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POPULATION, RESOURCES, AND ENVIRONMENT: IMPLICATIONS OF HUMAN BEHAVIORAL ECOLOGY FOR CONSERVATION

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Had we but world enough, and time,
This coyness, lady, were no crime.

-Andrew Marvell, To His Coy Mistress

It was certainly no accident that Repetto (1986) titled his essay on conservation management problems *World Enough and Time,* after Marvell's lament to his mistress. Most of us agree that today we face global problems of environmental degradation and extinction, that these have reached unprecedented proportions, and that time grows ever shorter. Brown (1990,1991) suggests that we are witnessing an "illusion of progress": progress because on the surface, many of the traditional scourges of mankind are diminishing. We have seen progress made toward feeding more people and increasing standards of living in many places, and we have lived through the longest span of economic growth in history. This progress is an illusion, Brown argues, because there are high prices attached to the good fortune: destruction of non-renewable resources and rainforests (e.g. Hecht and Cockburn 1990), desertification (Chiras 1988, Revelle and Revelle 1988), increased pest outbreaks and pollution from increased use of pesticides, fertilizers, and artificial irrigation systems (Revelle and Revelle 1988), resource scarcity for much of humanity (Smith 1982), global warming (Edgerton 1991). It is likely that thousands of species will be extirpated before they are even described (Myers 1984, Wilson 1988). Locally, landfills are being closed because they are simply too full. We protest against the dumping of nuclear wastes as we use the power from nuclear plants.

Conventional wisdoms exist about the way humans used resources in the past, and our strategies to promote conservation in the face of devastating global problems are in part based on these wisdoms. If they are wrong, our strategies will not work. These conventional wisdoms include our perception that people in pre-industrial ("traditional") societies, being more directly and immediately dependent on the ecology of the natural systems around them, were more conserving and respectful of those resources (e.g. Bodley 1990). Thus, as we have developed technological insulation against ecological fluctuations, we feel we have, in important ways, "lost touch" with ecological realities and constraints, and have, to some degree, lost our respect for them. We also commonly think of ourselves, as ethical individuals, giving value to the common good; thus, because none of us wishes to cause destruction of resources, each of us will accept some level of personal cost to ensure the common good.

If these conventional wisdoms were true, simple information about the effects of our actions would be sufficient to solve ecological problems, as individuals accept costs for the common good. It should be relatively easy to get each of us to accept some small cost for the good of all. Conventional wisdoms generate normative prescriptions: that we should all become more reverent, that we need more information about the impact of our actions on ecological balances. Yet today we seem trapped, with repeated examples of cases in which we all agree at some level, for example, that we need certain solutions, though we are unable to make ourselves accept the cost: for example, safe storage for hazardous wastes (but "not in my back yard"), avoidance of highly toxic chemicals (yet years after DDT was banned in the US, we allowed its production - and accompanying profit - for export), more recycling as our landfills overflow (yet, in the US we recycle only about 13 per cent of solid wastes, and as we show later, most of that is material for which we get refunds).

What is wrong? This litany of environmental problems could be expanded; that is not our purpose. We can see that our current efforts are discouragingly minimal in their effects. Perhaps we need a new paradigm for analyzing these problems. The examples above, for all their variability in scope, particulars, involvement of lesser-developed countries (LDCs) or developed countries (DCs), all have in common an underlying theme, and are all predictable from a behavioral ecological approach to human resource use.

Here we examine human resource use in a behavioral ecological context, generating testable predictions about resource use patterns, and making specific recommendations about strategies to promote wise resource use which should be adopted if a behavioral ecological, rather than the traditional view, is correct. As we explain in the next section, a behavioral ecological approach argues that humans, like all other living organisms, evolved to get resources in order to survive and reproduce, and that individual and familial well-being has always been central, while the good of the group has never been relevant. *We argue that natural selection has shaped all living organisms to exploit resources effectively, in competition with each other, and that our problem is that through our cleverness,we have created a novel evolutionary circumstance -- we have such technology that the very behaviors we evolved to perform are those likely to ruin us.*

No organism has evolved to be aware of how its behavior affects its survival and reproduction, only of immediate feelings. We humans are no exception. We have evolved, we will argue, to maximize short-term rewards that have, in our history, correlated with reproductive success - now these strategies may be harmful, not helpful. If we could simply set aside our evolutionary past, perhaps we could easily act as if the earth were our family, regardless of personal rewards. But that seems to be difficult (see Hawkes and Charnov 1988), and today in developed countries we have enormous technology for resource exploitation and high proximate rewards for exploitation of status and power, giving us an ability to cause massive extinctions, deforestation, global warming. Even the crucial problem of overpopulation (e.g. Ehrlich and Ehrlich 1990) arises from individuals satisfying proximate desires. We literally can destroy the earth to satisfy our proximate goals.

If we evolved, like all other living things, to be genotypically selfish, to strive for resources for ourselves and our kin, then we have evolved to apply our considerable intelligence to do just that, and Devil take the hindmost. When technology sufficiently limited, the results were as for other species: occasional population explosions, occasional resource constrictions, occasional local extinctions. We have reached a state in which our population density and developed technology mean that we can cause our own global extinction. Appeals to all of us to make relatively small sacrifices, for the ultimate good of all people everywhere, have had limited success. We have not evolved to consider the global population our family. This is the problem Boulding (1977) tackled when he spoke of the difficulties and complexities of building a "public" -- a large group willing to bear individual costs for a common good.

A BEHAVIORAL ECOLOGICAL APPROACH

If human resource use has followed the same behavioral ecological rules as other species, people are unlikely to give up short-term individual or familial benefits for long-term societal or global gains, and this is likely to have been true throughout our history as a species, rather than a new phenomenon associated with technological innovation. This prediction is in striking contrast to the conventional wisdoms.

We know a great deal about the evolution and ecology of resource use in other species: the costs and benefits; the influence *of* environmental extremeness, predictability, and patchiness, the evolution of sex differences (e.g., Dawkins 1976, 1982, 1986; Dewsbury 1978; Wittenberger 1981; Daly and Wilson 1983; Alcock 1984; Trivers 1985; Krebs and Davies 1991; and specific studies cited therein). The organisms we see today are the descendants of those that most successfully survived and reproduced in past environments. Strategies for survival and reproduction are all-important, though their appropriate analysis may be complicated. This simple logic, first employed explicitly by Darwin (1859, 1871), gives rise to complex and profound effects. Although only heritable variation is important, with complex social animals, there can be significant cultural heritability, and interaction between cultural and genetic transmission can certainly complicate analysis (Cavalli-Svor/a and Feldman 1981, Lumsden and Wilson 1981, Boyd and Richerson 1986, Dawkins 1986).

In this large body of theory and empirical data, two things stand out: [1] genetically selfish behaviors, those which enhance an individuals' reproduction, are always favored; and [2] fertility responds to the richness, controllability and predictability of important resources, and to the sources of juvenile mortality. All living things have evolved to acquire and use resources to survive and reproduce. The ways they do so are constrained by ecological conditions; the most effective and efficient resource strategies in any particular environment are those that tend to prevail over time. *Ceteris parabus,* those individuals using efficient strategies leave more offspring in the next generation than their competitors.

Not immediately apparent is that successful reproduction does not necessarily mean producing the most offspring, or even the most surviving offspring. Even for relatively non-social animals, success is seldom achieved by the strategy "eat and reproduce all you can." In non-human species, for example, infanticide, lethal conflict, delayed reproduction, sterility (e.g., non-reproductive helpers at the nest, Woolfenden and Fitzpatrick 1984; sterile honeybee workers, Seeley 1985; infanticide, Hausfater and Hrdy 1984) are all phenomena that at first glance look as though they decrease, rather than increase, reproductive success - but further analysis makes it clear that, except for rare pathologies, these behaviors are found in specific ecological and social circumstances, and that their impact is increased lineage success. Each individual has reproductive interests, but these interests are shared by other individuals who share common genes - genes identical by descent - and thus several avenues are open to enhance net reproductive success (inclusive fitness maximization; Hamilton 1964). We expect organisms, including humans, to engage in activities that benefit relatives; the extent to which this is true will depend on the degree of relatedness. Thus helping relatives, even at some cost to oneself, can be genetically profitable.

Individuals (and their genetic lines), can also prosper through reciprocity — cooperation (Trivers 1971). Cooperation can be a highly effective competitive strategy. Again, producing the maximum physiologically possible number of offspring is not always the best reproductive strategy. Humphrey (1983) and Alexander (1971, 1979, 1987) argue that even our powerful human intelligence probably evolved in the context of resource and mate competition. Reciprocity occurs only in long-lived, social species - species in which individuals recognize each other and are likely to interact repeatedly. Organisms in long-lived, social species including humans, are likely to do things which benefit potential reciprocators without immediate profit, because there is some probability that there will be future interactions between/among the individuals (indirect reciprocity). If individuals interact only rarely or occasionally, indirect reciprocity is extremely vulnerable to invasion by cheating, and individuals will mirror the behavior of others in a "tit-for-tat" manner (I'll start by co-operating, but if you default, I will, too; see Axelrod and Hamilton 1981). When risks are high, helping behaviors are likely to occur only or primarily among kin.

The relevance of these patterns to resource problems (e.g., "not in my back yard") should be immediately obvious. It is easy to say strategies should be followed, but only if our individual cost is low, or if we see an immediate benefit - to ourselves - will we be likely actually to do what we say is important. Many examples spring to mind: we know that rainforests need protection, but non-farmed teak, for example, is not banned. Many behaviors that we call in ordinary parlance "altruistic" have evolved because they were likely to benefit the inclusive fitness of those who did them. Alexander (1974) separated these behaviors in a clear fashion; it is obvious that genotypically altruistic behaviors, which benefit reproductive competitors at a reproductive cost to the doer, cannot evolve through natural selection. While they may occur, are always vulnerable to competition from genotypically selfish (lineage-enhancing) behaviors (Table 1). Thus true genotypic altruism, paying a real individual and familial cost for the sake of non-relatives, seems likely to remain rare. Only if selection worked to favor the group, rather than genetic lineages, would genetic altruism be common.

In light of this evolutionary background, it should not be surprising that ecological conditions change the costs and benefits of helping. For example, Minnis (1985: 38), in a discussion of pre-industrial societies, notes that as food stress increases, sharing of food increases to a point, and then decreases. In really extreme cases, dependent kin (children) can be abandoned (e.g., Boswell 1988, Turnbull 1972). Even in good times, sharing, as we would predict, is not random; it tends to be directed toward kin, and toward individuals from whom the giver might hope to receive benefits (Hill and Kaplan 1988a, Chagnon 1982, Turke and Betzig 1986).

Levels of Selection and Conservation Issues

To conservationists, the most familiar "levels of selection" problem is probably that of the commons (e.g., Hardin 1968). These are resources to. which all have access (and which, if destroyed, will hurt all), but which give short-term profit to individuals when used exploitatively. Typically, when many unrelated individuals simultaneously have common access to resources, whether the resources are grazing lands or whale populations, they tend to exploit the resource more than is wise from community's long-term perspective, in order to gain personally.

Such problems should be rare if our conventional wisdoms were correct, and we all felt our interests were identical to those of humans as a group - if selection were most potent at the level of the group. It has been tempting to think of selection acting strongly on groups, without specifying relationships among individuals, or the impact of behaviors on individual inclusive fitness; in part because kin selection involves individuals other than direct lineal descendants, and reciprocity may involve completely unrelated individuals. For example, Wynne-Edwards (1962) and others hoped to find the answer to limited population fluctuations of many species in terms of group benefit. He argued that individuals behaved in ways that, while costing each individual reproductively, helped maintain the population below the carrying capacity, thus allowing the population to persist through time (true genetic altruism in Table 1).

Such an approach has a serious failing. Selection cannot favor individuals who act for the benefit of a group of non-relatives at the expense of their own inclusive fitness; only behaviors which enhance reproductive success (such as behaviors which are selfish, parental, reciprocal, or help relatives and therefore enhance inclusive fitness), can evolve by natural selection. Situations in which the costs are paid by individuals other than those gaining the rewards are unstable. Yet this doesn't mean that we are simply harsh and fierce competitors, with no redeeming features. First, and importantly, helping our family and friends, common through individual-level selection, is common (phenotypically altruistic, genotypically selfish behaviors in Table 1). Sometimes, too, the group may appear to benefit as a result of the cumulative selection on individuals (e.g., Williams 1966) even though natural selection has acted on the level of the individual. Interestingly, Wynne-Edwards (1962) argued that all species except humans were group-selected, because human populations seemed not to be "regulated." He said this because even when he was writing, the conflicts between individual profit and group good were already clear. In fact, humans alone may show any evidence of group selection at all (laws, for example, are inflictions of constraint on individual behavior by coalitions of others in the group; Alexander 1987).

There is little evidence that we can count on the rationale that potential group benefits will change individual behavior substantially. Although research for some decades now has produced no evidence that any organism has *evolved* to assist unrelated individuals while costing the doer, this is not to say such altruistic behaviors will never occur; it's just that because they can not spread by natural selection they will be rare. Mother Teresa, Mahatma Gandhi, and the Dalai Lama are/were certainly altruistic by any standards. All are noteworthy in part because they are rare exemplars. The obvious outcome to genotypic altruism (Table 1) is that the genetic altruists decline in the population, being steadily replaced by individuals who behave to their own reproductive benefit. Of the great religious leaders mentioned above, only one (the Mahatma) left any known descendents. Darwin (1859: 260) himself recognized the problem of altruism when he stated "if it could be proved that any species does something for the sole good of another species, my theory is annihilated, for such could not have evolved by natural selection."

This particular result of natural selection is absolutely key to understanding human resource use. When we urge, as in the 1970s environmental movement, that we should all pay an immediate, relatively small cost (e.g., taking shorter showers, taking the trouble to recycle materials), in the interests of gaining long-term global benefits, involving non-relatives and competitors, we are asking for behaviors that have no evolutionary precedent, and could only have arisen through group selection. The result? Countless proximate reasons why "it's too much trouble," why "my part won't make any difference," and burn-out from those who do undertake the short-term costs. In sum, when we have asked people to do things that cost them individually in the short term, no matter how laudable and reasonable, we see considerable defection. In part, we have made mistakes in our scenario-building. If we forecast utter doom by some date, we run the risk of people imagining it, but then finding, when the time comes, that things are bearable — when that happens, the next gloomy scenario is less potent. And all of this complicates the fact that making things "bearable" may involve real short-term exploitation, combined with externalization of costs, and this can't be done forever.

Asking for altruism just has not worked as a widespread strategy. We suggest that when short-term gains accompany short-term individual costs, results beneficial to the group (e.g., long-term reduction in resource consumption) are more likely.

Novel Evolutionary Environments

In other species and in pre-industrial human societies for which we have sufficient data, individuals who have more resources typically have greater reproductive success. Now, however, we may have broken the link between resource accumulation and inclusive fitness (Figure 1). If we evolved, like other organisms, to strive for resources, using them for ourselves and our families, one powerful corollary is that we typically derive proximate rewards of satisfaction and pleasure from that struggle. What we perceive has always been some proximate cue like pleasure or pride, although the reason the behavior persists or dies out is its effect on inclusive fitness. Whenever some behavior has an evolutionary history of reproductive advantage, and conditions change ("novel evolutionary events"), there is a possibility for that behavior to continue be driven by proximate cues that in the past correlated with reproductive advantage, even when the proximate cues are currently unhinged from that functional advantage. We argue that humans are in precisely this situation with regard to the use and conservation of resources (Figure 1).

There are many cases of novel evolutionary events influencing the behavior and demography of animals. For example, Great Tits in Great Britain began to feed out of (evolutionarily novel) milk bottles although their probing behaviors evolved to forage on bark and twigs (Krebs and Davies 1981); a male chimp in a well-studied group gained status by banging empty metal containers together instead of the more traditional branches (Goodall 1986); and gulls which evolved as generalist feeders showed marked increases in population density as a result of more garbage dumps on the east coast of the US (Kadlec and Drury 1968, Drury 1973), while other seabirds declined in abundance due to gull predation (Podolsky 1985). In fact, the most frequent reason that animals become rare or endangered is that their habitat is altered by humans (Ehrlich and Ehrlich 1981).

Because no organism, including humans, has evolved to be aware of ultimate selective effect, but only of proximate cues, selection acts such that those things which enhance our survivorship or reproduction — forming friendships, having sex — tend to be be perceived as pleasurable, and acts which typically detract from our survivorship or reproduction — getting burned — are perceived as unpleasant or painful. Consider a simple example of how novelty complicates this process. In nature, sweet foods are seldom harmful, and sour and bitter tastes are often correlated with the presence of harmful alkaloids. Thus a preference for sweet tastes became widespread in omnivores, including humans. In natural situations, it was difficult to obtain sufficient sugar without other nutrients and fiber, to create problems of obesity. Once we humans invented technologies for refining and concentrating sugar, we created foods that had enormous concentrations of sugar, breaking the selective link between sweet taste, the proximate cue, and good food source, which results in enhanced survivorship and reproduction. But proximate cues drive the system, and selection, as a passive sieve, operates. So, we retain a preference for sweet taste that is often currently counter-adaptive (health risks, and perhaps sexual selection). It is our thesis that humans are in precisely the same situation with regard to the use and conservation of resources (Figure 1).

NATURAL SELECTION AND HUMAN RESOURCE USE

We humans do not often think of ourselves as having evolved in response to pressures on our reproductive success, yet here we argue that there is much evidence that this is so. A behavioral ecological approach makes several predictions about resource use, fertility, mortality, male-female differences, and about how those are predicted to differ in various environments. We do not argue that particular genes force particular behaviors, and we assume learning is important. A variety of proximate mechanisms might mediate any particular pattern. We simply ask: Under the described environmental conditions, what strategies will be favored (will result in enhanced lineage success) compared to alternate strategies? What patterns would we predict as a result of specific environmental conditions?

If humans, like other organisms, did evolve to gamer resources in order to succeed reproductively, specific predictions follow about human resource use and reproductive patterns. Ideally, of course, we would like to assemble here a series of tightly controlled statistical tests; however, some of these predictions are sufficiently new that data have not been systematically gathered. Part of our purpose here, in fact, is to urge data collection to test these predictions. To test these predictions, we [1] examine data from several literatures: cross-cultural, ecological, historical, demographic and economic; and [2] review both systematic and simple descriptive data bearing on the hypotheses. We hope to bring together the clues that will allow us to falsify these predictions, or to suggest the kinds of data we need.

PREDICTION [1] Resource Types **Conservatively** Used.

If enhancement of individual and familial survival and reproduction is the trait favored by natural selection, in traditional societies, resources will be most conservatively used when there is rapid and clear feedback regarding the impact on family and individual welfare (when overexploitation carries clear individual and familial costs).

Evidence from many sources shows that under some conditions, human resource use does not result in resource degradation. Evolutionary theory predicts that these conditions would include [1] exclusive management by small groups of relatives and neighbors likely to interact for long periods of time, and [2] resource types with feedback that allows people to assess what rates of harvest may be unsustainable. People in such cases have individual incentives, through kin selection and reciprocity, to manage resources conservatively, and they have the information to see how their use affects the resource. They are likely to have resource-use rules, and punish cheaters.

A review of some cases may shed light on how humans perceive costs and benefits, and how they behave in varying economic and ecological circumstances. Small groups of people cooperatively manage Amazonian fisheries; such small communities are typically made up of relatives and neighbors likely to interact over long periods of time, with exclusive or near exclusive access to the resource, provide an exception to Harden's "tragedy of the commons." Chapman (1989) discussed the exploitation of Amazonian fisheries in the political context of changing relations of common and private property resources. She contended that political ideologies favoring large-scale development and use caused decline of the fisheries through the lack of local control. She argued that this was related to variations in the "GINI" coefficient (a measure of inequality in wealth, Murdock 1980, Smith 1982). Similarly, Bunker (1985) contended that extractive economies have led to the enrichment of dominant classes at the expense of the poor, and to the depletion of timber and other Amazonian resources. Wealth inequalities do seem to be an important concomitant of overexploitation; if humans strive to acquire resources to enhance reproductive success, overexploitation can result as a side effect. In interacting groups of kin with exclusive or near-exclusive use of a resource, overexploitation should be less likely, and sustained harvest may be the best reproductive strategy.

If control of local resources is removed, it may be in individuals' interests to increase exploitation (cf.Dove 1988). It is an emerging paradigm in the international development literature that the most effective management strategy for some natural resources (e.g., tropical forests) may be to turn at least some control over to local communities (e.g., Pragtong and Thomas 1990, Peluso et al. 1990). The Nepalese Government is addressing this to some extent with the Annapurna Conservation Area Project, a new kind of protected area for the country, which includes a great deal of local participation regarding the use and conservation of resources in the heavily visited Annapurna region of central Nepal (Hough and Sherpa 1989). "Local control" is not a panacea, and external markets are important; in another area of the Himalayas, Moench (1989) reported that even purely local consumption of forest products in traditionally-managed areas can lead to resource degradation, albeit at a much slower rate than if all local controls are removed. All of Nepal's existing parks and reserves have management conflicts with local people to some extent (Heinen and Kattel, in press). We predict that the more local the control within different zones of the reserve, the more sustainable will be the management strategy. The results of the Annapurna Conservation Area Project will be an interesting test of these ideas; an evaluation is currently underway (N. Jain, personal communication).

Many cases in the international development literature suggest overexploitation is common when local people are marginalized and have no immediate incentive to conserve (e.g., Harrison 1987, Shaw 1989). McNeely (1988), in a new and provocative view of economics and conservation, proposed that various kinds of incentives and disincentives implemented at the local level are needed to sustain conservation activities in protected areas. Young (1991) discussed incentives to reduce waste, and Daly and Cobb (1989) proposed that economic policies must be directed to much smaller scales to promote environmentally conservative practices. Essentially these authors argue that new costs and benefits are needed to replace the (previously unrecognized) costs and benefits of familial resource management. On a similar note, Crowfoot and Wondolleck (1990) contended that incentives are needed by all parties to assure participation in environmental dispute settlements. Although these authors do not address the issue directly, their conclusions are similar to ours: people respond most readily to immediate costs and benefits. We argue that they do so ultimately because those are the types of rewards which led to greater reproductive success throughout our evolutionary history.

These examples all involve local communities, often comprising several kin groups and with a preference for cousin marriages, in which people are essentially involved in subsistence use of local resources. In these cases, the exploitation of resources for economic profit was initiated by outsiders - central government, foreign investors. In contrast, control by unrelated individuals in market economies, with highly developed transportation, may not result in the most conserving use: we have only to think of examples like the old-growth forest in Oregon, or conflict over salmon management and forestry in the Pacific Northwest, for example. In these cases, local individuals may find the "get mine and get out" strategy all too tempting. When this is so, coalitions of others, working through central government agencies, can have a moderating influence.

If conservation benefits can be made to outweigh costs for people through a system of economic incentives which confer immediate or short term benefits to people and their families, conservation strategies will succeed; if not, we argue, they will more often fail. Examples of local incentives in the case of protected areas include the sustained removal of some forest products, or providing employment to villagers. In a similar vein, Repetto (1986) suggested promoting conservation strategies that have proven effective, mostly by providing benefits to local people (e.g., improved health care and lowered infant mortality rates). Other recent volumes on economics and conservation which address the general problem of economic valuation of biotic resources are: Prescott-Allen and Prescott-Allen (1987), Oldfield (1989), and Dixon and Sherman (1990). These approaches may prove important for justifying conservation activities to policy makers, but we suspect the activities can only persist with systems of incentives and/or benefits to local people such as those discussed by Repetto and McNeely. Such systems would approximate the ultimate, evolutionary reward systems of human hunter-gatherer societies throughout most of our history. Pearson (1985) contended that many multi-national corporations are implementing new policies in LDCs which involve moving away from direct ownership of natural resources, and toward contractual relations with locally-owned and managed businesses, with the rationale that this will increase profits over the long term.

PREDICTION [2] Resource Destruction in Pre-Industrial Societies.

Deliberate overexploitation in traditional societies is likely when [a] it yields individual genetic profit (and/or its proximate cues, status or wealth enhancement), and [b] technology is sufficient to accomplish overexploitation. Thus the impact of introduction of more efficient technologies will vary, depending on whether their use will result in greater (short-term) individual and familial benefit.

Exceptions to the conventional wisdoms about pre-industrial societies' resource-use patterns are common. The general rule is that if any species, or local population, exceeds its "carrying capacity" more than briefly, it heads for extinction. Humans, successful resource users, should generally use resources at an "appropriate" level. When do exceptions occur? Humans can cause destruction or extinction in a variety of ways. They may do so directly, as in hunting a species to extinction (e.g., moas in New Zealand). Deliberate exploitation is predicted to cause extinction or environmental degradation most often when technology is sufficient, individual payoffs exist, and feedback on human impact is slow. Throughout most of our evolutionary history, these conditions were seldom met, although humans have apparently always modified their environment — even hunter-gatherers deliberately changed the environment by burning, for example, and there is evidence that tribal people are capable of over-hunting (Clay 1988, Bodley 1990). Typically, however, the technology was not widespread, and had principally local and limited environmental impacts (but see Lowdermilk 1953). Thus, it is not surprising that widespread group concern about a conservation ethic is more or less a twentieth-century phenomenon (e.g., Spoehr 1956, Hargrove 1988, Strong 1988, Callicott 1989).

In addition to deliberate exploitation, humans may also introduce crop plants or domestic stock, or inadvertent "weeds" or animal pests (e.g., rats). Exploitation is most likely to be directly related to individual striving, while introductions result more often from a lack of information (sometimes not only about the ecological relationships, but even the existence of the introduced species). What data actually exist about the effect of humans on other species? From the

Quarternary, documented extinctions have occurred as a direct result of human activity (Martin 1984). On the Hawaiian Islands, 54 per cent of endemic birds went extinct due to activities of early Polynesians (Olson and James 1984), and the same case, better-or-worse documented, can be made for most other continents or islands (Martin 1984).

Diamond (1984) analyzed factors associated with resource destruction and human activity. "Man's arsenal" included weaponry, stock, pigs, dogs, swift predators like cats, agriculture. All of these were usually deliberately brought. Rats often accompanied humans inadvertently. Faunal susceptibility was an independent consideration, arising from fire risk, absence of native swift predators, rats and land crabs, and previous absence of humans. Of the four prehistoric extinction waves definitely attributable to man, three "resemble what literate Europeans have been doing on numerous oceanic islands" (Diamond 1984: 852). Patterns of particular extinctions varied. In Pleistocene North America, human-caused extinctions included large mammals, few small mammals, and some relatively large birds.

Though less well known, the late Pleistocene extinctions in South America and Australia followed much the same pattern. In New Zealand, the Polynesian settlement extinguished all of the giant flightless birds, local populations of marine mammals, numerous species of both small and large flightless and flying birds, frogs, lizards, and flightless insects (Anderson 1984, Cassels 1984, Trotter and McCulloch 1984), as well as numerous plant species (Crosby 1986). Only part of the pattern is attributable to weaponry and hunting, which might be seen as more relevant to human intent. Other impacts arose from introduced stock, predators, and plant species (in which prediction of impact might have been difficult), and unwanted commensals like rats (in which case there was certainly a lack of information). The situation is further complicated by incomplete information on extinctions, and variability in faunal resistance (Diamond 1984). Other examples, perhaps less detailed, suggest that these problems have existed throughout time. Current work suggests that the abandonment of Mayan cities was related to agricultural failures (Deevey et al. 1979, Turner 1982). Ancient Sri Lankans, by forest clearing on mountainous regions, created flooding and reservoir siltation (Lowdermilk 1953), causing serious problems.

Both technology and profit are important. In North America, for example, Great Lakes Indian societies had sufficient technology to have great impact on beaver populations; nonetheless, these populations remained relatively stable until the Hudson's Bay Company entered the area, introducing a market economy, and made extra beaver pelts useful. A male beaver pelt, according to company records (Albany Fort, 1773), was worth a brass kettle, or twenty steel fishhooks, or two pounds of Brazilian tobacco (Newman 1989: 60). In this case, the technology was sufficient for some time without resulting overexploitation; what was lacking was immediate advantage to continued hunting.

Plains Indians who hunted bison were, regardless of the hunting technique, highly selective in their use of meat, hides, and other by-products of the hunt (Haines 1970, Speth 1983), seeking particularly fat and fatty meat, and leaving heavy, less nutritious parts at the kill. When cliff jumps were used, the hunt could become inefficient in terms of the amount of the kill actually used. Cliff jumps produced far more bison meat for less effort than competing technologies, but were certainly inefficient, and hardly "conserving" in that storage and preservation techniques were inadequate. Huge amounts of meat rotted at the base of cliffs; hunters took only the choicest meat. In this case, certain technologies were more than adequate; others lagged behind.

Hames (1979) found that among the Ye'kwana, enhanced technology increased hunting efficiency, but did not increase exploitation. Game could neither be stored nor traded in a market economy; its availability did not lead to feast and famine conditions. Thus, already efficient hunters simply had more spare time. When such time is used in male-male bonding and negotiations, it may constitute "politics," and may indeed have some reproductive payoff for individuals (e.g., Hames 1979, Chagnon 1988, Low 1990a). On the other hand, when steel axes were introduced in New Guinea, with a market available (Salisbury 1962), serious ecological degradation followed.

One might think that normative beliefs would strongly affect these patterns. Religious beliefs can be an important proximate cause of conservation, although we argue they are unlikely to be very effective if no individual or familial benefits accrue. In all major religions it is considered noble and just to aspire to poverty or limited resource use of some form (e.g., Durning 1991). In many Asian religions there is a great reverence and respect for nature (Callicott and Ames 1989).

Here we are interested in the environment-behavior correlation, rather than the particular mechanism such as spirituality, by which it is achieved. The evidence suggests that humans the world over behave in a genotypically selfish manner, sometimes in accord with their religious inculcation, sometimes in spite of it (cf. Callicott and Ames 1989). Although cultural and religious beliefs about important affairs may well have considerable inertia, making them slow to change, sometimes as slow as genetic algorithms, when environmental conditions change, religious beliefs can sometimes be altered rather quickly. We can convert from stewards and protectors of the earth, to believers that God has given man "to have dominion over the fish of the sea, and over the fowl of the air, and over the cattle, and over all the earth, and over every creeping thing that creepeth upon the earth" (Genesis 27).

We suspect that protective religious reverence for nature is more strongly practiced when kinship structures are strong and families benefit from conservative management, and further, that conservation philosophies relying on generalized and diffuse group benefits (e.g., Lovelock 1979, Devall and Sessions 1985, Taylor 1986) are probably doomed to failure in the absence of individual or kinship benefits to conservative management. We would be delighted to be wrong, but suspect we are not. In most hunting and gathering societies, while religious activities may surround hunting, men who are good hunters can get more wives, and men's attitudes about hunting (and various achievements) center on how hunting skill helps their social and reproductive success (e.g., Chagnon 1988).

Thus, two conditions apparently must exist for active rather than incidental environmental degradation to occur: the technology must be sufficient to accomplish it, and there must be some reward to individuals who, for example, hunt or clear land at destructive levels. If, in addition, the size of the resource pool is unknown or feedback is slow (e.g., whaling, sealing), overexploitation is even more likely.

PREDICTION [3] Information and Resource Destruction in the Industrial World.

Indirect or incidental damage, as through habitat destruction, is most likely when information or feedback about the resource is limited. Even when we move from considering traditional societies to modern industrial conditions, those resources most likely to be over-exploited should be those with slow feedback cycles — those on which it is hard to see the impact of resource use. This is especially critical for resources in which the size of the resource pool is difficult to measure and there are many potential users: many non-renewable resources like coal, oil, gas, and pleistocene water deposits, and renewable resources like whales and large secretive terrestrial mammals (e.g., many fur-bearers). The most profitable individual strategy is "get mine and get out."

Humans, like other organisms, evolved to use resources primarily for individual gain, even when this generates incidental expenses for the group; further, this is most likely in the case of resources with slow feed-back cycles, unknown sizes, and/or externalized costs. For example, consider the whaling industry. Harvests by several countries did not abate until the large baleen species, one by one, reached commercial, though apparently not biological, extinction (Oldfield 1989); that is, until it was no longer profitable to hunt.

Sometimes the costs to the group as a whole, or of to those receiving no profit from the resource use, can be dramatic. Our high rate of fossil fuel consumption is causing unprecedented pollution problems which contribute to increasing atmospheric CO2 and possibly to global warming (Mintzer 1987, Renner 1989), and a series of public health concerns (Ogden and Williams 1989). Gaps in the supply of these fuels raise serious concerns for global security (Anonymous 1985). The United States recently concluded a ground war in the Persian Gulf, yet the 1991 energy proposal from the Bush Administration made no concessions for decreasing foreign oil dependence or increasing gas mileage, and few for research and development of alternative fuels. Despite initial concerns about the use of chlorofluorocarbons in the early 1970s, their potential global consequences were ignored until the mid 1980s, when more definitive data made it apparent that ignoring the problem forever was not an option (Miller and Mintzer 1986, Shea 1989). Over-exploitation of some resources leading to widespread ecological problems continues (e.g., Silver and DeFries 1990, Hecht and Cockbum 1990, Miller and Tangley 1991).

These cases all involve resources in which the size of the pool is difficult to measure and/or the costs of profligate use are externalized. Thus, the short-term benefits outweigh the short-term costs for users (people in DCs, or wealthier people in LDCs in these cases), and users have no individual incentive to conserve, but strong individual incentives to exploit.

Walters (1986) discussed the importance of feedback policies in managing renewable natural resources. Policies which mandate that harvest should decline if there are signs of stock depletion may well be essential for sustained harvest for the reasons discussed here. Unfortunately, the quantities (pool size) of many resources are too poorly known, and the costs of use are so externalized, frequently across national boundaries, that adopting such policies at a local or even national level is sometimes not possible. International treatises and commissions are probably the only answer, if sufficient incentives can be applied for individual nations to comply. Of course, other more localized conservation problems occur in the industrialized nations as well. However, the global issues discussed above are largely caused by industrialized nations, and will be, we predict, the most difficult to solve because the benefits of industrialization may far outweigh the costs for citizens in those nations, because the costs dissipate over the earth.

PREDICTION [4] Sex Differences in Resource Use.

Because of the different shape of mating versus parental return curves (Low 1990a), male and female humans, like other male and female mammals, should differ in the amount of resources they strive to acquire, and the risks they are willing to take:

[a] Societies in which women's resource-use patterns approximate men's should be those societies in which their return curves are similar (i.e., matrilineal societies in which a very large amount of resources, while not increasing a woman's fertility, may, because she can pass them to her son/s, increase her number of grandchildren).

[b] Because women's reproductive value, related to age, is important in mate selection, while for men, resource control is likely to be more important than age (Low 1989a,b, 1990a,b), women's reproduction is unlikely to correlate with wealth, power, or status. Instead, even in cultural milieus (such as 19th century Sweden; Low 1989b, 1990b) in which marriage ages were late, women who marry earlier are likely to have higher lifetime fertility than women who marry later, while men's fertility tends to be related to their wealth and/or status, and not to their age of marriage.

[c] Because of the interplay of resource (male) and reproductive (female) values, in polygynous societies, men controlling more resources should marry more (and younger) women than do men with fewer resources. Even in monogamous societies, wealthier men may marry younger wives with higher reproductive value *(serisu* Fisher 1958).

All of these predictions argue that in most societies, men can benefit more directly from resource exploitation, and are likely to be the driving force in risky, high-stakes resource garnering.

Men and women, like other male and female mammals, appear to seek access to and control of resources toward somewhat different reproductive ends. Men's striving centers around the mating aspects of reproductive effort, and operates in the community sphere (Whyte 1978, 1979, Low 1990a). Male resource competition and male-male coalitions are associated with status or resource competition (Chagnon 1979, 1982, 1988), and with resources that can be more effectively obtained and protected by groups of males - war, heritable land of lasting value, some large game. While such coalitions are likely to be among brothers, and associated with patrilocal residence, more-or-less fluid coalitions of this sort arise among men of various relatedness, and among non-relatives in many societies. Men's coalitions typically are broad-reaching, involve both more risk and higher reproductive stakes than women's coalitions, and exert considerable power and control significant resources (e.g., Low 1990a). Coalitions in other male and female mammals also follow these patterns.

Men in most societies for which there is information use resources to gain reproductively, typically through polygyny — additional wives. In polygynous human societies (the majority of traditional societies), like other mammalian species, variance in male reproduction is relatively high; great expenditure and great risk-taking may be profitable (Low 1989a,b, 1990a,b). In more than a hundred well-studied societies (Betzig 1986), there are clear formal reproductive rewards for men associated with status: high-ranking men have the right to more wives, and have significantly more children than others. In most societies the relationship is quite straightforward: in the Turkmen, Irons (1979 a,b) found that richer men had more wives and more children than poorer men. Borgerhoff Mulder (1988,1990) found that in the African Kipsigis, richer men married younger wives (of higher reproductive value; Fisher 1958) and produced more children than poorer men, although with the introduction of western technology and medicine, differentials were reduced. Even in societies such as the Yanomamö, in which few physical resources are owned, male kin for coalitions represent a resource, and men manipulate kinship terms in ways that make more women available for mates, and more powerful men available as partners (Chagnon 1982); men who establish their bravery in revenge raids also have more wives and more children (Chagnon 1988) so that reproductive success is uneven. In the Ache, too, good hunters have more children than other men (Hill and Kaplan 1988 a,b). On the island of Ifaluk, men who hold political power have more wives and more children than others (Turke and Betzig 1985). Even in ostensibly monogamous societies, monogamy may be far from absolute. In the Kalahari Bushmen, living in a resource-limited environment, 5 per cent of the men manage to have two wives (Lee 1979). In 10 of 12 societies reviewed in less detail by Hill (1984), resource control enhanced reproductive success. There is an intriguing parallel in non-human species: in ostensibly monogamous songbirds, males will sometimes take another mate -- if resources are abundant (Gowaty et al. 1989).

For women, sufficient resources to raise healthy children are important, but there is little evidence that control of large amounts of resources has enhanced women's reproductive success throughout evolutionary history, or cross-culturally today (Irons 1979a,b; Borgerhoff Mulder 1988, 1990). This is true despite the fact that in many societies, women actually provide the majority of the calories to the family's diet. Female-female coalitions may arise among female relatives or co-wives, and appear to function for the exchange of information (e.g., location of good foraging spots), child care, and subsistence- related work (cf. Irons 1983, Low 1990a). Resources garnered are used for offspring, family, and important reciprocators, and significant resource control is rare or unknown. These coalitions are almost never significant beyond the household boundaries; even female solidarity groups tend to be among relatives.

The fact that resource striving can have a limited effect on women's lifetime reproduction is reflected even in cross-cultural patterns of sexual dimorphism in political activity, and probably also the politics of resource use. Women's ability to hold political office does not appear to be a function of men's absences, biased sex ratios, women's contribution to subsistence, subsistence type, group size, mobility, political level of sovereignty, or hierarchical political organization (Low in press a). Most societies in which women do hold political office are matrilineal or duolineal — societies in which women, if they gain very large amounts of resources, can invest them in their offspring, presumably would enhance reproductive success through more grandchildren (Low in press a). Thus, though women cannot enhance their own fertility through increased resources, and there is a generation's lag, women can invest in their sons' mating effort curves for increased numbers of grandchildren (Low in press a). Resources strongly affect women's reproduction when they are limiting (e.g., malnutrition), but can only be used by women to gain the extraordinary reproductive success of highly polygynous males (Betzig 1986) in societies in which the descent system allows highly successful women to concentrate resources in their sons (Low in press a).

Have we changed today? During the demographic transition, when family sizes fell in western Europe, there is considerable variation in pattern, but when we examine resource levels and family size correlates, a common pattern emerges: when great resource differentials exist, they are reflected in family size differences (e.g., Low 1989b, 1990b, Low and Clarke in press). Thus, the demographic transition typically proceeds at locally very different rates, and is frequently reversed locally (e.g., Lockridge 1983, Knodel 1988), something that has puzzled demographers. In Sweden, Low (1989b, 1990b) found that landowning men, but not women, had greater reproductive success than non-landowners. Landowning men married younger women, of higher reproductive value. Drake (1969) similarly reported from 19th century documents that in Norway, daughters of rich men were marriageable at about age 18, while daughters of poorer men were not considered marriageable until their mid-twenties. Poorer men of the time specified the value of marrying an older woman, who had accumulated household goods and knew how to run a household well -- explicitly trading reproductive value for economic value.

In western technological "monogamous" societies today, including the US, men typically remarry more often than women, and have children in second marriages more often than women; when this occurs, the society is rendered effectively polygynous (Daly and Wilson 1983, Hartung 1982, Essock-Vitale 1984). Further, US census data suggest that family size increases with a man's income, even when second marriages are not considered (Daly and Wilson 1983: 334). When we look within societal groups in contemporary society, rather than across nations (e.g., Birdsall 1980), richer men and families (but not women richer through their own employment), even today, have larger families (e.g., Voland 1990, Hughes 1986, Flinn 1986, Daly and Wilson 1983: 334, Mueller 1991, Rank 1989; see review in Low and Clarke in press). Some (e.g., Vining 1986) have argued that these trends (richer men reproducing more than poorer men) are spurious, and that they seem to disappear when population growth stops. However, these analyses (e.g., Vining 1986, Tables 2-5) use proxy measures like education rather than resources, and do not consider lifetime fertility; they are, at the very least, difficult to interpret. Thus even in industrialized societies, the possibility exists that richer men may derive immediate familial (reproductive) benefits from their resource acquisition.

PREDICTION [5] Conservation Strategies Likely to Succeed.

If enhancement of individual and familial survival and reproduction is the evolutionary context of resource striving, then our strategies for convincing people to shift resource use to more conserving patterns must appeal to their perceived short-term, familial and local, interests. No other species has evolved to behave in the long-terms interests of the larger group (unless that group comprises only close relatives), at the expense of short-term individual and familial interests, and we propose that this is also true of humans.

If humans have evolved to use resources in reproductively selfish ways, then the most successful conservation strategies will be those whose benefits to individuals can be made to outweigh costs, through a system of economic or other incentives which confer immediate or very short-term benefits to individuals and/or their families and friends. If this is the case, governments and organizations may find it productive to implement policies that create systems of incentives to conserve; *the more immediate the benefit, the more successful should be the outcome.*

The actual monetary value of the proximate rewards need not be great. Consider, for example, "bucket" drives to collect money for various causes on the campus of a major university. Our argument suggests people will be more likely to give to a bucket drive if they get some immediate reward such as a pin or tag indicating that they gave: there are two rewards — the pin advertises the giver's generosity (which may elicit reciprocity) to everyone, and warns other bucket collectors not to bother the giver again. To test this hypothesis, we interviewed students on the main campus of the University of Michigan, asking them to which drives they gave, and whether they received some sort of tag or pin for their gift. Students were much more likely to give to drives in which a pin or tag is provided ($n=84$, $X^2=8.4$, $p<0.01$). Yet the cost of each tag is a fraction of a cent, and most donors give a dollar or more. The American Red Cross uses a similar strategy during blood drives; pins are given which advertise "be nice to me: I gave blood today." Blood donors can aspire to become a "one gallon donor" or a "five gallon donor," with more badges (i.e. pins are given for each additional gallon, advertising the number of gallons donated). Other factors may operate in this case. Barbara Pate (personal communication), Regional Representative for the American Red Cross in Washtenaw County, Michigan, reports that the main reason people state for giving blood is that a friend or relative was in an accident or had an operation, and thus needed blood; people appear to be reciprocating consciously.

We are asking what people actually do, given the costs (a few bucks or a pint of blood) and the benefits (nothing versus a tag to advertise one's goodness, or help to a friend or relative versus help to a stranger), in such generalized reciprocity situations; this may provide clues for eliciting more widespread forms of conservation activities. We argue that, while many proximate motivations can prompt behavior, the greater the immediate individual benefit, or the lower the immediate individual cost, the more likely the behavior will be.

Consider further examples of this general principle. Why would anyone want to spend two or more years of their lives living in near-poverty to work in an LDC? In other words, how does the American Peace Corps gain recruits? One of us (JTH) can speak from personal experience after over three years of service to the organization in Nepal, and as a member of the Council of Returned Peace Corps Volunteers. The Peace Corps Volunteer Service is not truly volunteer; volunteers are paid salaries equivalent to those of host-country nationals in similar professions. Though these salaries are modest by American standards (e.g., less than $100 per month in the mid-1980s in Nepal), they are generally quite adequate for national standards. In addition, all travel, health and dental care, vacation pay, and funds for home leave in the case of extensions of service or family emergencies, are provided by the organization; living costs (rents) are provided by the host country. The US government saves $200.00 per month of service for each volunteer, and all academic loans can be deferred until service is completed. All returned Peace Corps Volunteers are eligible for non-competitive status for federal jobs for one year after service is completed, or for up to three years if the former volunteer pursues a degree, allowing former volunteers much easier access to federal employment. This alone may be a powerful incentive, particularly when employment markets are tight; the federal government is a major employer for people in the natural resources and agricultural professions, two areas in which the Peace Corps recruits actively. Finally, many institutions and organizations favor hiring former volunteers, and several universities offer scholarships specifically for former volunteers.

The Peace Corps actively advertises all of these direct benefits to prospective recruits. Beyond direct monetary incentives, the organization offers travel opportunities, challenges, opportunities for personal growth, and pre-professional experiences not available to most people in our society, resulting in greater employability. This organization uses extremely effective techniques, predictable from a evolutionary/behavioral approach, by developing direct and indirect incentives that appeal for many reasons to talented people to serve basic needs of the poor in lesser-developed countries; the Peace Corps seems to us an excellent example of promoting group-level benefits through offsetting some personal costs with individual benefits.

Other examples are closer to home. Consider the recycling of bottles in states with and without "bottle bills." Many communities in states without such bills have voluntary recycling centers, but few people use them. The cost of stopping at a center on the way somewhere is trivial, yet it is a cost that apparently few *of* us are willing to incur. We predict that the rate of recycling of the same bottles in states with bottle bills is much greater, probably approaching 100%, though the incentive is also seemingly rather trivial ($0.05 to $0.10 US for cans and bottles in the state of Michigan). For example, the Ann Arbor Ecology Center (personal communication) reports that over 90% of redeemable beverage containers are returned by the buyer in states with bottle bills such as Michigan; this is reported to be the most effective type, of recycling program. A small monetary reward (or fine if one doesn't collect) is sufficient to bring the point (and the bottles) home. Furthermore, in areas where people have to pay for garbage disposal on a volumetric basis, and recycling is provided free of charge, though not mandatory, up to 90% of households do at least some recycling. Compare this to the approximately 23% participation in cities like Ann Arbor, Michigan, in which there was free voluntary curbside recycling, but garbage fees were assessed per household, not on a volumetric basis (the laws in Ann Arbor have been changed recently, and recycling is now mandatory). People are much more likely to recycle bottles and cans redeemable for even a trivial reward (Figure 2). The lessons from these minor examples should be obvious for states or municipalities wishing to reduce solid wastes as landfills reach capacity (e.g., Young 1991): people are more likely to take part in programs whose benefits are societal if they have direct individual incentives. These benefits do not have to reach economic parity; often, rewards that would be ridiculously small in any economic analysis can be effective.

Can we apply the same principles to wider-ranging resource issues? The most difficult resource-use problems have the following characteristics: resource base inadequately known and feedback slow, used by many, unrelated individuals, and externalized costs. Even in these cases, if incentives can be provided to individuals we expect use patterns to change. Monetary incentives, as we noted, need not be great. The work of several environmental psychologists and environmental educators suggests that other, non-monetary incentives can be effective (especially if they play on our evolved psychological mechanisms). Most frequently studied proximate motivators are: education, and intrinsic and social motivation (e.g., DeYoung 1985, Kaplan and Kaplan 1982, DeYoung and Kaplan 1988, Monroe and Kaplan 1988, and Stapp et al. 1988). Educational techniques seek to change behavior by increasing understanding/information about the impact of behavior. Several components are felt to be necessary: awareness, knowledge, attitude modification, skills and participation (Monroe and Kaplan 1988, Stapp et al. 1988). Feedback (including information about impact, and implicit "goals") has been very effective in promoting energy conservation (Seligman et al. 1981). However, the overall effectiveness of information on encouraging conservation is unresolved. DeYoung (1989) found that information on recycling procedures to be very effective; while Hopper and Nielson (1991) found that while information increased recycling behavior, it was less effective than other strategies.

In our review, certainly the most intractable resource abuse examples involve slow feedback cycles and sparse or unreliable information; we also would argue that, for example, problems like local recycling efforts (which have some relatively immediate and personal costs and benefits) would be more easily tackled with educational efforts and appeals to help the community by "doing the right thing" than, for example, drought in Ethiopia or the price of gasoline. The cost of gasoline is currently much more costly (three to six times) in Europe versus the USA; use per capita in Europe is much lower, as a consequence of price, distances between living and working places, and availability of alternative transportation. In the US, we are certainly aware of the problem, but it is obviously politically difficult to pass new taxes in the US (for precisely the reasons we have outlined). The recent analysis of energy policy by Cowhey (1985) is a sterling example of "crisis" policy management in the face of conflicts of interest at a number of levels: government, individual politician, company CEOs. For the reasons Cowhey gives in more detail than we can here, it would be difficult to raises gas taxes even though it is clear that if this were done, incentives for alternative energy sources and alternative (mass) transit would be created. The difficulty in this case would be to convince voters and members of congress from the industrialized states to pass such a tax, due to the immediate costs of taxation to consumers and to the auto industry; the immediate individual costs to a politician promoting tax increases are seldom seen as counterbalanced by the long-term societal gain. Such an attempt would internalize the costs of fossil fuels, and reduce consumption by forcing consumers to pay immediate costs.

Precisely for the reasons we review here, this part of the process is difficult to achieve, and more difficult the larger and more diverse the society, because it requires coalitions of individuals willing to impose costs on themselves as well as on others in the short term. As Daly and Cobb (1989) pointed out, the rational behavior of an individual, given the current incentive system, is not necessarily a rational policy for society as a whole. With these complex problems, the question then becomes how to change incentives so that individuals will behave in ways that benefit society.

CONCLUSIONS: WHAT CAN WE DO?

Conventional wisdoms about resource use include our perceptions that [1] people in pre-industrial ("traditional") societies, being more directly and immediately dependent on the ecology of the natural systems around them, were more conserving and respectful of those resources, and [2] as ethical individuals, each of us will accept some level of personal cost to ensure the common good. If conventional wisdoms were true, resource abuse would increase with degree of technology, and information about the effects of our actions would be sufficient to solve ecological problems, as individuals accept costs for the common good. Information appropriate for analyzing these complex problems is scattered, and often it is difficult or impossible to accomplish the level of analysis we would wish. Yet it is clear that neither of the predictions from conventional wisdom are supported: resource abuse sometimes accompanies technological innovation, but only if individuals can benefit in the short term. When shifts in cultural values occur, they are secondary. Of conservation efforts in the last twenty years, those based solely on information are arguably less successful than those incorporating an individual cost-benefit leverage. Note, though, that, particularly at local levels, social costs and benefits - e.g., "doing the right thing" - can be very effective. Thus, education seems most effective when employed on relatively local problems, problems with individual costs and benefits (e.g., recycling and landfills).

The principal alternative to our conventional wisdom, the behavioral ecological paradigm, suggests that our complex human intelligence, like our co-operative behavior, evolved in competition with other human groups, and has always been directed toward our own familial short-term benefit ~ even when we can see clearly that long-term societal, or even global, detriment may result.

The behavioral ecological paradigm predicts that one effective way to change patterns of resource use is to examine people's perceived short-term benefits and play on those, creating individual (and corporate) short-term benefits (for compliance), or costs (for defection) in cases in which the behavior will have long-term societal benefit. As Mclntosh (1985) pointed out, it is only recently that there has been acceptance of the idea that humans are governed by the same physical, physiological, and ecological rules as are other species. Here we extend this statement to evolutionary principles. At one level, the logic we propose, that individuals "calculate" (though not necessarily consciously) their benefits and costs in any action, has been said or implied by others (e.g., Cosmides and Tooby 1987, McNeely 1988, and many entries in Harden and Baden 1977).

We argue that the cost and benefit currencies were not originally, and need not be, monetary. Our costs and benefits as a social primate are older than the invention of barter and money, though not older than family structure and reciprocity. If we are right, some solutions may come more easily than if we had to rely solely on economic levers; potentially important rewards include advertising one's status as a good co-operator. We evolved as a highly social species, and reciprocity is a powerful force, one we have probably underestimated in our attempts to encourage such behaviors as recycling. Even our brief review above suggests this. It may even be possible to manipulate an extension of our definitions of "family" or shared interest in real ways, to the benefit of conservation programs. These techniques have been extraordinarily successful in the service of ends many of us think less than ideal (e.g., training for warfare; Holmes 1985). Throughout our evolutionary history, most conflicts were fought by individuals or small groups of related men, and most conflicts were fought over reproductively important matters (Manson and Wrangham 1991, Low in press b). It is not coincidental that successful training eliminates many differences in appearance with haircuts and uniforms; that it uses kinship and reciprocity terms; that units are trained and moved together, so that one's life depends on men one knows (with notable failures like Vietnam, where individuals were rotated; Hackworth 1989). In short, training mimics the kin warfare situation of our evolutionary past. If we can call more widely on analogous strategies in the service of conservation (e.g., Peace Corps, Conservation Corps), perhaps we can add a powerful strategy with group-level benefits.

How can we foster strong normative conservation ethics, if we wish to? Williams (1989) called evolution "immoral," because it fosters the traits we described. While we would call natural selection amoral, because the traits it favors in all living organisms evolved long before, and outside the context of, our cultural perceptions of them, Williams makes an important point: If we try to overlook the fact that selection **uniformly** favors genotypically selfish behavior, we have no hope of countering these pressures. The only strategies likely to work consistently are those that manipulate individual costs and benefits. It is time to examine what such costs and benefits might be.

Defining manageable portions of the problems to be tackled ("think globally, act locally") seems to be an important strategic device, related to our evolutionary past in small groups with shared interests. As we have argued, shared interests are key. It is simply too overwhelming to think concurrently of whole litanies of problems, like the lists we made in our introduction; our response is to sink into passive despair. As Weick (1984) noted, such litanies disable the very resources of thought and action necessary to change them. Instead, he argues, building a series of "small wins" creates a sense of control, reduces frustration and anxiety, and fosters continued enthusiasm.

Information about the effect of our behavior is obviously important; ultimately, self-interest dictates avoiding our own destruction. However, probably because of the great changes in the scope of time and space involved, our recent history suggests that information alone will not be sufficient to change people's behavior. If the change is seen as costly in individual time, money, or even "attention," more than simple information may be required to effect change. Many solutions to resource problems may lie in adopting conservation strategies that provide direct individual or familial benefits, or advertisements to potential reciprocators, as well as monetary advantages.

Because of our inescapable history as a long-lived, social primate, we also possess evolved proximate mechanisms to maximize our functioning in the social context. If we can play upon these evolved mechanisms, again, we may be able to promote conservation strategies more effectively than if we require conscious cost-benefit calculations, or rely solely upon economic costs and benefits. Because cultural transmission is so very important (though not unique) in humans (e.g., Lumsden and Wilson 1981, Cavalli-Svorza and Feldman 1981, Boyd and Richerson 1985, Hamilton 1975), we have evolved to be "docile" — disposed to be taught (Simon 1990). Though there are sex differences in the intensity of training to be obedient, even boys in highly polygynous societies in which ferocity and aggression abound are taught to obey their elders (Low 1990a). Thus it will not surprise us that children raised in a conservation ethic might, as adults, find it less onerous than their parents did to perform slightly (phenotypically) costly behaviors which will have a longer-term benefit for the group. Similarly, the promotion of conservation ethics as a social norm (if one "ought" to do it, it can be socially costly to defect; e.g., Myers 1990) may be helpful.

In the "think globally, act locally" approach, not only can the problems be made more manageable, but the strong forces of social norms and reciprocity may be brought into play. That is, among non-relatives, our neighbors are those with whom we are most likely both to have had (socially) profitable reciprocal relationships, and those on whom we are least likely to defect (e.g., in tit-for-tat games, repeated interaction is important; Axelrod and Hamilton 1981, Axelrod 1984, Axelrod and Dion 1988). As we promote a normative standard regarding conservation, compliance is likely to be higher the better we know, and the more we interact with, our neighbors (e.g., the well-known "bystander effect" [Latane and Rodin 1969] notes that when there are sufficient bystanders, people defect - their chance of remaining anonymous is greater). Thus, information (recycling, above), reciprocal interactions, and promotion of social norms, are all likely to be more effective when translated into a more local scenario. The question remains: how much time do we have? If it takes a generation or two to create socially altruistic, group-benefit oriented individuals, what will remain for them to save? We need to work in in both the short and long term, using both economic and social (familial, reciprocal) costs and benefits, and designing education and social norm strategies on the most local scale we can.

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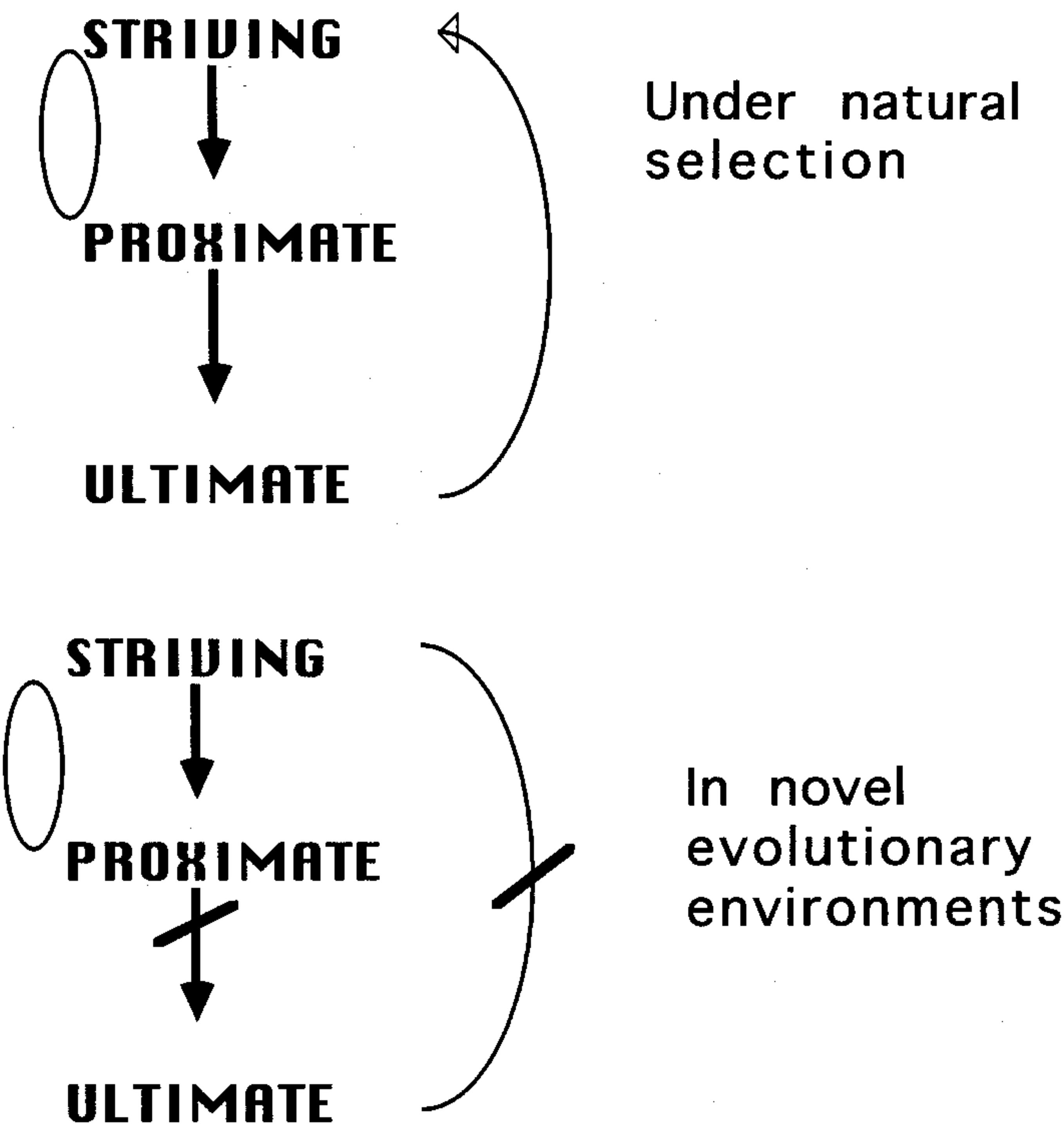
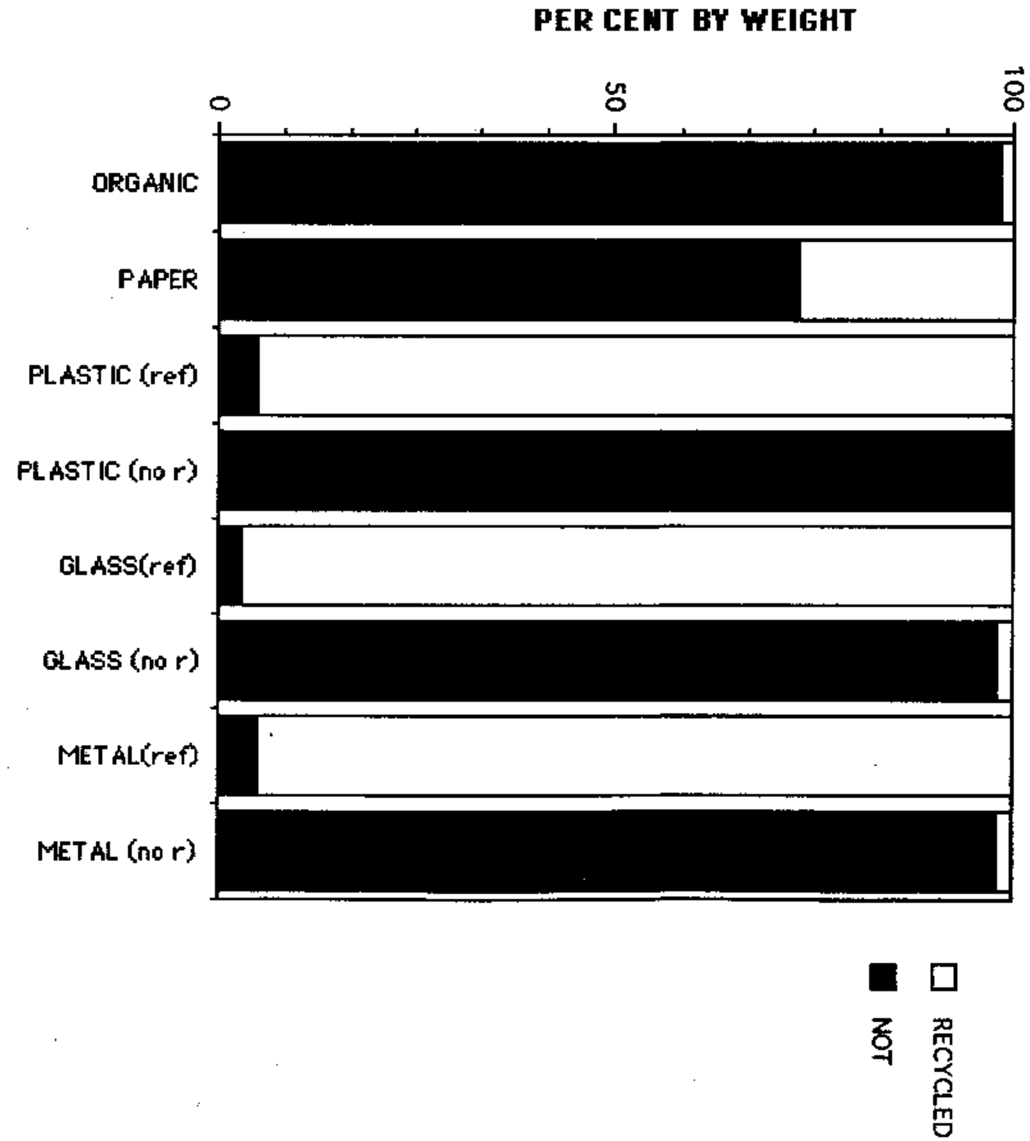
FIGURE CAPTIONS

Figure 1. The role of proximate and ultimate processes in behavior [a] in ordinary selective environments; [b] in novel evolutionary environments. While ultimate reproductive impacts actually drive the striving (arrows), organisms respond to proximate cues (closed loop). Thus, in novel evolutionary environments, if the link between proximate cues and ultimate reproductive gain is lost, the organism may persist in behaviors no longer reproductively profitable.

Figure 2. For most materials, whether recycling occurred depended on whether a refund was offered. Organic materials were defined as recycled when composted. Data from 240 University of Michigan undergraduates, 1989.



STRIVING
PROXIMATE
ULTIMATE
Under natural selection
STRIVING
PROXIMATE
ULTIMATE
In novel evolutionary environments


PER CENT BY WEIGHT
0
50
100
ORGANIC
PAPER
PLASTIC (ref)
PLASTIC (no r)
GLASS(ref)
GLASS (no r)
METAL(ref)
METAL (no r)
NOT
RECYCLED

PHENOTYPIC EFFECT?	GENOTYPIC EFFECT?	EXAMPLES
PROFITABLE ("selfish")	PROFITABLE ("selfish")	**numerous; all overt competition**
COSTLY ("altruistic")	PROFITABLE ("selfish")	**parenting, nepotism, reciprocity**
------------------	------------------	BECAUSE NATURAL SELECTION FAVORS ONLY GENOTYPICALLY PROFITABLE BEHAVIORS, UNDER NATURAL SELECTION, BEHAVIORS ABOVE THE LINE SHOULD BE COMMON; BELOW THE LINE, RARE
PROFITABLE ("selfish")	COSTLY ("altruistic")	?? Perhaps a rich miser who disinherits his family, leaving an anonymous gift to a home for unwed mothers
COSTLY ("altruistic")	COSTLY ("altruistic")	**Mother Theresa**

TABLE 1. Categorization of the impacts of behaviors on phenotypic and genotypic condition (modified from Alexander 1974).