# *Controversy*

## HUXLEY'S EVOLUTION AND ETHICS IN SOCIOBIOLOGICAL PERSPECTIVE

*by George C. Williams*

*Abstract.* T. H. Huxley's essay and prolegomena of 1894 argued that the process and products of evolution are morally unacceptable and act in opposition to the ethical progress of humanity. Modern sociobiological insights and studies of organisms in natural settings support Huxley and justify an even more extreme condemnation of nature and an antithesis of the naturalistic fallacy: what is, in the biological world, normally ought not. Modern biology also provides suggestions on the origin of the human moral impulse and on tactics likely to be effective in the combat against nature urged by Huxley.

*Keywords*: Darwinism; morality; natural selection; philosophy; selfishness.

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> Let us understand, once for all, that the ethical progress of society depends, not on imitating the cosmic process, still less on running away from it, but in combating it.
>
> Thomas H. Huxley

Thomas Huxley first presented "Evolution and Ethics" as his Romanes Lecture in 1893. The published version and "Prolegomena" first appeared in 1894. They have been favorites among anthologists and

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[*Zygon*, vol. 23, no. 4 (December 1988).]

have excited comment ever since. In my view most of the better known comments (e.g., Dewey 1900; Julian Huxley 1947; Waddington 1971) would have been better left unsaid. Their main errors have been ably rectified by D. Daiches Raphael (1958) and Anthony G. N. Flew (1967), who make it clear that Thomas Huxley's views were far more tenable than those of twentieth-century critics.

I think Flew (1967, 50) fails in one respect. He accuses Huxley of going too far in recognizing a negative moral value in nature rather than mere moral neutrality. I also criticize Huxley on this point, but in the opposite way. I will attempt to show that Huxley did not go far enough in his condemnation of the evolutionary process. We now have a far deeper understanding of evolution than Huxley had, and far more information on what this process has wrought. Huxley, for instance, understood nothing of forces favoring the development of nepotism or of parent-offspring and other sorts of conflict in nature. He knew little of the prevalence and violence of infanticide and cannibalism.

There are several important themes in Huxley's essay. One deals with the evolutionary origin of human ethical motivations and attitudes, and what he calls "the apparent paradox that ethical nature, while born of cosmic nature, is necessarily at enmity with its parent" (Huxley 1894, viii). This topic is ably discussed by Peter Singer (1981) and Richard Alexander (1987), with whom I am mostly in agreement. Although his "paradox" is not a matter that can be ignored, I will deal here mainly with Huxley's more prominent theme, his moral evaluation of nature, succinctly summarized: "Thus, brought before the tribunal of ethics, the cosmos might well seem to stand condemned. The conscience of man revolted against the moral indifference of nature, and the microscopic atom should have found the illimitable macrocosm guilty" (Huxley 1894, 59). Condemnation and guilt are dubious verdicts for mere moral *indifference*. Huxley clearly implies something worse, and the inconsistency makes the statement vague and disappointing. I would prefer something more along these lines: "Thus, brought before the tribunal of ethics, the cosmos stands condemned. The conscience of man must revolt against the gross immorality of nature."

I attribute the defects of Huxley's version to two factors. The first is that despite his accomplishments Huxley was, after all, only an Englishman and no doubt afflicted with the English habit of understatement. Secondly his grasp of natural selection was inferior to that of Charles Darwin and a few other nineteenth-century biologists, (Leonard Huxley 1900, 12, 372; Mayr & Provine 1980, 133). No one of his generation could have appreciated our modern concept of natural selection, which can honestly be described as a process for maximizing short-sighted selfishness. Moral indifference might aptly characterize the physical universe. For the biological world a stronger term is needed.

My concept of *gross immorality* here is similar to that of pacifists who claim that war is immoral. It need not imply any intentional evil or personal accountability. Pacifists' realization that wars start for complex reasons, and seldom merely from anyone's consciously evil decision, need not make them prefer Huxley's *moral indifference* to my *immorality*. War is immoral to pacifists because it systematically produces results that they find morally repugnant.

There is a morally important difference between being struck by lightning and being struck by a rattlesnake. Only the intellectually dead could fail to see that the snake has what are clearly weapons, precisely designed and used to produce a victim. The distinction between pain and death produced by aggressive use of weapons and those produced by accident is important but is obscured when a term such as *moral indifference* is used for both. They illustrate a basic contrast between physical nature and biological nature, and one that Huxley did not fully appreciate. I grant the major difference between a morally accountable human mind and a snake mind, but this is widely appreciated, and I can more confidently discuss the difference between the behavior of a rattlesnake and that of lightning. I hope that my discussion will show, at least to those who would concede that war is or at least may be immoral, that natural selection may be worse than warfare, and worse than Huxley imagined.

## RECENT UNDERSTANDING AND MISUNDERSTANDING OF NATURAL SELECTION

The process of natural selection requires the events of successes and failures: an early bird gets the worm, a later one does not; one worm gets eaten, a different one escapes. It also requires the keeping of records on such events. This means changes in gene frequency. The eating of worms by early birds and deprivation of late risers will affect bird evolution only if these processes affect gene frequencies in the bird population. Recognition of this distinction between events taking place and the record being kept had to await a thorough appreciation of the relationships among genes and genotypes and characters. Neither these relationships nor their moral implications could have been comprehended in Huxley's time. The comprehension is essential to any understanding of the role recognized by modern biology for an individual organism in Huxley's cosmic process. Its role is to transmit its genes to future generations to the maximum possible extent. This summary of current understanding of natural selection is, of course, grossly oversimplified, but perhaps adequate here. More detailed discussions are available (Dawkins 1976; Williams 1984; Williams n.d. In press).

The principles of population genetics as developed by R. A. Fisher, J. B. S. Haldane, and Sewall Wright around 1930 clarify the process by which the genetic record is kept and elucidate the nature of that record. It is a store of information about what has succeeded at transmitting genes in the past and a prediction as to what will succeed in the future. An important implication of this advance, especially important for social behavior and its moral implications, was first recognized by William Hamilton (1964). The survival and reproduction of a relative are partly equivalent, in evolutionary effect, to one's own survival and reproduction. Hamilton proposed an expansion of Darwin's concept of fitness to include any ability to get one's own genes represented in future generations. It does not matter whether these genes are present in one's own cells or present, for genealogical reasons, in relatives. He termed this broader concept *inclusive fitness*. His key formulation was that assistance to a relative will be favored if the benefit to the relative, times the coefficient of relationship, exceeds the cost to the donor.

Consider the problem of maximizing the fitness of individual *5* (Figure 1). The distribution of her special set of genes in herself and her relatives is shown by the stippling. Her fitness is measured by her ability to get these genes passed on to future generations. A useful device is to consider such questions as: What is the probability that an arbitrarily chosen gene in the focal individual (*5*) is also present in her father (*1*)? In sexual reproduction half of one's genes come from one's father. So the probability is .5, and this is the coefficient of relationship of *5* to *1*. The gene would be favored if it tended in any way to make *5* behave towards *1* as if his genes were half as important as hers. Her fitness will be enhanced, up to a point, by a willingness to jeopardize her own well-being to increase his.

The extent of the self-sacrifice favored would be determined by the .5 coefficient and the cost-benefit relationship, with costs and benefits measured as effects on the likelihood of transmitting genes. On the assumption of exactly equal prospects for future reproduction and an absolute certainty that *1* is *5*'s father, natural selection would favor her risking her life up to a .5 probability of loss, if she can surely save him by taking the risk, and if he will surely die if she does not. With conditions otherwise similar except that it is nephew *7* who is endangered, .25 would be the maximally tolerable risk.

Such *kin selection* normally deals with less than life-and-death matters. A more likely problem is whether to give a food item to a nephew (*7*) or a daughter (*8*). The daughter's coefficient of relationship is twice that of a nephew. So the nephew's potential benefit would have to exceed twice that of a daughter to justify giving it to him and depriving her. Selection thus favors nepotism towards close relatives over distant ones. In the symbolism of the diagram, the evolutionary role of individual *5* is to devote her life to the proliferation of that represented by the stippling. The agent that assigns this role to every individual is what Huxley called "a tenacious and powerful enemy" (Huxley 1894, 85).

I believe that this is a fair summary of the concept of kin selection, but I also realize that specialists in any subject may use common terms in uncommon and potentially misleading ways. For instance, when I discussed how an individual ought to behave towards her father, I did not mean literally that. I meant how she could be expected to react to stimuli normally associated with fatherhood. Neither a wild animal nor a primitive tribesman knows anything of coefficients of relationship or of roles assigned by a tenacious and powerful enemy. A male bird can

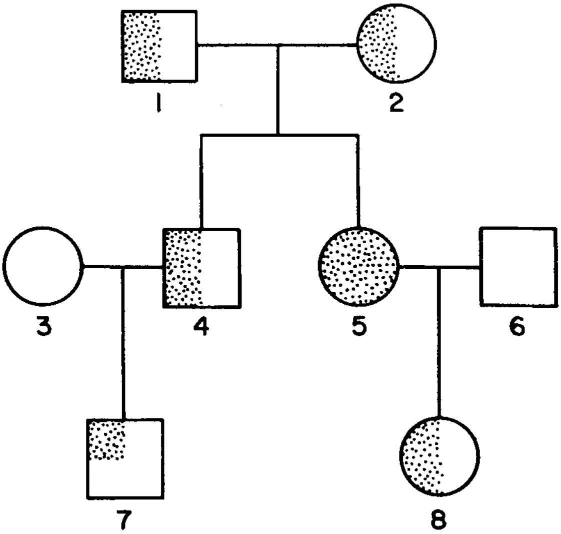

FIG. 1—Hypothetical pedigree diagram, applicable to any outcrossed diploid organism with separate sexes. Males are represented by squares, females by circles, mating by horizontal lines connecting males and females, offspring by verticals from the horizontals. Stippling shows the proportion of the genes in each individual that are necessarily identical with those in *5*. Her fitness is measured by her ability to pass these genes to future generations. Unstippled regions represent random samples of genes on which *5* can have only random effects.

be expected to react to hatchlings in his nest according to his likely coefficient of relationship with such hatchlings. If he is indeed their father, the coefficient is at least .5, but, as discussed below, sexual infidelity and nest parasitism may be common. A sociobiologist would expect his behavior to be closely determined by the average coefficient during recent history for males in his position.

I will mention one more of the many possible misunderstandings. Even a complete kin-selection argument would still give a grossly incomplete view of the natural selection at work on social relationships. Kinship is merely one of many important factors. The individuals diagrammed in Figure 1 must vary in many ways, not merely in kinship to the one I picked for special attention. She may have established mutually beneficial reciprocation with others, some perhaps unrelated. Her mate (*6*) would be an obvious example. Her sister-in-law (*3*) is also unrelated, but even if she has no other significance she has value (to *5*) if she is helping nephew *7*.

Individuals also vary in the amount of benefit they would realize from a given donation. A post-menopausal mother and adolescent daughter are equally related to each other, but it obviously makes evolutionary sense to be more generous to the girl than to the old woman. Questions such as why animals concern themselves so much more with their offspring than with equally related brothers and sisters are based on the assumption that kinship, to be important in evolution, has to be the only factor. A complete answer to such a question would have to consider the relative reliability, for adults of reproductive age, of available evidence for parenthood and that for other kinds of relationship; the reproductive potential, likely survival, and needs of recipients; needs and capabilities of prospective donors; alternatives for the investment of resources; and many other factors.

## RECENT EVOLUTIONARY THOUGHT AND THE MORALITY OF HUXLEY'S COSMIC PROCESS

It is only twenty-five years since Hamilton (1964) elucidated kinship as a factor in the evolution of social behavior, and less than that since Robert Trivers's (1971) insights on conditions for the evolution of reciprocity. Prior to these developments there was no consistent way of interpreting what animals were doing with each other. This absence of theoretical guidance and the outwardly benign appearance of some social interactions made it possible to paint a morally acceptable picture of nature. Romantically inspired naturalists found wholesome lessons in the mutual grooming of monkeys, the feeding of one bird by another, the brave self-sacrifice of worker bees for colony and queen. Such observations served as parables for moral guidance in a system that Donald Campbell (1978) called *normative biologism*. The noble-savage myth is a part of this larger complex. It persists despite abundant evidence of personal cruelty, group bigotry, and environmental destructiveness of primitive societies (Day 1953; Guthrie 1971; Speth 1983).

Romantics could deal with overt selfishness and destructiveness in nature by name changing and selective attention. Territorial disputes could be seen, not as truculent striving to garner resources for oneself at one's neighbor's expense, but as a wise program of birth control through limitation on the number of breeding territories. Verbal obfuscation is not merely practiced, but may be explicitly advocated. Objections have recently been made to accusing animals of practicing slavery, adultery, rape, or other sins (Gowaty 1982; Leacock 1980; Power 1980). The usual form of argument urges that some human practice, such as slavery, is largely determined by culture rather than genes and differs in many descriptive details from anything practiced (for example) by ants. So one must not use the term *slavery* for any kind of ant behavior.

Objections are never made to biologists' using such terms as *courtship*, *migration*, *fasting*, or many others that normally refer to culture-laden and descriptively unique human activities. The essential requirement for objection is for a term to refer to something wicked. There may even be an explicit decision not merely to relabel wickedness but to ignore it. Sarah Blaffer Hrdy found a superb example in a treatise on Antarctic penguins: "Occasionally some of the colonies are plagued by little knots of 'Hooligans' who hang about their outskirts, and should a chick go astray it stands a good chance of losing its life at their hands. The crimes that they commit are such as to find no place in this book" (Hrdy 1977b, 3).

Times have changed. Biologists today realize that unpleasant behavior can be important, and they are increasingly willing to study it. They often conclude that unpleasantness may be normal and adaptive, and they are also reinterpreting various seemingly benign or cooperative behavior. Armed with insights from Hamilton and Trivers they usually find that apparent generosity is limited to special situations in which it can be explained by one or more of three possible factors, none especially laudable.

The first and more prevalent is the nepotism explicitly discussed by Hamilton (1964). Cues available to a donor indicate an expected coefficient of relationship with a recipient, and the value of the aid given times the coefficient of relationship exceeds the cost. The service rendered is an investment by the donor in its own genes, as these are represented in the recipient. As the conditions differ, so does the behavior. Full sibs are nicer to each other than half sibs. Mother-love seems to be greater for offspring that are more nearly mature and therefore more likely to mature, but younger mothers are expected and found to be less loving than older ones (Andersson et al. 1980; Bierman & Robertson 1981).

Manipulation is the second reason why one individual may provide benefits for another. A mouse can provide nutritive benefits to a cat, and when handled by the cat's paws is literally manipulated, but the term normally has a metaphorical meaning. For example, threat of physical force may substitute for force itself, as when a subordinate monkey relinquishes a feeding site to a dominant. More interesting kinds of manipulation result from deception, most obvious when practiced against another species. A snapper may swim eagerly towards the jaws of an anglerfish that deceives it with its lure. Social-insect pheromones that suppress reproduction by workers are interpreted as both a kin-selected response by workers and manipulation by the queen. *Manipulation* may imply exploitation by a manipulator, but it may be that communication within a species is usually adaptive for both sender and receiver. A hen may use vocal signals to get her chicks to behave in ways that serve her genetic interests, but obedience will usually serve a chick's interest. The same might be said for most verbal exchanges between human parents and their children. Richard Dawkins (1982) argues convincingly for the prevalence of manipulation in nature.

The third reason for one individual acting in the service of another is reciprocity. Whatever is given up by the donor costs it less than some expected repayment. Neither the expectation nor the repayment need be conscious or even behavioral. The secretions of an aphid may later repay an ant that protects it from a predator. In cooperative ventures the mutual benefits may be simultaneous. Two hyenas in a cooperative attack on a wildebeest calf defended by its mother are more than twice as likely to succeed as one acting alone (Gould 1982), and one calf can be a feast for several hyenas. A cooperative hyena may therefore eat while a loner goes hungry. In application to human behavior Darwin (1871, 163) called reciprocity a "low motive."

Reciprocity in nature is strictly limited by the necessity of safeguards against cheating. No matter how great the collective benefit might be from a cooperative venture, the necessary behavior will not evolve if the benefits can be enjoyed by freeloaders. It might be that a gregarious species could reduce its rate of loss to predators by having each individual warn the others with a loud call when it sights an enemy. This would in no way assure favorable selection for calling. If the call attracts the notice of the predator it may increase the caller's likelihood of being the victim. This cost would not be borne by a silent freeloader that merely seeks its own safety on seeing a predator. It would survive better than the callers so that sounding the alarm would not be favored.

This sort of reasoning has led students of animal behavior to prefer kin selection over reciprocity as an explanation for known alarm calls, and predictions based on the kin-selection model have been borne out in recent studies. Alarm calls of various sciurid rodents are given mainly by those age-sex categories most likely to have close kin nearby, and the actual presence of individuals with a coefficient of relationship of .25 or more (grandchildren, nephews, aunts) increases the likelihood of calling (Dunford 1977; Sherman 1980). Animals sound alarms to warn close relatives. If such benefits also benefit the group as a whole, that is an incidental consequence of selection for nepotism and has no bearing on the evolution of alarm calls in gregarious animals.

It could work the other way around, with alarm calls being important in the evolution of gregariousness. If my neighbors shout at their children when they see a bear approaching, it behooves me to stay close enough to hear their alarm calls. The more such neighbors I have, the greater my safety. I should stay with them if I can, and encourage them to stay with me. More important is the *selfish herd* factor formulated by Hamilton (1971). The advantage comes from maximizing competition for the bad things in life. If I were a Christian in the Flavian Amphitheater, I would want as many Christian companions as I could muster to share the attention of the lions. Perhaps the best technical term would be the *St. Ignatius Strategy*, after the Bishop of Antioch who was the earliest on record to make use of this principle. Various groups of animals seem to use it more successfully than St. Ignatius did (Altman 1974; Kaufmann 1974).

As a general rule today a biologist seeing one animal doing something to benefit another assumes either that it is manipulated by the other individual or that it is being subtly selfish. Its selfishness would always be defined in relation to its single ultimate interest, the replication of its own genes. Nothing resembling the Golden Rule or other widely preached ethical principle is operating in living nature. It could scarcely be otherwise. Evolution is guided by a force that maximizes genetic selfishness.

Even if it turns out that natural selection among (as opposed to within) populations is more potent than is admitted by current orthodoxy, it would make little difference for a moral evaluation of Huxley's cosmic process. If some populations are consistently better than others at maintaining themselves and giving rise to new populations, they achieve their success by causing the extinction of less favored groups. To claim that this is morally superior to natural selection at the level of competing individuals would imply, in its human application, that systematic genocide is morally superior to random murder. There is no level of inclusiveness of selected entities at which the survival of the fittest is morally acceptable. The morally acceptable goal in relation to survival has to be "the fitting of as many as possible to survive" (Huxley 1894, 83).

## EXAMPLES OF THE TRIUMPH OF SELFISHNESS

Until now I have mainly discussed phenomena that seem benign, such as sharing food with relatives, or sounding an alarm that warns others of danger. Now I will deal with behavior that is not only selfish in some theoretical sense but patently pernicious. Only the morally and intellectually dishonest could label it otherwise. My intent is to present representative phenomena in straightforward fashion, not put on a horror show. More clinically detailed or melodramatic accounts are available (Gargett 1978; Dillard 1974). Scientific writing is supposed to be free of emotion, but occasionally the emotional trauma of observing some routine destruction sneaks into the technical literature, as in the fragment of field notes on ground squirrels published by Paul Sherman (1981), and Hrdy's (1977b) admission that her own tears were among the problems to be overcome in pursuit of data on family life in langurs.

Kin selection does not assure that relations between relatives will be friendly, nor need a mutually advantageous coalition like that between mates be really amicable. Trivers (1974) was the first to perceive the near universality of conflict within the family. He showed that evolution favors offspring that try to get more than their fair share of resources from parents. Any success in this attempt is achieved at a cost to parents and other offspring. The same evolutionary process favors parents that try for maximal reproductive success per unit of expenditure. They can achieve this by a precise optimum compromise between numbers of offspring and benefits to each. If the parents succeed, it means that each young gets less than its own optimum allotment.

Trivers discussed this conflict mainly for weaning. There comes a time in the development of a litter of kittens when weaning is in the best interests of the mother, but continued nursing is best for each kitten. The kitten ideal is to continue nursing but not have its litter mates do so. Members of nuclear families have coefficients of relationship of 0.5, not 1.0, and this means partly different genetic interests and different individual optima. A result is the noisy weaning conflict often observed in mammalian family life. Even in primates and other mammals that normally have one young at a time, the conflict can be intense (J. Altmann 1980). Continued nursing may delay the next pregnancy or reduce nutritive reserves on which the mother depends for survival to the next breeding season. Thus successive young are ultimately in conflict with each other, just like litter mates. Only mammals can have a weaning conflict, but analogous strife can be found in all groups in which parents provide services for developing offspring. Joanna Burger (1981) describes the lively dissention over termination of parental feeding of young in herring gull colonies.

Conflict between mates or potential mates is often bellicose. Recent accounts of reproductive behavior in wild animals are tales of sexual intrigue full of deception, desertion, strife, and sometimes lethal violence. Conflict arises because of basic physiological differences between males and females in most species (Trivers 1972). A female may need to mate with a male to produce offspring, but one mating may be enough to fertilize all the eggs she has or all she can produce in a breeding season. Mating once with the best male available can be a better strategy than mating once with the best and once with the second best. The female can be expected to try to optimize her choice of male and the timing, locality, and all other circumstances that might influence the ultimate success of the eggs to be fertilized. For the male, reproductive success may be largely a matter of how many females he can inseminate. He can be expected to make use of every available opportunity to fertilize eggs and to seek out or try to produce such opportunities. The common outcome is for males to spend much time and effort in mating attempts that females just as persistently avoid. A tank full of guppies is a scene of endless conflict between males and females. Such is the power of romantic self-deception that many people find such displays attractive. Mating conflict exacts a high cost for survival and well being in many species (Daly 1978).

The possibility of cuckoldry gives another dimension to male-female conflict for species in which fertilization is internal and males contribute to the care of offspring. A female songbird may be fertilized, willingly or unwillingly, by a neighbor rather than her apparent mate, or her mate may die or desert. Her best strategy is then to behave as if she has a full complement of fertilizable eggs and allow herself to be courted and won by a suitable male. He could still sire a fraction of her clutch but would waste part of his parental investment on another male's offspring and raise fewer of his own than he otherwise might. The result is an evolutionary arms race between a female's ability to deceive and a male's ability to detect deception. Many details of courtship in birds have recently been interpreted as a dialog based on male suspicion and female representations of fidelity. An essential part of courtship may be a male's effort to sequester and monitor his mate long enough to minimize the possibility of cuckoldry. Evidence for such interpretations is provided by swallows (Beecher & Beecher 1979), bluebirds (Gowaty 1982; Power & Donner 1980), and doves (Lumpkin 1983).

There may be benefits to a female in undetected adultery with one or more of her mate's rivals. A female mouse can perhaps make the rival less likely to kill her young later on (Elwood & Ostermeyer 1984). Adultery can also be a safeguard against a mate's sterility. If a male bird has a 10% probability of being partly or entirely sterile, a strictly monogamous mate has a 10% probability of losing all or part of her brood. Insemination by two males would reduce the hazard to 1%. That females often copulate with males other than their mates has been shown by surgically sterilizing males. About half of the mates of sterilized redwing blackbirds studied by Thomas A. Roberts and James J. Kennelly (1980) produced fertilized eggs, and similar observations have been made in many other species (McKinney, Cheng, & Bruggers 1984).

These observations need not indicate adaptive bet hedging by females, a possibly costly tactic. Actual or suspected adultery may expose a female to rejection or even violent attack by her mate (Barash 1980), and it may be that much of the illegitimacy results from rape. Even a brief absence of her mate may make a female vulnerable to rape by neighboring males in the goose colony studied by Mineau and Cooke (1979). An unguarded female mallard may be attacked so persistently by gangs of males that she drowns (Barash 1977). Joanna Burger and C. G. Beer (1982) observed 162 males that succeeded in mounting unwilling females in a gull colony, and many more that did not succeed. Apparent rape has been documented in eighty-one species of birds (McKinney, Cheng, & Bruggers 1984).

In some insects it would appear that females mate only as a result of male violence (Parker 1979), and in some sharks it appears that mating takes place only after injurious attack by males (Pratt 1979). Rape occurs in turtles (Berry & Shine 1980) and newts (Verrell 1982), and homosexually in a parasitic worm. The male victim may later find it difficult to fertilize a female with his own sperm (Abele & Gilchrist 1977).

The concept of rape would most clearly include mating as a result of threat or actual violence by males. A more theoretically useful definition would include any circumvention of mate-choice mechanisms used by females. By this definition it would be of common occurrence in plants (Janzen 1977; Willson & Burley 1983). In animals it should include the use of deception and stealth. A subordinate male frog may hide near a calling dominant. A female attracted to the caller may be intercepted and mounted and have her eggs fertilized by the unwanted subordinate (Forester & Lykens 1986). Subordinate male sunfish may lurk about the nests of dominants, sometimes with the color and behavior of females. They may then dart into the nest of a spawning pair, release a cloud of semen, and flee any attack by the dominant male (Dominey 1980; Gross 1979). Similar phenomena in diverse species are reviewed by Anthony Arak (1984).

Related phenomena occur in species with internal fertilization. For example, James Farr (1980) showed that by a combination of stealth and speed a male guppy may sometimes circumvent attempts at rejection by females. Even in species in which mating does not normally occur without female consent, an incapacitated female may be quickly inseminated. Male fruit flies mate more readily with anesthetized females than with active ones, and fish hybrids can be produced routinely by presenting males of one species with anesthetized females of another (Bowden 1969).

Besides adultery and rape, just about every other kind of sexual behavior that has been regarded as sinful can be found abundantly in nature. Brother-sister matings are the rule in many species (Hamilton 1967). Masturbation is common in mammals (Beach 1964), and especially common in juvenile male marmosets whose mothers are in heat (Hershkovitz 1977). Males may mount obviously pregnant females or other inappropriate objects (S. A. Altmann 1962). Homosexual behavior is common in a wide variety of vertebrates (Beach 1978), and perhaps homosexual preference (Weinrich 1980).

The killing of other members of the same species is a frequent phenomenon in a wide variety of forms and contexts. Simple cannibalism is the commonest and can be expected in all animals except strict vegetarians (Polis 1981). It is a general rule among fishes. Aquarium keepers find that speedy separation of young from adults is needed to prevent consumption of the young in many species. The phenomenon is widespread in nature, an extreme example provided by the walleye (Cuff 1980). Stomachs of large walleye contained smaller ones, which had eaten still smaller ones, for at least a fourfold cycle of cannibals within cannibals.

Conspecific destruction can also take special forms in fishes, several shown by the mottled sculpin (Downhower & Brown 1981). Large males are better egg guarders than small ones, and females prefer them, but if there is too great a difference in size he may find her more tempting as a meal than as a mate. Egg guarding is a stress for males, because it does not allow productive foraging. The required fast is justified only if it results in a certain minimum of hatched young. If the male gets only a single clutch of eggs and no more for a few days, he may eat them and abandon the attempt to reproduce that year. If he gets a succession of clutches from different females, and is sufficiently hungry after a long bout of egg guarding, he may eat the last batch instead of waiting for them to hatch. The eating of eggs or young in other individuals' nests is common in many fishes (Keenleyside 1972; Rohwer 1978) and amphibians (Crump 1983).

Sherman (1981) showed that about eight percent of the young in a colony of ground squirrels are killed by members of their own species. A male may raid a nest to kill and eat one of the young. A female may raid the nest of a competitor and kill all the young but not eat them. Nearly half the litters in a prairie dog colony were victimized by infanticide, sometimes by close relatives (Hoogland 1985). Cannibalism among insects is common, often the eating of young or of mates or potential mates (Buskirk, Frolich, & Ross 1984; Eichwort 1973; O'Neil & Evans 1981).

Destruction of the young of rivals can be a major source of mortality in birds (Picman 1977; Trail, Strahl, & Brown 1981). Destruction of one of a pair of young, with consumption of the victim, is frequent in birds of prey (Stinson 1979), and this killing may be by a brother or sister. Valerie Gargett (1978) recorded hundreds of attacks by a larger black eagle chick against a smaller nest mate over a period of three days, when the smaller finally died of its wounds and starvation. An authoritative compendium on infanticide in the animal kingdom is now available (Hausfater & Hrdy 1984). It is now generally realized that infanticide rates of some primitive human populations were sufficient for important demographic consequences (section 5 in Hausfater & Hrdy).

Mammalian infanticide may evolve as a male adaptation to female reproductive physiology because lactation may inhibit ovulation. For a male's reproduction the essential resource is an ovulating female. A female deferring ovulation while nursing another male's young is only a potential resource. She can be changed from potential to actual by the death of the unweaned infant. For females such young are of highest importance because with a bit more investment they can be turned into self-feeding juveniles. So the death of the young would be a major loss for the female but only a minor gain in time for the male. Unfortunately such issues are not settled by any principles of justice or net costs and benefits, but strictly on a might-makes-right basis.

Hrdy (1977a; 1977b) describes dramatic examples of this sort of male-female conflict for a monkey that often lives in groups of related adult females, their young, and one temporarily dominant male. Males keep such harems only so long as they can avoid being deposed by rivals. Sooner or later some rival will succeed in defeating any currently privileged male and in taking over his mates. When this happens there is an immediate conflict between the new male and any female with an unweaned infant. The sooner the infant stops nursing, the sooner its mother will turn into a valuable resource, and the only way to get it to stop nursing is to kill it. This is not always an easy task. The male is bigger and stronger than the female, and can kill an infant with one efficient bite into the skull, but he may fail despite repeated attempts. A female's motivation to protect her infant may be greater than his desire to kill it, and it may be necessary for him to fight both the mother and one or more other relatives of the infant. Members of the harem are closely related, and a grandmother or aunt or older half-sister has half as much at stake in the infant's survival as the mother has. Kin selection results in the formation of coalitions of related females in opposition to infanticidal males.

In the absence of ideology, only nepotism can produce such a coalition, and never anything analogous to feminism or an urge for justice or group welfare. If infanticide by a male raises his fitness even slightly, it is in a mother's interest to have her son practice it if and when he succeeds in taking a harem from some other mother's son. There is no way for the female sex to constitute a group for which group selection could produce any kind of change. If she loses her infant, the mother quickly comes into estrus and accepts her infant's killer as the father of her next offspring.

Many conspecific killings result from contests over resources, a common event among insects (Parker 1979). The disputed resource is most often a female ready to reproduce. In large mammals with horns or antlers, death or debilitating injury from fighting over females may claim five to ten percent of adult males every breeding season (Clutton-Brock et al. 1979; Wilkinson & Shank 1976). Death from strife among neighbors tends to be recorded for any wild animal population carefully observed for a thousand hours or more (Wilson 1975). Consider for comparison the annual homicide rate of 0.0003 for Houston, apparently the most murderous of major American cities (World Almanac and Book of Facts 1983, 966). It would be necessary to keep ten Houston residents under continuous observation for three centuries to make it likely that one murder would be seen.

Males of our own and most other mammalian species are more likely than females to kill or injure others of their own kind, but competition among females may not be so much of lesser intensity as of greater subtlety. They commonly deprive each other of resources in various ways, aggressively interfere with each others' courtship, attack each others' young, and actively aggravate male competition when it serves their interests (Silk et al. 1981; Wasser & Barash 1983).

Losses from sexual conflict may go far beyond direct results to participants. Males in combat may accidentally injure or kill females or young in such diverse animals as seals (LeBoeuf 1974) and dung flies (Parker 1979). Bright colors useful in attracting females or intimidating rivals may attract predators. This is certainly true in many fishes (Endler 1978) and insects. Elaborate sexual and competitive behaviors also increase vulnerability either by their conspicuousness or the inattention of participants. George Schaller (1972, 243) found that predation by lions was especially high on fighting warthogs or courting reedbucks. Merlin Tuttle and Michael Ryan (1981) noted that a predatory bat used frogs' mating calls to locate such prey. Other losses are less dramatic but real. In many species a large size is advantageous for males in winning females, but is deleterious in other respects. Myron Baker and Stanley Fox (1978) found that larger male grackles were especially vulnerable to a chemical eradication technique.

Such observations support the common assumption that females more closely approximate the engineering optima for a species but that males compromise these optima with requirements of sexual competition. Adult male modifications may go far beyond scaling for larger size. Antlers and horns are nutritionally expensive structures, and there may be major structural modifications related to the offensive use of these weapons and to withstanding violent collisions with rivals (Schaffer 1968). Russell Lande's (1980) calculations support the recently common assumption that increased effectiveness in sexual competition can increase the likelihood of extinction. The consistently higher human male rates of mortality and morbidity measure the price of features useful in sexual rivalry.

Many of the unpleasant phenomena reviewed above have been described only recently. They are likely to be impressive only if unexpected as a result of the blindness of romanticism. None are really needed for the argument being advanced. The inescapable arithmetic of predation and parasitism should be enough to show that nature is morally unacceptable. This should be so even if some romantic fictions were really true, which they are not. It is sometimes claimed, for example, that predators take only what they need and avoid unnecessary killing. The excess carnage in attacks by bluefish or swordfish on fish schools are a well known example of wasteful predation (Bigelow & Schroeder 1953). Foxes raiding gull colonies often kill far more prey than they use (Kruuk 1976). Prehistoric Indians would sometimes drive bison herds off cliffs and then only harvest foetuses. Andrew Sih (1980) and Jeffrey Lucas (1985) argue the general importance of individual optima of wastefulness.

The survival of one organism is possible only at great cost to others. The moral message in this obvious fact has been recognized by many philosophers and humanists, despite the general prevalence of romanticism. Tennyson (*In Memoriam*, 55) confessed to a confusion and pessimism about Nature when

considering everywhere
Her secret meaning in her deeds
And finding that of fifty seeds
She often brings but one to bear,

He must have realized that one-in-fifty would be extraordinarily favorable odds for all but a small minority of the world's species.

## PROSPECTS FOR MORALITY IN AN IMMORAL WORLD

Huxley viewed the cosmic process as an enemy that must be combated. Mine is a similar but more extreme position, based on the more extreme contemporary view of natural selection as a process for maximizing selfishness. If the enemy is worse than Huxley thought, the more urgent is the need for biological understanding. As Singer (1981, 168) stated it in precisely this context, "The more you know about your opponent, the better your chances of winning." Inadequate knowledge is likely to lead to counterproductive tactics, as Donald Symons (1979) noted for feminist issues.

Modern insights may help resolve Huxley's (1894, viii) paradox. How could the maximization of selfishness produce an organism often capable of advocating, and occasionally practicing, charity towards strangers and even towards animals? Huxley dealt only sketchily with this problem, but anticipated that biology would someday ". . . arrive at an understanding of the aesthetic faculty . . ." that makes people want a society that ". . . demands self-restraint; in place of thrusting aside, or treading down, all competitors, it requires that the individual shall not merely respect, but shall help his fellows; its influence is directed, not so much to the survival of the fittest, as to the fitting of as many as possible to survive" (Huxley 1894, 80-82).

A number of recent sociobiologists have concerned themselves with Huxley's paradox, most notably Alexander (1987). Not surprisingly, all invoke kin-selected altruism and adaptations for taking advantage of reciprocation. They attempt to show why such factors operating in stone-age society should produce attitudes that favor the development, in modern societies, of broadly inclusive ethical systems. A similar attempt is made by Singer (1981), a philosopher admirably knowledgeable on modern evolutionary theory. He proposes that the human capacity for reasoned argument constantly imposes a necessity for publicly presentable justification of personal action. If the chief of the Eastern Mohawks wants to achieve a trade agreement with his Western counterpart, he must be able to argue convincingly that the agreement would benefit all Mohawks. Some such need led Plato to urge consideration of the welfare of all Greeks, not merely of all Athenians (Singer 1981, 117). As the necessity for dealing with an ever broader range of groups arises, comparably expanded ethical systems must be advocated and followed.

As Singer's ever expanding circle of consideration reaches individuals of negligible relationship or likelihood of reciprocation it puts an altruist into ever more basic conflict with Huxley's cosmic process. This combat being urged, between the "microscopic atom" and the "illimitable macrocosm" may seem a bit one-sided. Is not Annie Dillard showing a pathetic megalomania when she exclaims "I came from the world, I crawled out of a sea of amino acids, and now I must whirl around and shake my fist at that sea and cry shame!" (Dillard 1974, 177). Are Huxley and Dillard perhaps like Job's neighbors urging him to rebel against oppression by an arbitrarily malicious, all-powerful, and omniscient god?

No, not omniscient. The evolutionary process is immensely powerful and oppressive, but unlike Job's god it is abysmally stupid. It can reliably maximize current selfishness at the level of the gene, but is blind to future macroscopic consequences of current action. It does not have the sense to realize that mechanisms evolved for practicing unfair nepotism or making self-seeking deals with others can be subverted in the interests of broad altruism. All through evolutionary history there have been such changes with important future consequences entirely unrelated to the selfishness that brought them about.

I will mention two of many possible examples. Manipulation was designed in the service of selfishness, but can play a positive role in human society. Anyone who makes an anonymous donation of money or blood or other resource, as a result of some public appeal, is biologically just as much a victim of manipulation as someone whose self-sacrifice serves the interests of a tyrant. In his otherwise enlightened treatment of ethics and sociobiology Singer (1981) misses the role of manipulation in philanthropy and social activism. He maintains that the prevalence of anonymous blood donation shows an altruism in human nature that defies evolutionary interpretation. It is indeed correct that truly altruistic acts cannot be favored by selection, but the ability to induce others to behave altruistically certainly can be.

My second example is anatomical. The subtle and versatile engineering of the human hand was fully appreciated by Galen about 1800 years ago (May 1968). In the last million years it has been modified by selection for precise manipulation of objects, but such selection could only be brought to bear on an organ already adapted to grasping and rotation. This earlier stage was produced by selection for special sorts of arborial locomotion, such as brachiation, which demands an ability to turn the body with a hand holding an overhead limb. The production of an organ capable of turning doorknobs was made possible as an incidental consequence of selection to be better than one's neighbors at swinging through the trees.

The helping hand of the Good Samaritan and the motivation for its use raise no question on the malice or power of natural selection. They merely show that Huxley's tenacious and powerful enemy is a mindless fool. The stupidity of the enemy is the one advantage enjoyed by those who would follow Huxley's banner into combat. It is hardly a cause for complacency. The enemy is in fact powerful and tenacious, and we need all the help we can get to overcome billions of years of selection for selfishness.

If biology can aid our understanding of our enemy it could be of great value. A key insight is the need to be suspicious of attitudes that arise from the biology of family life and group loyalties. They are based on narrow genetic self-interest and must be there to serve the enemy's cause, not ours. As Singer states it: "Discovering biological origins for our intuitions should make us skeptical about thinking of them as self-evident moral axioms. . . . Far from justifying principles that are shown to be 'natural,' a biological explanation is often a way of debunking the lofty status of what seemed a self-evident moral law" (Singer 1981, 70-71). In natural selection there may be a parallel to the doctrine of original sin as a partial explanation for human misconduct. This was noted by Huxley (1894, 27) and more recently by Campbell (1975, 103-104) and Harry Power (1981, 17).

Human speech is so effective a form of communication that once evolved it gave rise to a system of information transfer to rival the transmission of genes in reproduction. It made elaborate teaching possible, and it enormously augmented a purely cultural evolutionary process. The mechanism of cultural evolution is fundamentally different from that of genetic transmission, but the resulting evolutionary processes have many formal features in common. The transmission of cultural information by verbal messages or direct imitation can be followed, like genes, by phenotypic effects on recipient individuals. Recognizable cultural elements (Dawkins's *memes*) can wax and wane in a population, and such quantitative effects can be treated by mathematical devises not very different from those of population genetics (Cafalli-Sforza & Feldman 1981).

A meme (e.g., a new song, food fad, religious cult) will spread wherever society provides a favorable environment for its spread. There is an obvious analogy with selection acting on a gene. Perhaps the natural selection of memes is a bit less deplorable than that of genes. Human beings are not as stupid as nature. They can sometimes anticipate the social effects of adopting a meme.

But ultimately the ethical problems are much the same. The one necessary and sufficient reason for a meme spreading in a human population is that it is good at getting itself spread. It is not necessary that it enhance the biological fitness or perceived well-being of its practitioners nor that it increase general prosperity. I am sure that cigarette smoking has spread more rapidly through many populations in recent decades than have many sound public health practices. Richard Dawkins (1976) identifies the natural selection of memes as another aspect of the tenacious and powerful enemy.

In its recognition of the evolutionary importance of manipulation and the added potential received from language, biology can add its voice to the chorus of warnings on the dangers of propaganda. Both the ability to use propaganda and an inclination to be suspicious of it were designed by natural selection to spread selfish genes in tribal microcosms. In its boundless stupidity this evolutionary process incidentally designed machinery capable of dealing with the question of whether a message is one of help or harm for what we really want for the macrocosm. We can use abilities developed for petty intrigue to deal with sermons coming from the pulpit, activists' (or sociobiologists') tracts, or manipulation by politicians on television screens. People can now espouse remote and inclusive ideals far removed from the selfishness that gave rise to the power to do so. It is understandable that people in the novel civic environments of the last few millennia will have aspirations for the dictatorship of the proletariat, or the triumph of the master race, or the saving of souls. Because such strivings are not directly favored by natural selection, I have hope that some such cause can provide the humane artifice that can save humanity from human nature.

Modern biology also helps us identify ourselves as apt soldiers for Huxley's army and clarifies the distinction between ourselves and the enemy. Each of us at conception received a unique genotype that never existed before. Unless there is an early division of the embryo it will never be duplicated. This genotype has no significance in evolution beyond its brief and minor influence on rates of increase and decrease of the component genes. It is of the utmost personal significance because it directs individual development and controls vital functions. In these processes each gene interacts in various ways with the rest of the genotype and with environmental conditions. On the average, a gene must produce results favorable to its own replication, but the particular interactions in our own development were unique and unpredictable and may deviate markedly from average effects. We are all special genotypically besides having unique individual histories that give us our own personal collections of memories and experience that constitute the self. There is no conceivable justification for any personal concern with the interests (long-term average proliferation) of the genes we received in the lottery of meiosis and fertilization. As Huxley was the first to recognize, there is every reason to rebel against any tendency to serve such interest.

Gunther Stent (1979) objects that Dawkins's concept of rebelling against one's own genes is a meaningless contradiction. He apparently missed the relevance of major technologies (hair dyeing, tonsillectomy, etc.) based on such rebellion. They are directed at individuals' perceptions of flaws in the development controlled by the genes in the special association of their own genotypes. The combat urged by Huxley and refined by Dawkins is against the much less personal multigenerational effects of our genes, and this is even less of a contradiction. It is what Joseph Lopreato (1981, 124) meant when he proposed that the goal of moral striving should be the "ultimate negation of the commandment of natural selection" which is very much in the spirit of Huxley's (1894, 63) urging that we "refuse any longer to be the instruments of the evolutionary process. . . ."

Like Huxley and everyone else, I have my opinions on what the world ought to be like and on the best ways of moving towards that goal. Huxley did not write his essay to champion his particular view of utopia, and my purpose is merely to update Huxley's message and to characterize the enemy more clearly than was possible in Huxley's time. The updated program for the betterment of the human condition is a twofold attack on the natural enemy and any institutional enemies favored by cultural evolution. In Dawkins's words (1976, 215), we must ". . . rebel against the tyranny of the selfish replicators."

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