

Darwin worried specifically that the self-sacrificial altruism of the worker honeybees was not in accord with his theory of evolution by natural selection. Then he saw the answer: in bees, wasps and ants, *workers are daughters of the queen*. Altruistic worker variants are cooperating, helping the queen produce other daughters and brothers, the reproductive. The altruistic worker's heritable variation for altruism is not passed on directly, but through its siblings who will replicate the cooperative impulse due to family resemblance. In other words, altruistic behaviors arose from shared heritable variation.

B. Inclusive Fitness or Kin Selection Theory

W.D. Hamilton (1964) extended and formalized Darwin's insight into one important mechanism, *inclusive fitness*, that can favor the evolution of altruism and cooperation. John Maynard Smith (1964) termed it *kin selection*.

Hamilton deduced the benefit-cost rule for altruistic behavior: $B/C > 1/r$, where r is the probability of getting the same gene as someone else by common descent. (r is also the fraction of genes a potential altruist has in common with a potential recipient of her largess—the fraction that they are *I*dentical by *C*ommon *D*escent, ICD). That is, it is only the genes that are shared by virtue of a known genealogical relationship that are entered into the calculation.

Let's examine the example of genes ICD between full siblings:

	<i>Mother</i>	<i>Father</i>	Each sibling gets 1/2 of each parent's genes. Because of independent assortment of chromosomes, this sample is independent; so, on average, each sibling will share 1/4 of each parent's genes.
	2n	2n	
<i>Offspring A</i>	1/2	1/2	
<i>Offspring B</i>	1/2	1/2	
$r =$	$1/4$	$+ 1/4 = 1/2$	

Half sibs are related by 1/4, first cousins by 1/8 and so on, and B/C calculation must be adjusted accordingly. This is true in any sexual reproduction system where each offspring's sample of its parent's genotype is independent³.

Put anthropomorphically, if I am an altruist, I can gamble there is at least a 1/2 chance that a given brother or sister is also an altruist because we are that likely to share the same altruist gene ICD. If I can help one of them raise 2 offspring at a cost of less than one to me, I will (on average) increase the number of copies of my altruist gene in the population. Inclusive fitness is like dollars—selection encourages individuals to get as much as possible.

Another evolutionary puzzle for you to think about: Chimpanzees are said to share some 90+ percent of their genes with humans. Human races are much more similar still. Why can't we substitute 0.9+ for r in Hamilton's rule, and predict near-perfect cooperation even between closely related species, much less between individuals within a species? Why does Hamilton's rule stress *identity by common descent*, rather than total number of genes in common? Hint: What happens to the frequency of an altruist gene in a population where there are also non-altruists if there is an act of indiscriminate altruism to completely unre-

3. Mendel formulated the "law of independent assortment" which is applied here when we calculate genetic relatedness. Mendel thought that "genes segregate independently at meiosis so that any one combination of alleles is as likely to appear in the offspring as any other combination. It is now known... that genes are linked together on chromosomes and so tend to be inherited in groups. The law of independent assortment therefore only applies to genes on different chromosomes (Tootill, 1981:132)."

lated individuals? A kin altruist needs to be quite discriminating to protect its altruism from going to waste. If you see altruism as allocated on the basis of direct kinship links, and why total% of genes in common is irrelevant, you understand kin selection pretty well.

*An individual's inclusive fitness is its own offspring + $r * x$ offspring of relatives (but only counting the relative's children that are due to the altruism of the donor individual). Hamilton's rule suggests that selection will act to increase inclusive fitness rather than simple individual survival and reproduction. In cases where relatives live close together, selection can thus favor a measure of nepotistic "altruism" if individuals can help their relatives reproduce in conformance to the $B/C > 1/r$ rule.*

In cases where relatives live close together, selection can favor a measure of nepotistic altruism if individuals can help improve their relatives' reproductive fitness, & the net reproductive benefit to altruists is greater than the costs they bear.

C. Empirical Evidence

Most animal societies in which cooperation is important are kin-based. Kin altruism is frequently observed in nature. In many primates, such as baboons and macaques, the basic social unit of the troop is a set of related females, say four or five sisters and their offspring. Males disperse from their natal troops and enter foreign troops in which they have no relatives. There is a good deal of cooperation among females of a matriline in encounters with females from other matrilinies, for example. Cooperation among males is limited to unstable coalitions and hostile relations are the norm. In some species, for example chimpanzees, the situation is reversed and a group of related males forms the core of the group. Jane Goodall has observed dramatic examples of cooperation among related males, especially in aggressive encounters with neighboring groups (one of her groups exterminated another as males went on collective, murderous raiding parties). The rule, that when there is conspicuous cooperation it is usually among relatives, thus commonly corresponds to observation.

Another famous example of the workings of kin selection is the case of the haplodiploid hymenoptera (bees, ants, and wasps). In these and some other arthropods, males result when females lay unfertilized haploid eggs (so that a male only has one set of chromosomes, while females have the usual double diploid complement). This leads sisters to be

related by 3/4 rather than usual half:

	<i>Mother</i>	<i>Father</i>	Since males are haploid, they transmit only one set of chromosomes, and the daughter's sets of father's genotype are not independent samples. The halves of daughter genotypes received from fathers are the same.
	2n	n	
<i>Offspring A</i>	1/2	1/2	
<i>Offspring B</i>	1/2	1/2	
$r =$	$1/4$	$+ 1/2 = 3/4$	

Hymenoptera (bees, ants, wasps), with haplodiploid inheritance structures, have several independent origins of eusociality. The colonies are associations of related daughters of the Queen, with this unusually close relatedness. Some sociobiologists argue that haplodiploidy is a preadaptation to sociality, and that is why there are so many examples of highly social species in this Order of insects. Since the worker sisters are even more closely related than normal sisters, altruism can more easily evolve. The threshold B/C ratio is lower. Termites are a bit of an embarrassment for this argument, as they are highly social but diploid.

Note that *this is another example where the structure of the inheritance system affects what selection can favor*. The social hymenoptera, the possible role of selection on non-parental cultural variation, and sex ratio distortion all illustrate the same point.

IV. Reciprocal Altruism

A. Theory of Cooperation With Repeated Plays of the Game

Another mechanism for producing (usually) small-scale altruism, is establishing trust between pairs of individuals who reciprocally help each other (Trivers, 1971). A political scientist Richard Axelrod has collaborated with W.D. Hamilton (1981) to study this mechanism in the context of repeated plays of prisoner dilemma. Suppose we imagine a game with the basic structure of our guarding game above. But let us suppose a somewhat more complex situation and a more complex strategy. Suppose that Attila and Ghengis don't just interact once, but rather live in the same camp for a fairly extended period. Also suppose they can use *contingent strategies*. For example, the first night in camp, Attila might figure "on the off chance that Ghengis is another good guy like me, I'll guard tonight. If he also guards, I'll keep guarding, but if he doesn't I'll stop guarding until he starts." Axelrod and Hamilton call this the "tit-for-tat" strategy. If Ghengis is a good guy, the herd will be guarded and both will get benefits for as long as they remain together. If Ghengis turns out to be a bad guy, Attila suffers the cost of altruism, but only for one night. If both are

bad guys, neither will pay the cost of guarding nor reap its benefits.

An evolutionary analysis of this game shows that the tit-for-tat strategy is an ESS if the game persists for enough nights. If the B/C ratio is high, any given game need not have too many iterations for tit-for-tat to be an ESS, but if the B/C ratio is closer to 1, the number of iterations must be large. A rare mutant non-guarder will be at a disadvantage because it will get only one parasitical payoff per set of turns, while the guarders will get multiple pay-offs for cooperating as long as the game persists. It is a little hard for guarding to get started when it is rare⁴, but there are ways around this. For example, a little kin selection will get tit-for-tat started.

To many people, the idea that tit-for-tat, as well as strategies with the same basic property, will work is quite intuitive. If you have some way of coercing and punishing other people you can induce them to cooperate, and the theory seems to support this idea. There are of course many strategies of this type and many as yet unexplored complexities in the reciprocal altruism problem. This is right now a booming field of research.

B. Trivers' (1971) Examples

Robert Trivers at U. C. Santa Cruz introduced the idea of reciprocal altruism in his classic paper with some nice examples. *There are fish and shrimp on tropical reefs that clean the insides of the mouths of larger fish.* Some mimics of these “cleaner-fish” take a bite out of the host instead. Of course, the cleaned fish can always cheat by eating the cleaner just as it finishes cleaning. Trust must be established on both sides. Cleaners have conspicuous coloration and stylized displays. They also have rather permanent stations where they display their willingness to clean. Apparently this allows enough trust to develop so that cleaners can evolve even when the possibility of mimic cleaners complicates things.

Trivers' other conspicuous example was humans. We live a long time and commonly form long-lasting friendships, trade relationships, and so forth. We are smart, so we can be very discriminating, stopping reciprocation with those that disappoint us⁵.

4. All bad guys is also an ESS, see if you can determine why.

5. Although non-altruists' deceptive tactics may also get more sophisticated as we get smarter. This can lead to an “arms race” where cheaters evolve new ways to cheat and their victims evolve new ways to detect and protect against cheaters. This insight is the basis for my own work examining how the nature and distribution of crime evolves in human populations.

V. Sociobiological Explanations for the Scale of Human Social Organization

A. Kin Selection + Reciprocal Altruism?

Alexander (1979, 1987) argues that simple kin selection plus lots of reciprocal altruism will explain human levels of cooperation. He introduces the term “indirect reciprocity” for the tendency of people in a diffuse network of cooperation to behave cooperatively to strangers on the premise that “what goes around comes around.” However, it is hard to explain costly altruism like military heroism with such a concept. The theory of reciprocal altruism runs into difficulties when groups get “large” (i.e. ≥ 10 individuals). This is the problem of the N sized group of herdsmen given above. So far, the theoretical work on this topic indicates that tit-for-tat works well in small groups (e.g. 2-3) but breaks down very rapidly as group size increases.

W.D. Hamilton (1975) and P. van den Berghe (1981) think that modern scale of human society is an evolutionary mistake. There is some group selection in ‘primitive’ human societies because of warfare and group endogamy (marriage within a group) which tend to reduce intra-group variation and raise group extinction rates. They suggest that the impulse to cooperate evolved due to kin or group selection in the relatively tiny, simple societies of our hunting and gathering past, and that this impulse misfires in the present because the rapid cultural evolution of social complexity has not given selection an opportunity to correct our tendency to treat large groups of strangers as if they were relatives or band-mates. General Watanabe is acting as if every Japanese is a close relative, as they might have been in the hunting and gathering societies in which the heroism impulse arose. Recall that all human groups were small and close-knit until relatively recently.

A major problem with the Hamilton/van den Berghe approach is that the common practice of victorious warrior groups is to incorporate vanquished women and children into their groups. This would produce a high flow of cowardly (or at least poor warrior) genes into the most successful warrior groups. This flow of women to victorious groups seems common, and means that group selection on human societies, even at the level of small, warring groups with lots of group extinction may be difficult.

B. Something Special About Culture?

This is an example of a research topic in human ecology where there is plenty of room for new ideas. *Nobel Laureate Herbert Simon (1990) recently suggested that two factors, human docility and bounded rationality, can account for the evolutionary success of genuinely altruistic behavior (i.e., behavior that cannot be explained by reciprocal altruism or inclusive fitness).* Simon defines ‘docility’ as receptivity to social influence. Since

being receptive to social influence often contributes to a person's genetic fitness in human species, Simon argues that the physical traits that tend to make one more docile will tend to be favored by selection. "As a consequence, society can impose a 'tax' on the gross benefits gained by individuals from docility by inducing docile individuals to engage in altruistic behaviors. Limits on rationality in the face of environmental complexity prevent the individual from avoiding this 'tax' (Simon, 1990:1665)." It is not clear to us from why docility in the sense of a susceptibility to altruism automatically has to arise from a tendency to imitate.

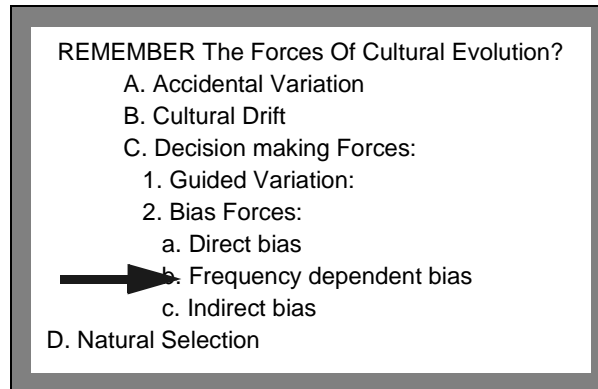
VI. Cultural Group Selection

A. Introduction

Human eusocial cooperation is unique and so is our dependence on culture. Is this coincidence or causation? The reciprocity mechanism just doesn't work well for large groups. The closest animal analog of human societies in degree of cooperation, coordination, and division of labor are those of the social insects, but our "queens" do not suppress the reproduction of our "workers;" so the kin selection with large mechanism isn't the exact answer. It is certainly probable that kin selection and reciprocity are important to explain parts of the small-scale parts of human cooperation, but they don't seem sufficient to explain the cooperation of dozens of weakly related Hunters and Gatherer, much less the millions of members of a modern society.

Simon's idea has the virtue of treating one unique feature of humans, culture, as the cause of another, large-scale cooperation among non-relatives. This is a natural approach to the apparent fact that humans are a unique special case as regards cooperation. In this section, we pursue a hypothesis of group selection on cultural variation, which is akin to Simon's idea, but with a more explicit mechanism. The hypothesis is that the use of frequency dependent bias (1) might have been favored by selection and (2) result in group selection on culture as a by-product. The argument is much like the hypothesis that haplodiploidy results in eusociality among the hymenoptera. Haplodiploidy is apparently (1) fairly widely evolved as a sex determining mechanism, which (2) makes haplodiploid species susceptible to exaggerated kin selection as a by-product.

B. Evolution of Frequency-Dependent Bias



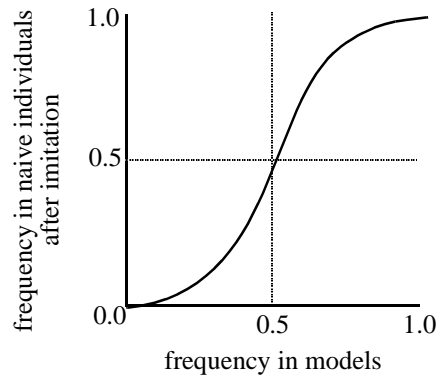
Frequency dependent biases are decision rules for adopting cultural traits that use the commonness or rarity of traits as a basis for deciding whether to imitate or not. If you are a non-conformist, you try to be as unlike most people as possible. If you are a conformist, you try to be as similar as possible. Here we are interested in conformist transmission.

A conformist bias might easily evolve by natural selection. When information is costly, and environments vary in space, the use of conformist rules of imitation tend to be favored by natural selection. “When in Rome, do as the Romans do” as the saying goes. Every adaptive process--direct bias, guided variation, natural selection--will conspire to make adaptive ways of behaving common. Imitating the common type is generally good sense. At the same time in an environment where the adaptive thing to do varies a lot from place to place, and where people move about, many people will be trying to do the Naples thing in Rome. Conformist decision rules discriminate against relatively rare Neapolitans in Rome. It is interesting that this trick requires at least three “parents;” the genetic system with only two is forbidden this trick. In the jargon of statistics, the reason is that a sample of two has only one “degree of freedom” and hence no information about the state of the population. A sample of three or more begins to have enough information to say something reliably about the state of Rome, and hence to implement a conformist strategy. As the number of cultural models you survey goes up, the more powerful conformity can be. (As in Chapter 11, we admit this idea is completely heretical. Professors are supposed to tell students to think for themselves! Conformity is supposed to be bad! If so, why do people conform???) Figure 13-1 illustrates how the conformity effect works.

B. Some Micro-evidence That Conformity Exists

The evidence that conformity is important as regards cultural transmission is weaker than you might think. There are many studies showing superficial conformity of behavior to what others expect. Few of the studies that have been done have tested specifically for the non-linear conformity effect as we have defined it, but some experiments show it (Ja-

Figure 13-1. Conformist-based rules for the transmission of culture are potentially a strong force for making common traits more common—and rarer traits more rare. It also increases and preserves variation *between* populations as it reduces variation *within* populations.



cobs and Campbell, 1961). We presume that the many studies demonstrating superficial conformity are indicative that deep conformity is common, but this certainly needs further study.

C. The Population Level Effects of Conformity

Conformity greatly affects the structure of variation in a population. Non-conformity preserves variation within a population, while conformity greatly reduces it. However, conformity has a powerful tendency to preserve variation between populations. To see this, imagine what happens to people who migrate from one population to another. As long as migrants are fairly rare, their differences will be discriminated against in cultural transmission in the populations they enter if there is conformist transmission. Young people will tend to ignore them just because they are unusual. Compared to the case of genetic transmission, this effect diminishes the effect of migration. It is much easier to maintain a cultural difference between Naples and Rome than a genetic difference, for the same amount of migration, if cultural transmission is conformist.

D. Evolutionary Biologists Hate Group Selection

Recall from Chapter 10 that the idea of group selection is in bad odor among evolutionary biologists. There we said that it would be theoretically possible for selection to favor animals that sacrifice their own reproductive success where selfishness would put the group in danger only if there is:

- (1) high variability between groups;
- (2) low variability within groups; and
- (3) substantial group extinction rates, or differential group success rates.

The problem is that migration between groups will tend to spread selfish individuals into

unselfish groups. Once in a group of unselfish individuals, selfish ones will have a special advantage. They can take advantage of the altruists, without bearing the costs of altruism themselves. This process is what makes it hard to imagine how the high levels of cooperation we observe in humans arose. It is very hard to see how the genetic transmission system can maintain enough heritable variation between groups to let group selection work. The general conclusion reached was that genes are selected to cooperate to make a reproductively effective individual, but individuals are not nearly so likely to be selected to make a successful group. Because an earlier generation of biologists, before George Williams wrote his famous book in 1966, often carelessly appealed to benefit to the group arguments, modern evolutionists have an almost dogmatic distrust of group selection arguments.

E. Group Selection on Cultural Variation Easier

The group variation-maintaining by-product of conformity makes group selection on cultural variation much easier to imagine than group selection on genetic variation. By preserving the variation between groups and suppressing the variation within groups, it tends to overcome the potent impediments to selection at the level of groups. According to the model described in the reading for this chapter, the rate of group extinction need not be very high to produce considerable change in the long run, and group “extinction” only needs to be *cultural*, it need not actually involve the physical death of members of a group. It is enough that defeated individuals are dispersed to other groups where they are a minority.

*Thus, if we can once get a group with strongly altruistic predilections going, it will persist in the face of a substantial **immigration** of selfish individuals, and will be able to replicate itself (colonize empty habitat) faster than a group composed of mostly selfish individuals.* This assumes that cooperation is an advantage, so that groups of mostly altruists will be rather better off compared to groups of mostly non-altruists. As we’ve seen, the relatively few eusocial animals that have evolved have been unusually successful. Us, the ants, the termites, and the eusocial jellyfish!

E. Some Empirical Evidence Supports Cultural Group Selection Hypothesis

In the reading, Boyd and Richerson argue that ethnic groups are potentially a result of a cultural group selection processes. There is no animal analog of the ethnic group in which a large number (hundreds to millions) of rather distantly related individuals show sentiments of solidarity and a propensity to cooperate. Such group sentiments as motivated Poles, Pathans, Armenians, Lithuanians, Estonians, etc. to defy the USSR in recent years—not to mention the ~350 year long attempt by the Irish to free their country from the British—are examples of individual risk-taking for the benefit of a very large, open group. It is

hard to see how this can arise by natural selection on genes.

Otterbein's (1966) study of the evolution of warfare turned up an interesting pattern of cooperation for violent conflict that is consistent with the cultural group selection model. He found that warfare existed only on a small scale in human societies with characteristics such as local group endogamy (within-group marriage), a tendency of males to reside with relatives, and no cross-cutting institutions such as men's warrior societies. When local groups were more exogamous (marry outside the local village), when males tended to live with unrelated males, or when there were strong cross-cutting institutions to bring unrelated males together, then warfare tends to be on a larger scale. In our terms, when the scale of the institution in which males are socialized regarding use of violence is small (i.e., the extended family) then the unit that is selected and that cooperates is small. Warfare is then limited to the level of feuds between families. Sicilians are reputed to use relatively narrow family loyalties, and can generate extremely effective small-scale conspiracies as a result of intense loyalty at the level of the extended family (the Mafia). On the other hand, Sicilians have weak loyalty at the whole-island level and have historically been prey to the imperialism of stronger states. It is the scale over which conformity is effective that is important. When the group that experiences a common socialization is large, large-scale sentiments of solidarity exist, and local peace is maintained; however, this makes large-scale violence possible.

Close Local Group Endogamy → Small-Scale Warfare
Local Group Exogamy → Small-Scale Peace, Large-scale Warfare

In modern societies, there are many cultural institutions that generate loyalty. Economists have worried that big economic firms like Chrysler Corp. should not exist. Shouldn't each individual employee of a firm act selfishly? Yet economists tend to assume that such firms exhibit organized profit maximizing behavior, rather than individualized anarchy. Suppose new employees are taught work norms by old employees in most firms. If there is a conformity effect, new employees will tend to conform to the existing "corporate culture" (recently a buzz word in business management circles). If the corporate culture is one of cooperation in pursuit of collective corporate goals, the firm is liable to prosper. On the other hand, firms full of selfish careerists, pilferers, and embezzlers are likely to go bankrupt. The bankrupt firms' employees will be dispersed to many surviving firms, and they will have to undergo a period of resocialization. Thus, the tendency to loyalty to the

company, honest hard work, and similar attitudes can spread, even if individuals have direct biases toward selfishness. Effective corporate socialization processes will be group selected to “fool” people into cooperating. Of course, everyone is better off if everyone cooperates; a prosperous firm can afford higher wages than a failing one. As Peters and Waterman (1982) argue in their best-selling book *In Search of Excellence: Lessons from America's Best-Run Companies*, we are all better off if most of us are fools in this sense.

Simple societies, such as might have characterized humans for the last 30,000 years or so, look as if they meet the main requirements for being group selected. Joseph Soltis et al. (1995) recently looked at the potential for group selection among highland New Guinea groups. These groups all engage in warfare and land competition between villages. The pattern of intense competition survived into the late 1940s, when contact with the outside world was first established. In most places, European contact disrupted patterns of intergroup competition before competent ethnographers arrive. Thus the Highland New Guinea situation is unusually interesting. Intergroup competition was intense and often violent. Soltis could make estimates of group extinction rates per generation (25 years) for 5 groups, and the values run from a few percent to about 30% depending upon group and method of estimation. “Extinctions” were counted whenever a group broke up and went to live with other groups. Complete genocide is rare; most often defeated groups disperse piecemeal to neighboring groups. This form of “extinction” is very hostile to genetic group selection, because defeated groups will inject any failed genes they might have into the groups that accept them as refugees. However, the conformity effect could protect host groups from the bad culture of the refugees they take in. He also documented considerable variation between groups in cultural traditions, and a pattern of new group formation by budding that preserves between group variation.

Soltis concluded that the cultural group selection hypothesis meets the test of the New Guinea data. The rate of change due to this process would be fairly slow; it would take something like 1,000 years for this process to make an innovative mode of social organization common in all groups in a larger population. This rate of cultural evolution may seem slow, but remember that in Eurasia, the evolution of the modern types of states is a product of 10,000 years of political evolution. Western Europeans were approximately at the level of political sophistication of New Guinea Highlanders for perhaps 3,000 years after the evolution of the first simple states in the Middle East. The evolution of political evolution does have a 1,000 year time scale, which is roughly correct.

VII. Conclusion

The extremely high level of cooperation exhibited by humans is an evolutionary anomaly. The only other animals where thousands of individuals can be organized into cooperative units are the social insects and the colonial lower invertebrates such as jellyfish. And in both of these cases, kin selection seems to provide an acceptable explanation; these are close families, albeit huge ones.

In our closest relatives, the higher primates, groups are often as large as hunter-gatherer bands, but the level of cooperation within such groups is very low. For example, males do not cooperate in defense, except in those groups where males do not disperse (e.g. chimpanzees). The levels of cooperation observed seem easily explicable in terms of kin-selected cooperation with close relatives plus a small amount of reciprocal altruism.

Humans by contrast, at least when it comes to post-agricultural societies, are organized on a very large scale and with lots of cooperation, coordination, and division of labor. It is clear that humans do not literally use the kin selection mechanism to achieve these levels of cooperation. We do not have the sterility-of-the-workers mechanism that ensures that all members of society are closely related.

Sociobiologists have advanced a series of hypotheses to account for human societies based on the classic kin and group selection, and reciprocal altruism mechanisms. We think these explanations all have fairly serious problems. An alternative explanation is that the use of simple decision-making rules, like conformist transmission (frequency dependent bias), to reduce the cost of acquiring adaptive cultural traits might lead to group selection on cultural variation as a by-product. Once altruism arose culturally, altruists could punish cheaters and set up selection against genes that encourage cheating. In this scenario, a peculiarity of the human inheritance system, the existence of culture, is invoked to explain a peculiarity of our behavior, a high degree of cooperativeness.

We might suppose that group-selected human culture has gradually (if imperfectly) domesticated our selfish genes over the last 100,000 years or more. The human docility that Simon refers to really does seem to exist. People have attempted to raise chimps like children, and all these animals become unmanageably aggressive as they approach sexual maturity. The wild progenitors of other domesticated animals, like cats and dogs, are practically unmanageable as pets. Somehow Simon must be right, we domesticated ourselves. If not by cultural group selection how?

The testing of all of these hypotheses is incomplete. Perhaps not even all the hypotheses needed have been formulated. Pieces of the puzzle are certainly missing, no matter

what your favorite hypothesis might be.

VIII. Bibliographic Notes

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