

THE QUARTERLY REVIEW of BIOLOGY



THE EVOLUTIONARY ROOTS OF OUR ENVIRONMENTAL PROBLEMS: TOWARD A DARWINIAN ECOLOGY

DUSTIN J. PENN

Konrad Lorenz Institute of Comparative Ethology

Savoyenstrasse 1a, A-1160, Vienna, Austria

E-MAIL: D.PENN@KLIVV.OEAW.AC.AT

KEYWORDS

evolutionary psychology, human conservation behavior, aboriginal overkill, demographic transition, conspicuous consumption, discounting, tragedy of the commons, environmental aesthetics, environmental education, social pressure

ABSTRACT

It is widely acknowledged that we need to stabilize population growth and reduce our environmental impact; however, there is little consensus about how we might achieve these changes. Here I show how evolutionary analyses of human behavior provide important, though generally ignored, insights into our environmental problems. First, I review increasing evidence that Homo sapiens has a long history of causing ecological problems. This means that, contrary to popular belief, our species' capacity for ecological destruction is not simply due to "Western" culture. Second, I provide an overview of how evolutionary research can help to understand why humans are ecologically destructive, including the reasons why people often overpopulate, overconsume, exhaust common-pool resources, discount the future, and respond maladaptively to modern environmental hazards. Evolutionary approaches not only explain our darker sides, they also provide insights into why people cherish plants and animals and often support environmental and conservation efforts (e.g., Wilson's "biophilia hypothesis"). Third, I show how evolutionary analyses of human behavior offer practical implications for environmental policy, education, and activism. I suggest that education is necessary but insufficient because people also need incentives. Individual incentives are likely to be the most effective, but these include much more than narrow economic interests (e.g., they include one's reputation in society). Moralizing and other forms of social pressure used by environmentalists to bring about change appear to be effective, but this idea needs more research. Finally, I suggest that integrating evolutionary perspectives into the environmental sciences will help to break down the artificial barriers that continue to divide the biological and social sciences, which unfortunately obstruct our ability to understand ourselves and effectively address our environmental problems.

The Quarterly Review of Biology, September 2003, Vol. 78, No. 3

Copyright © 2003 by The University of Chicago. All rights reserved.

0033-5770/2003/7803-0001\$15.00

INTRODUCTION

The one process now going on that will take millions of years to correct is the loss of genetic and species diversity by the destruction of natural habitats. This is the folly our descendants are least likely to forgive us (Wilson 1984:121).

IT TOOK OUR SPECIES hundreds of thousands of years to reach a population of 10 million, and we now are adding (net) 10 million people every six weeks (McMichael 1993). Global population is around 6 billion and it is projected to reach 7 to 11 billion in the next 50 years (Lutz et al. 2001). It is unclear, however, whether the Earth's ecological life-support systems can sustain this many people, at least at current standards of living (Meadows et al. 1992; Cohen 1995). Humans currently consume 40 percent of the food (net primary productivity) available to sustain land animals (Vitousek et al. 1986), and 45 percent of the available freshwater on Earth (Postel et al. 1996). Our toxic pollutants, such as PCBs, dioxin, and DDT, have spread across the planet and are causing insidious effects, which we are only now beginning to recognize, on the health and behavior of humans and wildlife (Colborn et al. 1996). Humanity has become a geological force and our pollution of the atmosphere is altering the Earth's climate (Gelbspan 1997). We are causing the first episode of mass extinction on the planet in 65 million years, with thousands of species vanishing each year (Wilson 1992, 2002). "*Homo sapiens* is poised to become the greatest catastrophic agent since a giant asteroid collided with the Earth sixty-five million years ago, wiping out half the world's species in a geological instant" (Leakey and Lewin 1995:241). By destroying our planet's natural resources, biodiversity, and ecosystem services, we are weakening its capacity to support our burgeoning populations, and subsequently creating violent conflicts and health, social, and economic problems for ourselves and future generations (Homer-Dixon 1999).

It is widely agreed that we need to change course and move toward greater ecological sustainability (Bloom 1995); making the necessary changes has proved to be extremely difficult, however. Most agree that we need to stabilize population growth (Cohen and Rich-

ards 1994), and yet family planning efforts have been met with considerable resistance (Ehrlich and Ehrlich 1990; Abernethy 1993; Hardin 1999). Some opponents argue that environmental degradation is not due to overpopulation as much as overconsumption and pollution by the rich. Indeed, industrialized countries consume the vast majority of the Earth's resources. This is why the world's leading scientists, including most living Nobel Laureates, have issued a "warning to the world," urging developed nations to reduce their consumption (Graham-Smith 1994). Yet efforts to address consumption are also strongly resisted and undermined by politically powerful interests (Helvarg 1994; Ehrlich and Ehrlich 1996). Most people—including economists and governmental leaders—still maintain that increasing consumption is desirable (Baltz 1999). Our environmental problems are clearly due to both overpopulation and excessive consumption (Waggoner and Ausubel 2002), but we face a global standoff: wealthy countries want poor ones to reduce their population, and poor countries want the rich to reduce their consumption (Porter and Brown 1996). As the World Commission on Environment and Development recognized: "The Earth is one but the world is not" (World Commission on Environment and Development 1987:27).

Why have people been so slow to respond to our environmental crisis? Why is there such resistance to family planning and efforts to reduce consumption and environmental destruction? Why do we discount the needs of future generations, and why do we blame our environmental problems on everyone and everything else but ourselves? And most importantly, how can we bring about changes needed to reduce our environmental impact?

My goal here is to show how efforts to address our environmental problems would benefit from a better understanding of the evolution of human behavior. The problem is that science currently lacks the integration necessary to understand ourselves or our relationship with the rest of nature (Wilson 1998a,b). Historically, biologists have not generally been trained in the human behavioral or social sciences, and social scientists have not generally been interested in the environ-

ment. This situation is improving, as the social sciences are becoming increasingly ecologically informed and new interdisciplinary fields are emerging, such as ecological economics (Costanza 1991) and environmental psychology (Gardner and Stern 1996). Researchers are beginning to address human behavior and environmental problems; most only consider only *proximate* explanations, however. For example, ecological economists recognize that our environmental problems are due to constraints on human cognition, such as discounting the needs of future generations. Such explanations are valid but incomplete. We also need to understand *why* such cognitive biases exist, why people discount future generations. Because humans are animals that evolved by natural selection, a complete understanding of why people do what they do requires *evolutionary* analyses of behavior.

Evolutionary biology provides fundamental insights into human behavior, including reproduction, cooperation, politics, ethics, and morality, which are gradually becoming integrated into the social sciences (human ethology, sociobiology, behavioral ecology, and evolutionary psychology) (Smith and Winterhalder 1992; Betzig 1997; Barrett et al. 2002). Contrary to what is often assumed, evolutionary approaches have much to say about human culture. For example, social learning evolves by natural selection and generates novel behaviors that can potentially create new sources of genetic selection (Lumsden and Wilson 1981; Richerson and Boyd 1992; Feldman and Laland 1996; Blackmore 1999). Ethology and sociology, which were once so controversial for applying evolutionary principles to humans, have become increasingly recognized as providing major contributions to understanding human behavior, and researchers in these fields have successfully addressed their critics (Alcock 2001). Their offspring disciplines, human behavioral ecology and evolutionary psychology, are helping to bridge the artificial division between the social and biological sciences. Evolutionary analyses are also providing important insights into applied sciences, such as medicine ("Darwinian medicine": Williams and Nesse 1991; Nesse and Williams 1994). Similarly, my aim is

to show that evolutionary analyses also offer important insights for addressing population, conservation, and environmental problems.

Evolutionary approaches to human behavior are generally ignored or rejected by environmental scholars, and it is important to understand why. First, most are simply unaware of the recent advances that have been made by integrating evolution into the social sciences. Human behavior is still generally viewed from the perspective of the obsolete "standard social science model," which assumes that the human mind appeared fully functional in its present state and that human behavior is determined solely by culture (Tooby and Cosmides 1992). Second, "human nature" is widely misunderstood as a constraint and something to overcome, rather than *enabling* our ability to change, adopt new behaviors, and produce social norms and culture; therefore it is mistakenly viewed as an obstacle to the efforts of environmentalists. Third, Darwinism is widely misunderstood as being useful only for explaining (and justifying) individualistic selfish greed, social inequality, and the pursuit of the political goals of the conservative right, which is another reason that it is misunderstood as an obstacle to change (Singer 2000). Unfortunately, these latter two misunderstandings have been reinforced by evolutionary thinkers who have sometimes overexaggerated self-interests (see de Waal 1996 for a thoughtful critic of such "Huxleyans"). Fourth, although some environmental thinkers have been forging bridges between the biological and social sciences, many are hostile toward biology and science (Lewis 1992, 1996). A large segment of the environmental movement—e.g., postmodernists, ecofeminists, ecotheologists, New Age and radical Greens—embraces mystical and religious views, and opposes scientific materialism and reductionism (e.g., Merchant 1980; Oelschlaeger 1994; Roszak et al. 1995; Sessions 1995). Part of the resistance is due to common misunderstandings about science (Gross et al. 1996). Many fail to recognize, for example, that scientists rely on holistic, integrative, and synthetic, as well as reductionistic, approaches. More importantly, some people view efforts to explain human behavior in

physical terms—or with the evolutionary principles used to understand animals—as a vulgar insult to human dignity (e.g., Berry 2000). Environmentalists may recognize that humans are ecologically part of nature, but most still refuse to accept our species' evolutionary origins. Environmentalists often point out that “we need new ways of thinking about our place in the world” (Raven 2002). Modern evolutionary biology offers a fascinating new way of viewing ourselves and our place in the world (Dawkins 1982), it is simply that most are still unwilling to give it serious consideration (Wilson 1998a).

In this paper, I will show how evolutionary perspectives of human behavior often provide a different view from those generally held by environmental thinkers. First, I review evidence that our species' potential for being ecologically destructive is more pervasive and older than “Western” culture. These findings directly contradict the conventional wisdom of environmentalists, and offer several important implications. Second, I review evolutionary research aimed at understanding why people create ecological problems, and also why people sometimes want to limit their reproduction and conserve natural resources. Third, I show how these evolutionary insights into human behavior offer practical implications for environmental policy, including education and political activism. Finally, I suggest that an interdisciplinary field of applied human behavioral ecology, “Darwinian ecology,” is emerging, whose central aim is to apply evolutionary insights about human behavior to address ecological problems. This is an extremely important endeavor. Indeed, achieving a better understanding of ourselves to address overpopulation and our environmental crisis is arguably the most important challenge currently facing science and the rest of humanity.

THE ECOLOGICAL NOBLE SAVAGE HYPOTHESIS

We have never quite outgrown the idea that, somewhere, there are people living in perfect harmony with nature and one another, and that we might do the same were it not for the corrupting influences of Western culture (Konner 1990).

When attempting to explain why humans are ecologically destructive, environmental scholars have long attributed the problem to “Western” culture, especially the anthropocentric and scientific worldviews (White 1967). Subsequently, many argue that addressing our ecological problems requires a rejection of the materialism of science, and an embrace of the animistic and spiritual beliefs of non-Western religions and traditional cultures. Aboriginal peoples, such as Native American Indians, have been represented as the major role model for the modern environmental movement because they are widely thought to have lived in harmony with nature before Western contact. Environmentalists often quote a famous speech by Chief Seattle of the Squamish tribe who reportedly stated that “Every part of this earth is sacred to my people . . . the earth does not belong to man, man belongs to the earth” (Gore 1992:259). Just as Jean-Jacques Rousseau thought that people in traditional cultures live as “noble savages,” environmentalists often assume that humans lived in harmony with nature as “ecological noble savages” until they became corrupted by Western culture (Redford 1991). The idea that our modern environmental problems are due to Western science and culture is central to modern environmental movements and philosophies such as Deep Ecology (Devall and Sessions 1985; Sessions 1995) and ecofeminism (Merchant 1980).

Evolutionary researchers have been uncovering a very different picture of the conservation behavior in traditional and other non-Western cultures (Smith and Wishnie 2000). Increasing evidence indicates that pre-Columbian American Indians and other traditional societies are not the conservationists often assumed (Edgerton 1992; Ridley 1996; Krech 1999). The low ecological impact of people in traditional cultures does not appear to be due to conservation practices per se, but simply their low population densities and inefficient technologies (Hames 1987; Alvard 1993, 1995; Kay 1994; Stearman 1994; Vickers 1994; Low 1996a; Alvard 1998; Miller et al. 1999; Ruttan and Borgerhoff Mulder 1999). Among the Piro Indians in Ecuador, hunters do not pay the opportunity costs of passing up prey for conservation;

instead their hunting behavior follows optimal foraging principles (Alvard 1993, 1995, 1999). Nor is there any association between societies that hold beliefs about the sacredness of nature and having a low ecological impact (Low 1996a). It turns out that the widely quoted speech by Chief Seattle is just a myth, a story created for television, that has been perpetuated by uncritical and wishful-thinking environmentalists (Ridley 1996).

Furthermore, increasing evidence indicates that our species has a long history of causing ecological destruction (Diamond 1988, 1992, 1995; Redman 1999). As humans have moved around the planet, they have caused massive extinctions in various ecosystems. For example, the megafaunal extinction in the Americas during the Pleistocene (in which 57 species of large mammals went extinct, including mammoths and mastodons, in a sudden ecological collapse) is usually attributed to climate change. Alfred Russel Wallace suggested otherwise: "I am convinced that the rapidity of . . . the extinction of so many large Mammalia is actually due to man's agency" (cited in Leakey and Lewin 1995:172). Much evidence now indicates that the Pleistocene extinctions in North America correspond to the time of arrival of human migrations from Asia (Martin 1978; Martin and Klein 1984). This major extinction event does not appear to have been due to climate change; other places experienced climate change at this time, but did not have similar extinctions. Instead, it appears that it was due to the vulnerability of North American fauna to a newly introduced and highly effective predator, *Homo sapiens* (Alroy 2001). This "Pleistocene overkill" hypothesis is somewhat controversial; it is still debated whether the Pleistocene extinctions in North America were due to human hunting alone, climate change, or some combination of these factors. Yet, the major extinctions that occurred on many South Pacific islands (Steadman and Olson 1985; Steadman et al. 2002), such as the disappearance of elephant birds in New Zealand, cannot be attributed to climate change and they coincide precisely with the arrival of humans who hunted them extensively (Anderson 1989;

Diamond 2000; Holdaway and Jacomb 2000; Roberts et al. 2001).

Once humans began to settle down and organize into larger and more complex societies, entire civilizations appear to have collapsed due to the overexploitation of their resource base (Diamond 1988; Ponting 1992). After arriving to Easter Island, the Polynesians turned a lush forested island into a treeless landscape, exhausted their resources, and their population and society collapsed (Diamond 1995). The sudden disappearance of the Anasazi Indians in North America, the Maya in Central America, and other non-Western civilizations may have been due to an ecological collapse (Culbert 1973; Deevey et al. 1979; Diamond 1992; Redman 1999; Stuart 2000). The precise causes for the demise of the Maya and Anasazi and other ancient civilizations are still unclear and controversial. Their downfall is still usually attributed to internal social turmoil or hostile invading groups (except Easter Island), though such events may have just provided the final coup de grace after resource depletion already undermined economic and political stability, as we are seeing today in many societies (Homer-Dixon 1999).

Thus, humans did not live in harmony with nature until the spread of "Western" culture, and these findings about our species' actual conservation behavior offer several extremely important implications. First, they indicate that environmentalists are not merely overreacting "alarmists"; we have very good reasons to be concerned about our species' potential for causing ecological destruction. Second, they indicate that achieving ecological sustainability may be more difficult than is often assumed and that we cannot simply abandon "Western" secularism and science for mysticism. Third, they show that we must be wary of romantic myths and wishful thinking about human nature. Becoming more critical, though, does not imply that we should not be open to new possibilities or try to learn from other cultures. Many societies have successfully managed their resources (Smith and Wishnie 2000), so there is room for optimism. What is needed is more research into how people in various societies have successfully managed

their natural resources, and to determine how to apply this knowledge toward designing adaptive strategies for dealing with ecological problems (e.g., Ostrom et al. 1999).

EVOLUTIONARY PERSPECTIVES ON ENVIRONMENTAL PROBLEMS

Evolutionary approaches are valuable, not because they tell us what is natural or what is good, but because they help us understand why people do what they do (Mace 1999).

In this section, I provide an overview of how evolutionary perspectives offer insights into why people create ecological problems, and also suggest why people sometimes want to control their fertility and reduce their environmental impact. Evolutionary analyses are not alternatives to the standard proximate explanations sought by social scientists (e.g., conscious motives, influences of social norms). They can, however, sometimes provide a different perspective from the conventional views of environmental thinkers and reveal flawed assumptions.

STABILIZING POPULATION GROWTH

The omission of Darwinian interpretations of contemporary reproductive patterns [from a recent book] reflects an omission in the whole field of human demography (Mace 1999).

Human overpopulation is one of the main reasons for our ecological problems, and stabilizing population growth is one of the greatest challenges for the 21st century (Ehrlich and Ehrlich 1990; Cohen 1995). Efforts to stabilize population growth would be aided by a better understanding about *why* fertility has declined in some societies. Fertility declines have long been attributed to improved infant survival that accompany economic development (“demographic transition” theory). The evidence to support this idea is not as strong as generally assumed, however. Fertility declines have occurred without reductions in infant mortality or economic development, and some populations in developed countries have high fertility (Kirk 1996; Mason 1997). Demographic transition theory was originally based on the erroneous assumption that nat-

ural selection favors altruistic population regulation checks to benefit the species (Bates and Lees 1979; Hawks and Charnov 1988; Turke 1989). For example, people were expected to curb their own reproduction when child survival is high because “otherwise population would grow at a rate which would upset the balance of population and the economic environment” (Andorka 1978:19). “One of the central ideas in demographic transition theory is that fertility decline is an adaptive response to improved survival chances. Under conditions of very high mortality with expectations of life of 20–30 years, five or so births per woman were necessary to ensure continuation of the species” (Cleland 1995:217). It has become all too clear, however, that we cannot count on people to automatically reduce their reproduction to benefit the common good.

More recently, researchers have been applying principles from evolutionary biology toward understanding fertility, including fertility transitions (evolutionary demography) (Turke and Betzig 1985; Low 1993; Rose 1997; Borgerhoff Mulder 1998; Voland 1998; Bock 1999; Kaplan and Lancaster 2000; Mace 2000; Strassmann and Gillespie 2002). This work was sparked by a challenge from the demographer Daniel Vining (1986), who asked why people in wealthy, developed countries do not use their wealth to make *more* offspring. Why do they have the lowest fertility? He called this problem “the central challenge of human sociobiology,” and claimed that it questions the validity of applying evolutionary principles to humans! As it turns out, reproductive success is actually positively associated with increased wealth *within* traditional societies (Kaplan and Lancaster 2000; Clarke and Low 2001), as predicted by evolutionary theory (Dawkins 1986). This still leaves the problem of explaining why fertility declines have mainly occurred in developed countries.

The leading explanation for fertility declines argues that people in developed countries are trading offspring quantity for “quality”; i.e., people in developed countries have fewer children because their children require more investment to make their offspring competitive (Becker 1991; Kaplan and Lancaster 2000). This idea assumes that there

is a tradeoff between number of offspring and their quality, and recent work has found evidence for this assumption (Borgerhoff Mulder 2000; Strassmann and Gillespie 2002). High investment into rearing children is not the whole story though, because fertility declines are not exclusively occurring in developed countries. Also, the quantity/quality tradeoff hypothesis is insufficient to account for a particularly striking observation: fertility declines have occurred in some poor countries, and they are often correlated with improvements in education for women. Consequently, most population policies now promote the “women’s empowerment hypothesis,” which suggests that stabilizing population growth requires a reduction of patriarchy and an improvement of women’s education and access to contraception. I have suggested that sexual conflicts over fertility are due to women bearing higher fitness costs for childbearing than men, and this “sex-specific optimal fertility hypothesis” has some empirical support (Penn 1999).

There appear to be several proximate factors that trigger fertility declines (child survival, parental investment, women’s empowerment), rather than a single encompassing theory. This is not surprising from an evolutionary perspective. More work is needed to integrate evolutionary perspectives on fertility with those of the social sciences. For example, Darwinians object to a common notion among economists that people in developed countries are “trading babies for durable consumer goods,” since the point of consuming resources is to reproduce. Yet economists might have it right if people’s instinctive emphasis on status seeking is being exploited by modern mass media (see next section) (Pratkanis and Aronson 1992). Also, when wealth is inherited, the rich may have an advantage by producing few but well-provisioned offspring (Rogers 1995; Mace 1998). Another hypothesis that needs more attention is the idea that people copy the fertility behavior of other individuals (e.g., the spread of modern contraception through cultural transmission). Biology is assumed to be irrelevant for such cultural behavior; and yet such behavior may function as a mechanism in which people use the fertility of others as a

cue to make adaptive reproductive decisions. The spread of low fertility in developed countries may be due to people copying the fertility of social dominants, who are likely to have more information about the environment and how many offspring are likely to survive (Borgerhoff Mulder 1998). Such behavior may have been adaptive in the past, but maladaptive in the modern world in which social dominants are trading babies for consumer goods in their quest to maintain status. Finally, it has been suggested that modern fertility declines are a pathological response due to exposure to evolutionarily novel chemical pollutants in the environment (“endocrine disruptors”) that cause reduced sperm count and other reproductive abnormalities (Jensen et al. 2002). These are all viable explanations that need more research if we are going to stabilize population growth.

Evolutionary research offers insights into human reproductive behavior, but its findings are not likely to be integrated or applied until some significant misunderstandings are cleared up. Many environmentalists distrust evolutionary biology, especially when it is applied to family planning (e.g., Ross 1998). This is understandable because some social elites in the past tried to address overpopulation through coercion and sterilization of the poor and nonwhite, who they saw as “unfit” to reproduce, and they invoked Darwinism to justify their goals. Evolutionary biology can help to explain these behaviors, but it offers no moral justification for racism or exploitation of the poor. Another complaint is that biologists have emphasized the dangers of population growth in poor countries, and ignored overconsumption in wealthy, industrialized countries. This is because biologists had little to offer on this topic, but this is changing.

REDUCING CONSUMPTION

How might we explain to our grandchildren why we pursued further embellishments of our outdoor cooking appliances at the expense of safer highways and clean air? Or why we found continued escalation in the amounts spent on Patek Philippe wristwatches and Hermés handbags more important

than cleaner drinking water and safer food? (Frank 2000:277).

We humans, especially those living in industrialized nations, consume an amazing portion of the Earth's available natural resources. Americans, for example, represent around 5 percent of the Earth's population, and yet consume 25 percent of the resources, release 20 percent of the carbon dioxide emissions that contribute to global climate change, and generate almost 50 percent of the hazardous waste produced on the planet. How can we explain why people in industrialized countries consume so much? Americans consume so many calories from fats and sugars that obesity and diabetes have become major epidemics! The evolutionary reason for overeating seems straightforward: selection appears to have favored open-ended cravings for fats and sugars that were difficult to obtain for our ancestors; modern fast foods satisfy our evolved dietary preferences but remove the energetic costs of hunting, foraging, and processing the food. Our environmental impact, however, is not simply from overconsuming food and other resources needed for sustenance and survival. It is mainly from the pursuit of *extravagant* goods, such as fashionable clothes, luxurious cars, and massive homes (Durning 1992; Frank 2000; de Graaf et al. 2001). Why do people spend so much time and trouble pursuing resources that have *no survival value*? What is the appeal of buying expensive large automobiles, designer watches, fur coats, and following the latest fashion trends?

To explain the evolution of conspicuous and extravagant traits in animals, such as a peacock's elaborate plumage, Charles Darwin (1871) proposed that they function to attract mates and repel rivals (i.e., they evolve through differential mating success or "sexual selection"). The problem has been to explain why traits that are handicaps to survival would be sexually attractive or increase status. Amotz Zahavi (1975) suggested that costly exaggerated displays enable high quality males to honestly advertise their quality to potential mates and rivals because only high quality individuals can bear the costs of the display. This "handicap principle" or "honest signaling theory" helps to explain the evolu-

tion of extravagant displays in animals (Zahavi and Zahavi 1997), and offers implications for many aspects of human behavior (Miller 2000).

Interestingly, honest signaling theory was first suggested by the economist Thorstein Veblen (1899) to explain the excessive consumption by wealthy people. He coined the term "conspicuous consumption" to describe extravagant and ostentatious displays of resources that function as a competitive strategy to demonstrate wealth and social status: "Conspicuous waste and conspicuous leisure are reputable because they are evidence of pecuniary strength" (p 181). "Since the consumption of these . . . excellent goods is an evidence of wealth, it becomes honorific; and conversely, the failure to consume in due quantity and quality becomes a mark of inferiority and demerit" (p 74). Veblen also suggested why this process tends to escalate into increasingly wasteful displays of fashion and consumption: people instinctively acquire items to demonstrate group membership, but to rise in social status they must be able to display items worn by high status individuals, which in the modern world means wearing the expensive designer clothes, driving costly and wasteful cars, and buying large homes in expensive neighborhoods. If low status individuals are able to acquire the luxury items (or cheap copies) usually reserved to the wealthy "leisure class," then the wealthy simply acquire more costly and ostentatious items to display their wealth. Veblen even attempted to place his ideas about conspicuous consumption within an evolutionary framework, but evolutionary biology was not yet a mature science.

Veblen's ideas have had surprisingly little impact on economists, but evolutionary researchers are beginning to give them serious consideration (Neiman 1997; Boone 1998; Miller 1999; Smith and Bird 2000; Sosis 2000; Bliege Bird et al. 2001). Their studies support the idea that conspicuous displays of wealth enhance social status and mating success. For example, people in nearly all human cultures (especially women) prefer mates with high status and good resources or prospects (Buss 1989), and conspicuous displays of resources (from hunting and fish-

ing) appear to enhance men's social status and mating success (Hawkes and Bliege Bird 2002). If our species' preoccupation with material resources and the display of wealth evolved through sexual selection, then these preferences may have been further exaggerated by runaway (positive feedback) selection, like other sexually selected traits (Grafen 1990). Moreover, handicap signaling behaviors may have become exaggerated by cultural evolution, in which people copy the behavior of others and engage in escalated contests of ever-increasing displays of wealth and power (e.g., temples, palaces, cathedrals, skyscrapers). The ecological collapse of some ancient civilizations, such as Easter Island, the Maya, and the Anasazzi (Diamond 1992, 1995), may have been the result of runaway escalation processes in which natural resources were converted into increasingly large and ostentatious architectural structures erected for displaying the wealth and power of social dominants (Neiman 1997). It is still unclear, however, whether conspicuous consumption functions as a handicap signaling behavior or is simply a by-product of some other adaptive behavior, perhaps exploited by modern media.

Evolutionary analyses help to explain why people are more concerned with *relative* rather than absolute wealth and status (Frank 1985, 2000). For example, some studies have found that as people have increased their absolute levels of wealth and consumption it has not made them happier; above a minimal threshold, it is relative not absolute wealth that matters most to people (Durning 1995). Though this was a complete surprise to many social scientists, it makes sense from an evolutionary perspective (because evolutionary "success" is always relative). People's concern about social status and other "positional goods" appear to become intense once their immediate survival concerns are satisfied (Hirsch 1976). In *How Much is Enough?*, Durning (1992) argues, "The happiness that people derive from consumption is based on whether they consume more than their neighbors and more than they did in the past . . . Consumption is thus a treadmill, with everyone judging their status by who is ahead and who is behind" (p 39). Yet Durning, like

most social scientists, assumes that conspicuous consumption was created by socially prescribed values of "Western" culture and mass media, and he does not consider its evolutionary origins. Overconsumption appears to be fueled by television, mass media, marketing, advertising, and other gimmicks designed to exploit our concern for "keeping up with the Jones's" (de Graaf et al. 2001). Contrary to conventional wisdom, however, consumer preferences were not invented by Madison Avenue, and worrying about the Jones's is not new to the modern world. Traditional peoples, like Westerners, often deplete their natural resources in "ostentatious displays of resource-acquiring potential and success in social competition" (Wilson et al. 1998).

Overconsumption by the wealthy is rapidly exhausting our natural resources, but we do not completely understand why this is happening. It seems likely that advertisers are fueling runaway consumption by exploiting our instinctive desires to maintain status in society and attract mates. For example, television programs and commercials show us how the other (upper) half lives, and advertisers appear to exaggerate the standard of living of actors to trigger consumption. As one advertiser quipped, "It is our job to make women unhappy with what they have" (cited in Durning 1992:120). The advertising industry's success may be possible because we lack evolved defenses in our nervous system against modern media. But if this is truly manipulation, then individuals must be harmed in some way. It is unclear, however, whether exposure to advertising or excessive consumption causes harmful psychological or other health problems, such as depression or overeating (Wright 1995). The problem is that social scientists since John Watson, the founder of behaviorism, have generally aimed to *increase* consumerism rather than to reduce it (Pratkanis and Aronson 1991) or to determine how advertising might be harmful. Fortunately, some scientists are beginning to consider how we might reduce consumption (de Graaf et al. 2001), and some are applying evolutionary insights to make specific policy recommendations for change (Frank 2000).

DISCOUNTING THE FUTURE

The difficulty created for the conservation ethic is that natural selection has programmed people to think mostly in physiological time (Wilson 1984: 120).

Our environmental problems are generally due to the fact that we humans place more emphasis on today's tiny pleasures than tomorrow's greater needs; i.e., we discount the future. To understand how we might reduce temporal discounting, we need to understand *why* people discount the future. Discounting, like other aspects of human preferences, are usually assumed to be just some pathological aspect of human behavior arbitrarily determined by culture or an aberrant pathology of "Western" civilization. In contrast, evolutionary theory views temporal discounting as an adaptation to enhance individual survival and reproductive success (Kagel et al. 1986; Rogers 1994, 1997; Henderson and Sutherland 1996; Kacelnik 1997; Wilson et al. 1998) (though I know of no direct evidence for this assumption). Squirrels that spend too much of their time preparing and storing food for the upcoming winter, rather than addressing their immediate survival needs (watching out from predators), are less likely to make it to see the winter. Also, discounting the future makes sense because individuals always face some uncertainty about whether potential future payoffs will ever be realized. Although the failure to delay gratification is often interpreted as an indicator of poor intelligence, evolutionary life-history theory suggests that how the future is optimally weighted depends on the expected present and future fitness payoffs (Wilson et al. 1998). If life expectancy is short, for example, then natural selection favors steep discount rates. Thus, evolutionary theory provides a foundation for understanding why it has been so extremely difficult to address long-term environmental threats, such as global climate change (Low and Ridley 1993; Wilson et al. 1998).

Evolutionary theory predicts that men generally discount the future more steeply than women for several reasons, e.g., men have a lower life expectancy than women, and use resources to compete for and attract women. Interestingly, several studies have found that

women express more of a concern about the pollution and the quality of the environment than men (Low and Heinen 1993; Low 1996b; Wilson et al. 1996; Wilson et al. 1998). As these studies point out, however, evidence based on such self-reports and interview data is not convincing because stated attitudes do not always reflect actual behavior. It is often claimed that environmental groups are frequently organized by women (Merchant 1980; Winter 1996), though I know of no evidence for this hypothesis. Many environmental thinkers, particularly "ecofeminists," blame our environmental problems on male-dominated or patriarchal societies, and argue that women are more inclined to protect the environment than men (Merchant 1980; Mies and Shiva 1993). Evolutionary research offers support for this view, though it does not support the notion that biology is irrelevant and that gender differences are simply "social constructions" arbitrarily determined by culture.

Efforts to understand the evolutionary psychology of temporal discounting are just beginning, and yet they already offer important implications for environmental scientists, activists, and policy makers (Henderson and Sutherland 1996, 1997). First, evolutionary analyses suggest that people will always discount the future to some degree, and therefore calls for people to value the needs of future generations as much as their own needs are unrealistic. Second, although zero discounting is unrealistic, evolutionary theory does not imply that institutional and other social changes cannot alter people's time preferences. We simply must find ways to work within the constraints of the evolved psychological mechanisms that control human time preferences. Third, evolutionary perspectives offer a more *optimistic* picture than is usually assumed by economists. Economists generally assume that humans discount "rationally," with an exponential function, whereas humans and other animals use a hyperbolic discount rate, which gives the future more importance (Henderson and Sutherland 1996; Kacelnik 1997; Wilson et al. 1998). Evolutionary perspectives offer some insights into why animals have evolved a hyperbolic rather than an exponential discount rate. Some economists argue that the concept of discounting should not be

applied beyond an individual's own expected lifetime, but evolutionary theory provides a different perspective. It recognizes that "one's descendants are an extension of one's self, and organisms may be expected to have evolved to act in ways that will promote their fitness both before and after their deaths" (Wilson et al. 1998:516). Integrating an evolutionary perspective on discounting into economics has policy implications. By using exponential rather than hyperbolic discount rates as a basis for policy decisions, we could be seriously underestimating the costs of environmental damage and the benefits of resource conservation and sustainable use (Henderson and Sutherland 1996).

Evolutionary perspectives help to understand why our species is so ecologically shortsighted, and why our species has a long history of creating ecological problems. If the human mind is evolutionarily "designed" to discount the future, then policies that do not recognize this aspect of human psychology are doomed to fail. We still have much to learn about the conditions under which people tend to value the future (e.g., we know almost nothing about how parenthood affects environmental attitudes or behavior). The main problem is that most researchers in the social sciences assume that human decisions and preferences are based on conscious and rational deliberation, and the people can (and will) express these preferences when questioned (Wilson et al. 1998). This is the central assumption that underlies the methods commonly used for evaluating discounting rates, such as the "contingent valuation method," which are currently being used to assign a monetary value to biodiversity and ecosystem services (Daily 1997). Evolutionary thinkers challenge this assumption because "natural selection favors the forces of psychological denial" (Hardin 1968:1244). Denial or self-deception, rather than being a design defect, may be a functional feature of human psychology (Trivers 1991). Fortunately, discounting rates appear to be flexible and change depending upon social and ecological circumstances. In the next section, I review how the biological and social sciences have converged on a general explanation for

why people sometimes discount steeply and overexploit their natural resources.

THE TRAGEDY OF THE COMMONS

Each man is locked into a system that compels him to increase his herd without limit—in a world that is limited. Ruin is the destination toward which all men rush, each pursuing his own interest in a society that believes in the freedom on the commons. Freedom in a commons brings ruin to us all (Hardin 1968:1244).

The tragedy of the commons has become central for understanding our ecological problems: why people tend to overexploit common-pool resources, such as public grazing lands, fisheries, and aquifers, and why they pollute (Hardin 1968; Hardin and Baden 1977). This model suggests that people are unlikely to conserve common-pool resources when they lack confidence that others will show similar restraint. As a resource becomes overexploited, prudent restraint only yields opportunity costs, and so users have incentives to get their fair share before it is all gone (i.e., this model extends the classic prisoner's dilemma to a multiperson game theoretical problem). Each individual faces a dilemma in which they ask themselves, "Why should I sacrifice and minimize my reproduction and environmental impact if others do not do the same?" The tragedy of the commons was first suggested as a general explanation for ecological overexploitation by the evolutionary ecologist, Garrett Hardin (1968). It has subsequently been corroborated by evidence from various fields and methods (Dawes 1980; McCay and Acheson 1987; Berkes et al. 1989; Ostrom 1990, 1999; Ostrom et al. 1999; Borgerhoff Mulder and Ruttan 2000; Wedekind and Milinski 2000; Milinski et al. 2002). This research is helping to integrate evolutionary approaches with economic approaches (via mathematical game theory) to address conservation and other collective action problems (Hawkes 1992).

Yet, ever since Hardin suggested the tragedy of the commons model, it has been widely criticized by environmentalists. This resistance was partly due to semantic misunderstandings. Hardin's original paper equated "common-pool resources," which belong to

no one and tend to be overexploited, with “communal resources,” which belong to a group and so are often managed and protected (Berkes et al. 1989). Hardin pointed out that this debate would have been avoided had he called his paper “the tragedy of the *unmanaged commons*” (Hardin 1991). The resistance has also been due to a widespread refusal to recognize that people generally value their own short-term self-interests over the common good. Still, the resistance has also been a reaction to Hardin’s cynical view of human nature, his emphasis on competition rather than cooperation, and his nice-guys-finish-last, lifeboat ethics (Hardin 1974, 1978). Hardin’s acrimonious attacks on Marxism and socialism reinforced existing suspicions of biology, genetics, Darwinism, and sociobiology from leftist environmentalists. As Abernethy (1996) noted: “Despite Hardin’s well-reasoned analysis, [Hardin’s] book will not persuade past detractors. The crux of their difference is an assumption about human nature. In the well-established tradition of Darwinism and modern sociobiology, Hardin shows how evolution favors selfishness (selects against altruism) so his reasoning begins from: ‘As a matter of principle, we should always assume that selfishness is *part* of the motivation of every action’ (p. 64)” (p. 277). This debate should disappear as more social scientists are recognizing the evolutionary constraints on human altruism and more evolutionary thinkers are rejecting unnecessarily cynical views of human nature (i.e., motivated only by egoistic self-interests and unconstrained by social norms) (Richerson and Boyd 1992; de Waal 1996; Sober and Wilson 1998; de Waal 2001).

Research on the tragedy of the commons illustrates how addressing our ecological problems has benefited and been improved by integrating perspectives from the biological and social sciences (Ostrom 1990; Ruttan 1998; Borgerhoff Mulder and Ruttan 2000). The debates over the tragedy of the commons between evolutionary (Kay 1997) and environmental thinkers (Anderson 1998; Sandvik 1999) are sterile for those that understand that biology and culture are not alternatives, and higher forms of cooperation and organization can arise out of individual self-interests

(Ridley 1996). The tragedy of the commons is not inevitable, and the model suggests that how people treat natural resources depends upon social circumstances. Yet we still need more research on whether and how social pressure might help to avoid the tragedy of the commons in more normal ecological and social circumstances, and not just simple laboratory experiments.

MALADAPTIVE BEHAVIOR

Homo sapiens has brought its old mind into the new world (Ehrlich and Ehrlich 1990:187).

It is puzzling that people are not more concerned about environmental threats, such as toxic chemical pollutants that harm their health. Also, it is also difficult to understand why people (even trained scientists) are so poor at evaluating the relative dangers of various modern environmental risks (Dawes 1988; Kammen and Hassenzahl 1999). Contrary to what is often assumed, irrational and maladaptive behaviors also require an evolutionary explanation (Dawkins 1982). For example, we understand that the reason that moths spiral into candle flames is because their navigational apparatus is fooled by an evolutionarily novel light source. People in modern industrialized societies live in a very different environment from the world in which their ancestors evolved, and such “evolutionary mismatches” may also result in inappropriate behavioral responses. Indeed, this is one of the central guiding principles of evolutionary psychology (Irons 1998).

The idea that we humans respond inappropriately to many environmental hazards because the human mind was designed for life in the Pleistocene rather than the modern world was first suggested by Robert Ornstein and Paul Ehrlich (1989). They also suggested that people tend to ignore large-scale environmental problems, such as global climate change, because our ancestors gained no advantages by reacting to them. Ornstein and Ehrlich’s attempt to integrate perspectives from evolutionary ecology and cognitive psychology was truly insightful, and has begun to influence environmental psychology (Gardner and Stern 1996). Unfortunately, however, they made the usual assumptions of

the standard social science model, including the notion that humans are capable of culturally reconstructing human nature. Their book *New World, New Mind* would have been more appropriately entitled “New World, *Old Stone Age Mind*” (also see Tooby’s 2001 critique of Ehrlich’s (2000) recent book, *Human Natures*).

Cognitive researchers have long been puzzled as to why people are so poor at evaluating probabilistic questions and assessing various environmental risks (Dawes 1988; Kammen and Hassenzahl 1999). Their findings raise the apparent paradox that the human mind is adept at solving extraordinarily complex problems, such as speech perception, grammar induction, facial and object recognition—outperforming the most powerful computers—and yet we fail at many simpler tasks. The problem is not that the brain is riddled with random errors in design, as often assumed. Evolutionary psychologists have found that poor performance at evaluating risks can be solved by rephrasing or representing the problem in a more natural ecological context (Cosmides and Tooby 1994, 1996). This is because human cognition and behavior are designed for *ecological rationality* and we rely on simple heuristics rather than complex algorithms to solve problems faced by our ancestors (Gigerenzer et al. 1999).

An evolutionary perspective suggests that humans need simple instructions rather than complex directions. It supports the idea that regulations are needed to mandate energy efficiency in manufacturing to remove the task of having to make environmentally sound decisions that are too complex for consumers to solve. An evolutionary perspective questions the traditional approach of providing information about the environment in *probabilistic terms*, and suggests that educators should provide more emotional and aesthetically appealing anecdotes and stories, not just statistics, to influence behavior (Pooley and O’Connor 2000; Anderson 2001). It also suggests that our failure to respond to modern environmental hazards is often due to our evolved sensory and cognitive constraints, and therefore we need to find ways to alter our perception of these threats: industries could be required to discolor their invisible but harmful emissions; authorities should alter the taste

and smell of public drinking water according to the level of pollutants detected. Integrating evolutionary and cognitive perspectives should provide many possibilities for addressing environmental problems, and should be a productive area for future research.

ENVIRONMENTAL AESTHETICS

Biophilia, if it exists . . . is the innately emotional affiliation of human beings to other living organisms (Wilson 1993:31).

In addition to explaining why humans are so ecologically destructive, we also need evolutionary explanations for why people cherish nature. People spend much time and money attempting to preserve nature, surround themselves with plants and pets, visit parks and zoos, and spend their vacations traveling to view natural landscapes. Environmental psychology has been only a small and peripheral subdiscipline within the social sciences, and it has mainly focused on determining how to alter the environment to suit people’s tastes. This field is now beginning to consider the evolution of human environmental aesthetics (Kellert and Wilson 1993; Gardner and Stern 1996). This transformation is largely due to E O Wilson’s (1984) book, *Biophilia*, in which he proposes that humans have instinctive aesthetic preferences for natural environments and other species (note that his use of the term “instinctive” correctly includes genetically programmed learning biases). Just as we easily learn to fear or dislike potentially harmful species, such as snakes and spiders (biophobia), we may have evolved psychological and sensory mechanisms to be attracted to other aspects of nature (biophilia) (Wilson 1993). Moreover, Gordon Orians and his colleagues have pointed out that habitat selection, which is an adaptive aspect of animal behavior, can help to explain our instinctive environmental preferences (Orians 1986, 1998; Orians and Heerwagen 1992).

Research on the evolution of environmental aesthetics has only just begun and yet it provides several interesting findings (Ulrich 1993). First, people generally prefer photographs of natural over artificial environments, and artificial environments are pre-

ferred when they contain trees or other vegetation (Ulrich 1993). Second, people appear to prefer environmental settings that offer possibilities for finding food, water, and a safe refuge from predators and human enemies (prospect/refuge hypothesis) (Kaplan 1987, 1992; Orians and Heerwagen 1992). Third, several studies have found that people prefer savannahlike landscapes, in which our ancestors largely evolved, over other types of biomes (the savannah hypothesis) (Balling and Falk 1982; Orians 1986, 1998; Orians and Heerwagen 1992). This may explain why people so often surround themselves with manicured lawns and gardens, and prefer paintings and photographs of landscapes similar to savannah environments (Kaplan 1992; Orians and Heerwagen 1992; Ulrich 1993; Gardner and Stern 1996). Fourth, there is evidence that viewing or spending time in natural environments helps to reduce stress, and offers other health benefits (Kellert and Wilson 1993; Ulrich 1993; Gardner and Stern 1996). The possibility that there may be emotional, psychological, and other health benefits for preserving natural landscapes is the most important implication of the biophilia hypothesis. These ideas need more investigation, especially to see how the findings might help to raise concern for the environment.

One potential problem is that our instinctive environmental preferences probably do not develop "normally" in artificial environments, such as modern cities (Morris 1994). Just as "environmental enrichment" is necessary for normal sensory and nervous development in primates and other mammals, it is likely that children also require natural environmental sensory inputs for proper mental development. Thus, we need to determine how natural selection has "designed" our environmental preferences, and how artificial environments in the modern world, such as pollution and television, might be adversely impacting the development of our decision making and our environmental tastes and preferences.

The ideas and findings of evolutionary research on human behavior are necessary to explain why people are environmentally destructive, and moreover, why people sometimes become environmental advocates—

e.g., why people reduce their fertility, cherish forests, castigate greed, and use social pressure to enforce group norms to protect natural resources. The evolved physiological machinery that controls human behavior enables, as well as constrains, the possibilities for change. This means that evolutionary perspectives on human behavior can help to find practical solutions for addressing our ecological problems.

EVOLUTIONARY PERSPECTIVES AND ENVIRONMENTAL POLICY

The suggestion that our evolved "human nature" is a source of environmental exploitation and degradation is not a claim that nothing can be done, but a warning that effective conservation and remediation strategies will have to incorporate an understanding of relevant evolved psychological processes in order to modify human action (Wilson et al. 1998:517).

Environmentalists generally agree that reducing our ecological impact requires a reduction of population growth and levels of consumption, but it is unclear how we can create the changes needed to accomplish these goals. We may agree to place legal limits on family size and consumption or to tax these activities; however, we still have to determine how to obtain the public support necessary to pass and enforce such policies (at least in democratic regimes). Therefore we need to know more about the conditions in which people want to reduce fertility and consumption. Evolutionary analyses may sometimes challenge the assumptions of environmental thinkers, but they do not necessarily imply that the efforts of environmentalists are a waste of time! Presumably, if we understand human nature better, we can find more effective solutions. In the next section, I examine the role of environmental education, policy, and activism from an evolutionary perspective.

ENVIRONMENTAL EDUCATION

Overexploitation and habitat degradation are serious problems, but they require thoughtful solutions that run with the grain of human nature (Henderson and Sutherland 1997:402).

Improvements in education and public information are widely thought to be the solution to address our environmental problems. The implicit assumption is that if people only had more knowledge about the importance of environment for other species or future generations, then they will want to reduce their environmental impact. It seems almost certain that we cannot successfully promote environmental policies without public education. We cannot possibly obtain widespread support for reduced emissions of greenhouse gases if people do not understand the problem. On the other hand, we cannot expect people to sacrifice their short-term interests for the long-term good of the planet. In addition, greater awareness of resource overexploitation might trigger *increased* consumption because people might want to get their share before it is all gone. So what role does education play?

Darwinians have criticized the assumption that people will automatically sacrifice their own consumption and fertility when they learn that their actions adversely impact the common good and future generations (Ridley and Low 1993; Kay 1997). Indeed, the available evidence indicates that education is not sufficient for evoking conservation behavior (Hirst et al. 1981; Caro et al. 1994; Whitehead 1994; Bloom 1995). For example, researchers attempted to persuade young students not to litter either by teaching them about ecology and pollution or by telling them that they were neat and tidy compared to others (instigating rivalry); only the latter had a positive effect (Miller et al. 1975). “[E]ducation is effective mainly with relatively simple, low-cost behaviors, such as depositing cans in curbside recycling bins or altering home thermostat settings. . . . Nevertheless, when protecting the environment requires great effort or expense, as it often does, there is no experimental evidence that education alone will do the job” (Gardner and Stern 1996:92).

Environmentalists often assume that they can spread conservation ethics throughout society like an infectious information virus or “meme” (Sandvik 1999). Humans are not simply passive recipients of new ideas, however, and they do not lack sensory filters or defenses in their nervous system against being manip-

ulated. *Some* ideas may spread like an epidemic (Blackmore 1999), but humans are facultative strategists that adopt behaviors most likely to provide an individual advantage (Daly 1982). How else can we explain why educated people are often resistant to passing environmental laws that require individual sacrifice? It is often pointed out that education has resulted in reduced fertility in many countries (Sandvik 1999). Education is associated with reduced fertility for women (though not usually for men); this is probably because schooling provides women with greater status and reproductive autonomy, however, rather than just being a product of education per se.

Although education is insufficient to elicit the sacrifices needed, it is still necessary. Moreover, an evolutionary perspective suggests that environmental education will be most effective for triggering changes when it shows how the destruction of the environment harms *individual* interests, though it is also important to remember that an individual’s evolutionary interests include close relatives, friends, and their group or tribe—as well as their own health, survival, and economic interests (Ridley and Low 1993; Heinen 1995a,b,c, 1996). The state of environment only became a major political issue when environmentalists, such as Rachel Carson (1962), increased public awareness about the dangers of pollution for people’s health. Similarly, ecological economics has been successful in showing how environmental degradation is adversely affecting the health and economic well-being of individuals and nations (Costanza 1991). Many environmental thinkers, such as Deep Ecologists, attack appeals to human and self-interests as “shallow ecology” (Roszak et al. 1995; Sessions 1995). They want people to protect the environment, not because it benefits their interests, but because of its “intrinsic value.” However, as E O Wilson points out: “A stiffer dose of biological realism appears to be in order. . . . The only way to make a conservation ethic work is to ground it in ultimately selfish reasoning An essential component of this formula is the principle that people will conserve land and species fiercely if they foresee a material gain for themselves, their kin, and their tribe” (Wilson 1984:131-132). This is *evo-*

lutionary-informed ecology rather than shallow ecology.

Conservationists emphasize the importance of biodiversity for its potential medical benefits and ecosystem services for humanity (Daily 1997). They are attempting to find how conservation might benefit local peoples, making them stakeholders. Some environmental activists are cleverly showing the public how we can reduce runaway taxes and governmental spending by eliminating environmentally destructive subsidies and projects funded by the government. For example, the *Green Scissors* report outlines 74 U.S. governmental programs that, if cut, would protect the environment and save taxpayers \$54 billion (e.g., subsidies for timber, mining, automotive, and petroleum industries) (Newport 2001). Environmentalists who criticize such appeals to human self-interest overlook the evolutionary design and constraints on the human mind. Making successful environmental policies requires considerations of the evolved psychological constraints on human behavior, as well as our ecological constraints for growth.

Environmental education may be sufficient for addressing some environmental problems, such as toxic pollution that threatens individual interests, but it is surely insufficient for addressing many others. Environmentalists have educated the public about greenhouse gases and global climate change, but there is still much resistance to change. Education is necessary but it is not sufficient because the solution requires individual sacrifice that can be exploited by others (i.e., the collective action problem). Conflicts between individual versus group interests are at the heart of most environmental problems, and evolutionary theory offers fundamental insights here (Ridley 1996).

SOCIAL PRESSURE AND THE TRAGEDY OF THE COMMONS

[R]esource users are compelled by social pressure to conform to carefully prescribed and enforced rules of conduct (Berkes et al. 1989).

Evolutionary research on human behavior is providing many insights into human cooperation and collective action problems (Hawkes 1992; Frank 1995; Kollock 1998; Nowak

and Sigmund 1998; Fehr and Gächter 2002; Hauert et al. 2002; Price et al. 2002). Contrary to what is often assumed, an evolutionary perspective does not imply that the tragedy of the commons is inevitable. Hardin (1968) argued that we cannot rely upon voluntary restraint, and he was skeptical that government will prevent the tragedy of the commons due to the age-old problem of "*Quis custodiet ipsos custodes?*"—"Who shall watch the watchers themselves?" He suggested that social arrangements could create the coercive feedbacks necessary: "the great challenge facing us now is to invent the corrective feedbacks that are needed to keep custodians honest" (p 1246). Hardin has been attacked for suggesting that we use coercion (Commoner 1971), but the only kind of coercion that he recommended—"mutual coercion, mutually agreed upon by the majority of the people affected"—was democratic (Hardin 1968:1247, 1991).

Since Hardin's classic paper, several studies provide support for the idea that common-pool resources can be successfully managed through shame, moralizing, and other forms of social pressure (Berkes et al. 1989; Palmer 1991, 1993; Ostrom 1999; Ostrom et al. 1999). For example, a recent experiment found that people were more likely to conserve a common resource when their *reputation* was at stake (Milinski et al. 2002). These findings contradict conventional economic models, which assume that an individual's behavior is unaffected by the costs imposed by social pressure and ignore the benefits of following norms. Instead, they match the actual behavior of environmental activists who instinctively use shame and other forms of social pressure to instigate changes and achieve compliance. For example, when American consumers learned which companies produced most of the toxic wastes in the U.S., environmentalists publicly shamed these companies and disseminated the information to others. These companies responded rapidly to avoid public humiliation and save their reputation (Graham 2000). When mandatory disclosure laws have forced companies to warn consumers about potentially harmful chemical additives in their products or the ecological impact of their industry (such as the impact on dolphins by tuna fishing), they

changed their practices to avoid lost profits from such public embarrassment (Graham 2000). Public shaming has also provided a strong deterrent against free-riding nations that have tried to veto or violate environmental treaties (e.g., whaling, ivory trade, dumping toxic wastes) (Porter and Brown 1996). People are tribal and nationalistic, but this is not always an obstacle since concern about national reputation provides a strong incentive to get countries to sign and comply with environmental treaties. Information plays a key role because it enables individuals to recognize their common interests and punish free-riders that are destroying common resources.

Some evolutionary thinkers have criticized the exhortations of environmentalists and their emphasis on information, ethics, and moralizing as being "unrealistic" (Ridley and Low 1993; Kay 1997). Evolutionary biologists are understandably uncomfortable with the mystical language of many environmentalists, but they often underestimate the potential power of social pressure for policing selfish behavior (Boyd and Richerson 1992; Frank 1995; Hammerstein 1995; Fehr and Gächter 2002; Price et al. 2002). They have not considered treating the religious moralizing of environmentalists as a subject worthy of study itself (i.e., why do environmentalists often adopt religious attitudes?). Humans are not simply egoists nor short-sighted, tit-for-tat reciprocators (Frank 1995; Kollock 1998; Nowak and Sigmund 1998; Wedekind and Milinski 2000; Fehr and Gächter 2002). As Alexander (1987) suggested, human cooperation relies on indirect reciprocity, such as reputation, moralizing, and social pressure, to enforce individual restraint. Concern for reputation might explain why people purchase solar equipment, an act that usually depends mainly upon the number of acquaintances they have that own such equipment (Leonard-Barton 1981), and why public commitment resulted in a 15% reduction in gas and a 20% decrease in electrical use compared to a control group that was not asked to commit publicly (Pallak and Cook 1980). Once people understand the importance of the environment for their own health, then they become more interested in *other's* envi-

ronmental impact. For example, rates of smoking dropped dramatically in the U.S. after people learned about the harmful effects of second-hand smoke (Gardner and Stern 1996). We should not underestimate selfishness and greed, but we should also be careful not to underestimate the potential power of social pressure for curbing self-interests.

Social scientists often argue that our environmental problems are not due to a scarcity of natural resources as much as social inequalities in distribution, but they often overlook that evolutionary analyses are necessary to explain why resources are not shared more fairly. Also, in their admirable defense of the poor, they sometimes ignore the possibility that the wealthy play a positive role in resource conservation. In small traditional societies, efforts to conserve natural resources are sometimes enforced by elites and social dominants who have the luxury of worrying about the long-term consequences of overexploitation (Ruttan 1998; Ruttan and Borgerhoff Mulder 1999). In modern societies, however, social dominants may generally be those with the most to lose from environmental protection (Porter and Brown 1996; Gelbspan 1997). When powerful parties have vested interests in environmentally destructive activities, this makes social change difficult, as every environmental activist knows. Education appears to be crucial in this situation for providing information so that individuals and groups organize against being exploited by more powerful and wealthy social dominants. The importance of information for organizing environmental protection is precisely why the chemical and oil industries oppose mandatory disclosure laws (Graham 2000), and why industry spends so much money disseminating misinformation about the environment (Ehrlich and Ehrlich 1996). Industries have been retaliating by secretly hiring third-party spin-doctors and front groups, who pose as objective scientific experts to disagree with environmentalists. This tactic probably works because it exploits our instinct to rely on neutral third parties to get unbiased information. Similarly, advertisers pay attractive and popular sports and film stars to endorse their products, apparently

exploiting our instincts to emulate social elites (Pratkanis and Aronson 1991). The relationships between social status and consumption are complicated, especially when mass media gets involved, and I suspect that neither education nor appeals to narrow economic interests will suffice to achieve environmentalists' objectives. Environmental activists will probably have to continue to use shame, moralizing, and other types of social pressure to encourage collective action.

In summary, an evolutionary perspective suggests that education and social incentives will be most effective when they emphasize how pollution and other types of environmental destruction adversely affect human and individual interests. Education provides the information necessary for making individuals aware of their common interests, and it is especially effective for employing shame and other types of social pressure. Because not all people stand to gain equally from conserving natural resources, social pressure and coalitional enforcement may be the only tools that individuals can use to resist manipulation from social dominants. Humans are highly social animals that care about their reputation, and social pressure appears to provide a strong incentive to change behavior. Environmental activists use persuasion, public shame, embarrassment, and moral indignation, as well as economic pressure (trade incentives, strikes, boycotts), to influence others. Some prefer to call such behaviors "persuasion" rather than "mutual coercion," but whatever we call it, social pressure appears to offer our greatest hope for preventing a global tragedy of the commons. Thus, education and social pressure must be used together to evoke support for environmental policies. "It is here that the twin tools of coercion and education can succeed where other methods may fail" (Warren 1998). It is difficult to see any alternative. No one enjoys social pressure, especially when it is aimed at them, but this is preferable to the violence and terrorism that people also use to settle disputes over natural resources (Homer-Dixon 1999). It is human nature to want more than what is necessary to survive and reproduce—more resources, more social status, more mates—but it is also

human nature to want fairness and to shame individuals that behave selfishly!

CONCLUSIONS

This ultimate aim of designing a new type of society . . . will involve drastic changes in our system of values . . . [that] will undoubtedly require a considerable lowering of our living standard. . . . I am often told that this view of the future is utopian. I submit that this is reversing the positions; it is those who believe that we can with impunity continue on our present course who live in a dream world (Tinbergen 1976:521).

We humans must reduce our population growth and consumption if we are going to prevent the destruction of the planet's ecosystem that supports us. To determine how we can more effectively reduce our environmental impact, we need to understand the conditions in which people *want* to reduce their fertility and consumption (Heinen 1994). Our species has a long history of creating ecological problems, and sustainability is not going to come easily, but this does not mean that the efforts of environmentalists are in vain. The wisdom of liberal democratic institutions has been their recognition of the limitations of human altruism by balancing the freedom of individual pursuits with coercive laws and taxes that maintain public goods. Communism failed precisely because it ignored important constraints on human altruism: e.g., Mao's agricultural reforms failed because they ignored the fact that humans place greater emphasis on their family than the common good. This is a valuable lesson for why an accurate model of human nature is crucial for environmental educators and policy makers. Like Marxism, neoclassical economics fails to recognize the evolutionary and ecological constraints on the human possibilities. Ecology has exposed the false assumptions of economists about *nature*, and now evolutionary research is challenging their assumptions about *human nature* (Gigerenzer and Selten 2001). It is human nature to place more emphasis on individual short-term interests than on the long-term common good, but it is also human nature to punish selfish individuals that behave unfairly and exploit collective interests (Tooby and

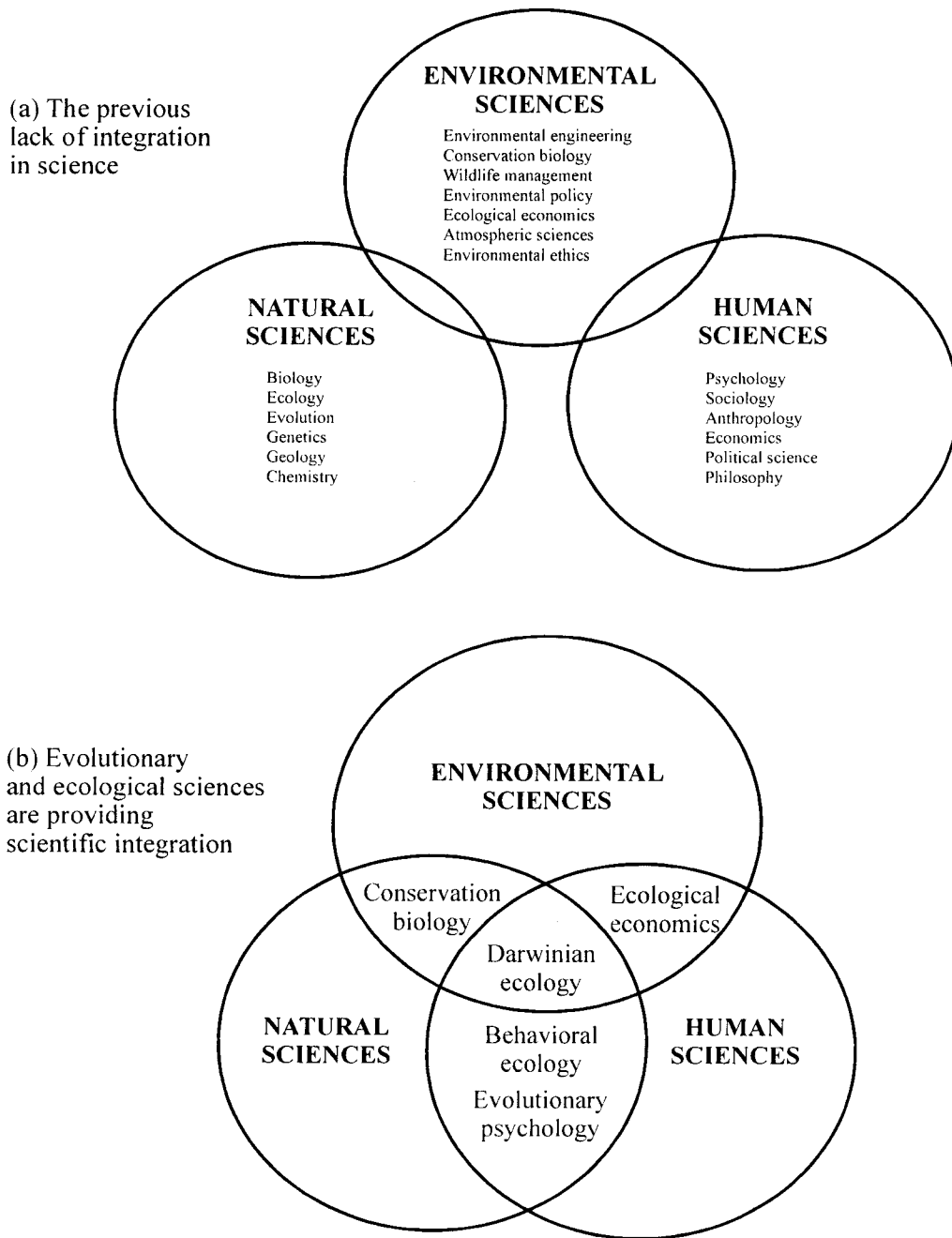


FIGURE 1. ENVIRONMENTAL SCIENCES CUT ACROSS TRADITIONAL DISCIPLINARY BOUNDARIES, ESPECIALLY BETWEEN THE NATURAL AND SOCIAL SCIENCES, BUT MORE INTEGRATION IS STILL NEEDED

(a) Environmental thinkers generally view the natural and human sciences as completely disconnected or bridged only by environmental and biomedical sciences (adapted from Meffe and Carroll 1994). (b) Newly emerging interdisciplinary fields, such as conservation biology, ecological economics, human behavioral ecology, and evolutionary psychology, are helping to integrate the biological and human sciences. A field of applied human behavioral ecology or "Darwinian ecology" is needed to complete this synthesis, however.

Cosmides 1992; Price et al. 2002). We are not “designed” to perceive or respond to long-term ecological problems, such as global warming, or to “think globally”; but we are not designed to live cooperatively in large nation-states, as we do, either. Thus, we must not ignore the evolved constraints on human behavior or underestimate our ability to change and solve collective action problems.

Attempts to understand our environmental problems from an evolutionary perspective are only in their infancy, and several major problems need to be solved. First, stabilizing population growth will require a better understanding of the conditions that motivate individuals to reduce their fertility (Borgerhoff Mulder 1998; Penn 1999). The challenge here is to find incentives that lower fertility without making counterproductive increases in consumption. Second, overconsumption is the major source of our ecological impact, but we have only begun to try to understand why people overconsume or how to put a brake on runaway consumption (Frank 2000). The problem is that social science research is still generally aimed at increasing rather than decreasing consumption. Third, most of our environmental problems are collective action problems, so we need a better understanding of how they can be solved through social pressure or otherwise (Ostrom 1990, 1999; Ostrom et al. 1999). This is an especially difficult challenge in the large anonymous societies of the modern world, though “globalization” might present new opportunities (as well as problems) for eliciting cooperation (French 1994; Wright 2000). Finally, evolutionary theory will have limited practical applications until it can help to explain human morals, political processes, and institutional arrangements (Wong 1994). Environmental issues are deeply moral and political, yet these aspects need not remain outside of the realm of science and biology. We can learn much about ourselves from research on chimpanzees and other species, which indicates that the roots of morality and politics are older than humanity (de Waal 1982, 1996; Alexander 1987; Wright 1994; Ridley 1996).

Integrating the various specialized and fragmented disciplines of science to address

our ecological problems requires more direct dialogue about the resistance to applying evolutionary biology to humans (Wilson 1998a). Many environmental scholars dislike evolutionary biology and view it as no better at improving our understanding of ourselves and our place in nature than astrology (Gross and Levitt 1994; Gross et al. 1996). Postmodernist rhetoric inspires much of the environmental literature, including Deep Ecology (Sessions 1995), ecopsychology (Roszak et al. 1995), ecofeminism (Merchant 1980), and ecotheology (Oelschlaeger 1994). Religious environmentalists claim to reject the human/nature dichotomy, yet they still embrace most of its forms, including the human/animal, nature/nurture, biology/culture, and mind/matter dichotomies. The human/nature dichotomy is also assumed in social ecology (Bookchin 1990), environmental psychology (Roszak et al. 1995; Winter 1996), ecological economics, and even in less anthropocentric disciplines, such as ecology and conservation biology. Surprisingly, the human/nature dichotomy has been assumed by many evolutionary thinkers since T H Huxley who mistakenly viewed humans as selfish by nature but moral and altruistic by nurture (de Waal 1996; de Waal 2001).

Perhaps the most common misunderstanding among environmentalists is that Darwinian analyses only lend support for social inequality and racism. This misconception has been propagated by Marxist scientists, especially Stephan J Gould and Richard Lewontin, who have ardently attacked sociobiology, apparently because it does not support their political views (Dennett 1995; Segerstråle 2000). What many fail to understand is that evolutionary perspectives on humanity can help to challenge the erroneous assumptions of the political right as well as the left (Singer 2000). It is true that evolutionary research has been and will continue to be distorted by those with radical political agendas (like any science). This does not imply that we stop research; it simply means that we should be on guard against efforts to distort or confuse science for political purposes—and this includes efforts from leftists and Greens, as well as right-wing capitalists and social conservatives!

Many prefer to keep Darwinism out of environmental classrooms, but this will not prevent its misuse. On the contrary, if we do not use all of the insights that science has to offer about human behavior for achieving the common good, then others will surely exploit this knowledge for their economic interests (Pratkanis and Aronson 1991). The findings of the social sciences have long been used by advertisers to drive the escalating levels of consumerism (Durning 1992; de Graaf et al. 2001). The “producers of conspicuous consumption goods do not merely *inform* us of the merits of their products. They also attempt to *persuade* us to believe we need them, using all the tools in the modern social psychologist’s arsenal” (Frank 2000:177). It is likely that advertisers are paying much attention to the latest findings from evolutionary research on human behavior; therefore, environmental thinkers can no longer afford to continue to ignore them.

Evolutionary biology provides the central organizing principles for understanding the behavior of humans, as well as other animals; therefore it is time to integrate it with the environmental sciences. An interdisciplinary field of applied human behavioral ecology, or “Darwinian ecology,” is needed to apply evolutionary insights on human behavior to address environmental problems (Figure 1). Darwinian ecology could help to integrate the biological and social sciences, a separation that interferes with our ability to understand our ecological problems. Such a synthe-

sis could bring valuable political as well as scientific advances. Environmentalists’ efforts to create social change have been limited, partially due to the philosophical, religious, and political differences that divide them (e.g., human-centered versus the ecocentric approaches) (Norton 1991; Lewis 1996). These differences are largely based on differences about human nature and our place in nature. Evolutionary perspectives provide a direct attack on the false human/nature dichotomy by showing the continuity between ourselves and other animals (de Waal 2001); yet they also show why stressing individual and human interests to evoke change is a practical necessity. Thus, evolutionary perspectives can help to mend the philosophical rifts among environmental thinkers and generate more solidarity, which is necessary for them to achieve their political and scientific objectives.

ACKNOWLEDGMENTS

I thank my friends and colleagues who have offered me their thoughtful insights on this subject, including Kevin Baldwin, Dave Bowling, Tom Kursar, Ron Edwards, Joe Fragosa, Kristen Hawkes, Bobbi Low, Monique Borgerhoff Mulder, Iver Myrsetrud, Carla Restrepo, Alan Rogers, Jon Seger, Jan Sendzimir, Mark Stowe, and Richard Wagner. I thank Edward Wilson for his suggesting the title of this paper. I also thank Margo Wilson, Martin Daly, and the other participants of the symposium that I organized on this topic at the 1999 Annual Meeting of the Human Behavior and Evolution Society. I especially thank my wife and colleague, Sarah Zala, for her input and support.

REFERENCES

- Abernethy V. 1993. *Population Politics: The Choices That Shape Our Future*. New York: Insight Books.
- Abernethy V. 1996. Review of *The Immigration Dilemma: Avoiding the Tragedy of the Commons*, by G Hardin. *Population and Environment* 17:275–277.
- Alcock J. 2001. *The Triumph of Sociobiology*. Oxford and New York: Oxford University Press.
- Alexander R D. 1987. *The Biology of Moral Systems*. New York: Aldine de Gruyter.
- Alroy J. 2001. A multispecies overkill simulation of the end-Pleistocene megafaunal mass extinction. *Science* 292:1893–1896.
- Alvard M. 1995. Intraspecific prey choice by Amazonian hunters. *Current Anthropology* 36:789–818.
- Alvard M S. 1993. Testing the “ecologically noble savage” hypothesis: interspecific prey choice by Piro hunters of Amazonian Peru. *Human Ecology* 21: 355–387.
- Alvard M S. 1998. Evolutionary ecology and resource conservation. *Evolutionary Anthropology* 7:62–74.
- Anderson A. 1989. Mechanics of overkill in the extinction of New Zealand moas. *Journal of Archaeological Science* 16:137–151.
- Anderson E N. 1998. Reevaluating the tragedy of the commons. *Conservation Biology* 12:1168.
- Anderson J L. 2001. Stone-age minds at work on 21st century science: how cognitive psychology can inform conservation biology. *Conservation Biology In Practice* 2(3):18–25.
- Andorka R. 1978. *Determinants of Fertility in Advanced Societies*. London: Methuen.
- Balling J D, Falk J H. 1982. Development of visual pref-

- erence for natural environments. *Environment and Behavior* 14:5–28.
- Baltz M E. 1999. Overconsumption of resources in industrial countries: the other missing agenda. *Conservation Biology* 13:213–215.
- Barrett C, Dunbar R, Lycett S. 2002. *Human Evolutionary Psychology*. Princeton (NJ): Princeton University Press.
- Bates D G, Lees S H. 1979. The myth of population regulation. Pages 273–289 in *Evolutionary Biology and Human Social Behavior: An Anthropological Perspective*, edited by N A Chagnon and W Irons. North Scituate (MA): Duxbury Press.
- Becker G S. 1991. *A Treatise on the Family*. Enlarged Edition. Cambridge (MA): Harvard University Press.
- Berkes F, Feeny D, McCay B J, Acheson J M. 1989. The benefits of the commons. *Nature* 340:91–93.
- Berry W. 2000. *Life is a Miracle: An Essay Against Modern Superstition*. Washington (DC): Counterpoint Press.
- Betzig L. 1997. *Human Nature: A Critical Reader*. Oxford and New York: Oxford University Press.
- Blackmore S. 1999. *The Meme Machine*. Oxford and New York: Oxford University Press.
- Bliege Bird R, Smith E A, Bird D W. 2001. The hunting handicap: costly signaling in human foraging strategies. *Behavioral Ecology and Sociobiology* 50:9–19.
- Bloom D E. 1995. International public opinion on the environment. *Science* 269:354–358.
- Bock J. 1999. Evolutionary approaches to population: implications for research and policy. *Population and Environment* 21:193–222.
- Bookchin M. 1990. *The Philosophy of Social Ecology*. Montreal (Canada): Black Rose Books.
- Boone J L. 1998. The evolutionary of magnanimity: when is it better to give than to receive? *Human Nature* 9:1–21.
- Borgerhoff Mulder M. 1998. The demographic transition: are we any closer to an evolutionary explanation? *Trends in Ecology & Evolution* 13:266–270.
- Borgerhoff Mulder M. 2000. Optimizing offspring: the quantity-quality tradeoff in agropastoral Kipsigis. *Evolution and Human Behavior* 21:391–410.
- Borgerhoff Mulder M, Rutten L M. 2000. Grassland conservation and the pastoralist commons. Pages 34–50 in *Behaviour and Conservation*, edited by L M Gosling and W J Sutherland. Cambridge and New York: Cambridge University Press.
- Boyd R, Richerson P J. 1992. Punishment allows the evolution of cooperation (or anything else) in sizable groups. *Ethology and Sociobiology* 13:171–195.
- Buss D M. 1989. Sex differences in human mate preferences: evolutionary hypotheses tested in 37 cultures. *Behavioral and Brain Sciences* 12:1–49.
- Caro T M, Pelkey N, Grigione M. 1994. Effects of conservation biology education on attitudes toward nature. *Conservation Biology* 8:846–852.
- Carson R. 1962. *Silent Spring*. Boston (MA): Houghton Mifflin.
- Clarke A L, Low B S. 2001. Testing evolutionary hypotheses with demographic data. *Population and Development Review* 27:633–660.
- Cleland J. 1995. Obstacles to fertility decline in developing countries. Pages 207–229 in *Human Reproductive Decisions: Biological and Social Perspectives*, edited by R I M Dunbar. New York: St. Martin's Press.
- Cohen J E. 1995. *How Many People Can the Earth Support?* New York: W. W. Norton.
- Cohen S A, Richards C L. 1994. The Cairo consensus: population, development, and women. *Family Planning Perspectives* 26:272–277.
- Colborn T, Dumanoski D, Myers J P. 1996. *Our Stolen Future: Are We Threatening Our Fertility, Intelligence, and Survival?—A Scientific Detective Story*. New York: Dutton.
- Commoner B. 1971. *The Closing Circle: Nature, Man, and Technology*. New York: Knopf.
- Cosmides L, Tooby J. 1994. Beyond intuition and instinct blindness: toward an evolutionary rigorous cognitive science. *Cognition* 50:41–77.
- Cosmides L, Tooby J. 1996. Are humans good intuitive statisticians after all?: rethinking some conclusions from the literature on judgment under uncertainty. *Cognition* 58:1–73.
- Costanza R, editor. 1991. *Ecological Economics: The Science and Management of Sustainability*. New York: Columbia University Press.
- Culbert T, editor. 1973. *The Classic Maya Collapse*. Albuquerque (NM): University of New Mexico Press.
- Daily G C. 1997. *Nature's Services: Societal Dependence on Natural Ecosystems*. Washington (DC): Island Press.
- Daly M. 1982. Some caveats about cultural transmission models. *Human Ecology* 10:401–408.
- Darwin C R. 1871. *The Descent of Man, and Selection in Relation to Sex*. London: J. Murray.
- Dawes R M. 1980. Social dilemmas. *Annual Review of Psychology* 31:169–193.
- Dawes R M. 1988. *Rational Choice in an Uncertain World*. Fort Worth (TX): Harcourt Brace Jovanovich.
- Dawkins R. 1982. *The Extended Phenotype: The Gene as the Unit of Selection*. Oxford: W. H. Freeman.
- Dawkins R. 1986. Wealth, polygyny, and reproductive success. *Behavioral and Brain Sciences* 9:190–191.
- Deevey E S, Rice D S, Rice P M, Vaughan H H, Brenner M, Flannery M S. 1979. Mayan urbanism: impact on a tropical karst environment. *Science* 206:298–306.
- de Graaf J, Wann D, Naylor T H. 2001. *Affluenza: The All-Consuming Epidemic*. San Francisco (CA): Berrett-Koehler.

- Dennett D C. 1995. *Darwin's Dangerous Idea: Evolution and the Meanings of Life*. New York: Simon & Schuster.
- Devall B, Sessions G. 1985. *Deep Ecology: Living as if Nature Mattered*. Salt Lake City (UT): G. M. Smith.
- de Waal F. 1982. *Chimpanzee Politics: Power & Sex Among Apes*. New York: Harper & Row.
- de Waal F. 1996. *Good Natured: The Origins of Right and Wrong in Humans and Other Animals*. Cambridge (MA): Harvard University Press.
- de Waal F. 2001. *The Ape and the Sushi Master: Cultural Reflections by a Primateologist*. New York: Basic Books.
- Diamond J. 1988. The golden age that never was. *Discover* 9:71–79.
- Diamond J. 1992. *The Third Chimpanzee: The Evolution and Future of the Human Animal*. New York: HarperPerennial.
- Diamond J. 1995. Easter's end. *Discover* 16:62–69.
- Diamond J. 2000. Blitzkrieg against the moas. *Science* 287:2170–2171.
- Durning A T. 1992. *How Much Is Enough?: The Consumer Society and the Future of the Earth*. New York: W. W. Norton.
- Durning A T. 1995. Are we happy yet? Pages 68–76 in *Ecopsychology: Restoring the Earth, Healing the Mind*, edited by T Roszak, M E Gomes, and A D Kanner. San Francisco (CA): Sierra Club Books.
- Edgerton R B. 1992. *Sick Societies: Challenging the Myth of Primitive Harmony*. New York: Free Press.
- Ehrlich P R. 2000. *Human Natures: Genes, Cultures, and the Human Prospect*. Washington (DC): Island Press.
- Ehrlich P R, Ehrlich A H. 1990. *The Population Explosion*. New York: Simon & Schuster.
- Ehrlich P R, Ehrlich A H. 1996. *Betrayal of Science and Reason: How Anti-Environmental Rhetoric Threatens Our Future*. Washington (DC): Island Press.
- Fehr E, Gächter S. 2002. Altruistic punishment in humans. *Nature* 415:137–140.
- Feldman M W, Laland K N. 1996. Gene-culture co-evolutionary theory. *Trends in Ecology & Evolution* 11:453–457.
- Frank R H. 1985. *Choosing the Right Pond: Human Behavior and the Quest for Status*. Oxford and New York: Oxford University Press.
- Frank R H. 2000. *Luxury Fever: Money and Happiness in an Era of Excess*. Princeton (NJ): Princeton University Press.
- Frank S A. 1995. Mutual policing and repression of competition in the evolution of cooperative groups. *Nature* 377:520–522.
- French H F. 1994. Making environmental treaties work. *Scientific American* 271(6):94–97.
- Gardner G T, Stern P C. 1996. *Environmental Problems and Human Behavior*. Boston (MA): Allyn and Bacon.
- Gelbspan R. 1997. *The Heat is On: The High Stakes Battle Over Earth's Threatened Climate*. Reading (MA): Addison-Wesley.
- Gigerenzer G, Selten R, editors. 2001. *Bounded Rationality: The Adaptive Toolbox*. Cambridge (MA): MIT Press.
- Gigerenzer G, Todd P M, and the ABC Research Group. 1999. *Simple Heuristics That Make Us Smart*. Oxford and New York: Oxford University Press.
- Gore A. 1992. *Earth in the Balance: Ecology and the Human Spirit*. Boston: Houghton Mifflin.
- Grafen A. 1990. Biological signals as handicaps. *Journal of Theoretical Biology* 144:517–546.
- Graham M. 2000. Regulation by shamming. *Atlantic Monthly* 285(4):36–40.
- Graham-Smith F, editor. 1994. *Population—The Complex Reality: A Report of the Population Summit of the World's Scientific Academies*. Golden (CO): North American Press.
- Gross P R, Levitt N. 1994. *Higher Superstition: The Academic Left and Its Quarrels with Science*. Baltimore (MD): Johns Hopkins University Press.
- Gross P R, Levitt N, Lewis M W. 1996. *The Flight from Science and Reason*. New York: New York Academy of Sciences.
- Hames R. 1987. Game conservation or efficient hunting? Pages 92–107 in *The Question of the Commons: The Culture and Ecology of Communal Resources*, edited by B J McCay and J M Acheson. Tucson (AZ): University of Arizona Press.
- Hammerstein P. 1995. A twofold tragedy unfolds. *Nature* 377:478.
- Hardin G. 1968. The tragedy of the commons. *Science* 162:1243–1248.
- Hardin G. 1974. Living on a lifeboat. *BioScience* 24(10):561–568.
- Hardin G. 1978. Nice guys finish last. Pages 183–194 in *Sociobiology and Human Nature: An Interdisciplinary Critique and Defense*, edited by M S Gregory, A Silvers, and D Sutch. San Francisco (CA): Jossey-Bass Publishers.
- Hardin G. 1991. The tragedy of the *unmanaged* commons: population and the disguises of providence. Pages 162–185 in *Commons Without Tragedy*, edited by R V Andelson. London: Shephard-Walwyn.
- Hardin G. 1999. *The Ostrich Factor: Our Population Myopia*. Oxford and New York: Oxford University Press.
- Hardin G, Baden J. 1977. *Managing the Commons*. San Francisco (CA): W. H. Freeman.
- Hauert C, De Monte S, Hofbauer J, Sigmund K. 2002. Volunteering as red queen mechanism for cooperation in public goods games. *Science* 296:1129–1132.
- Hawkes K. 1992. Sharing and collective action. Pages 269–300 in *Evolutionary Ecology and Human Behavior*

- ior*, edited by E A Smith and B Winterhalder. New York: Aldine de Gruyter.
- Hawkes K, Bliege Bird R. 2002. Showing off, handicap signaling, and the evolution of men's work. *Evolutionary Anthropology* 11:58–67.
- Hawks R, Charnov E L. 1988. On human fertility: individual or group benefit. *Current Anthropology* 29:469–471.
- Heinen J T. 1994. Emerging, diverging and converging paradigms on sustainable development. *International Journal of Sustainable Development and World Ecology* 1:22–33.
- Heinen J T. 1995a. Applications of human behavioural ecology to sustainable wildlife conservation and use programmes in developing nations. *Oryx* 29:178–186.
- Heinen J T. 1995b. A review of, and research suggestions for, solid-waste management issues: the predicted role of incentives in promoting conservation behavior. *Environmental Conservation* 22:157–166.
- Heinen J T. 1995c. Thoughts and theory on incentive-based endangered species conservation in the United States. *Wildlife Society Bulletin* 23:338–345.
- Heinen J T. 1996. Human behavior, incentives, and protected area management. *Conservation Biology* 10:681–684.
- Helvarg D. 1994. *The War Against the Greens: The "Wise-Use" Movement, the New Right, and Anti-Environmental Violence*. San Francisco (CA): Sierra Club Books.
- Henderson N, Sutherland W J. 1996. Two truths about discounting and their environmental consequences. *Trends in Ecology & Evolution* 11:527–528.
- Henderson N, Sutherland W J. 1997. Discounting and conservation: another final word. *Trends in Ecology & Evolution* 12:402.
- Hirsch F. 1976. *Social Limits to Growth*. Cambridge (MA): Harvard University Press.
- Hirst E, Berry L, Soderstrom J. 1981. Review of utility home energy audit programs. *Energy* 6:621–630.
- Holdaway R N, Jacomb C. 2000. Rapid extinction of the moas (Aves: Dinornithiformes): model, test, and implications. *Science* 287:2250–2254.
- Homer-Dixon T F. 1999. *Environment, Scarcity, and Violence*. Princeton (NJ): Princeton University Press.
- Irons W. 1998. Adaptively relevant environments versus the environment of evolutionary adaptedness. *Evolutionary Anthropology* 6:194–204.
- Jensen T K, Carlsen E, Jørgensen N, Berthelsen J G, Keiding N, Christensen K, Petersen J H, Knudsen L B, Skakkebaek N E. 2002. Poor semen quality may contribute to recent decline in fertility rates. *Human Reproduction* 17:1437–1440.
- Kacelnik A. 1997. Normative and descriptive models of decision making: time discounting and risk sensitivity. Pages 51–70 in *Characterizing Human Psychological Adaptations*, edited by G R Bock and G Cardew. Chichester (UK): Wiley.
- Kagel J H, Green L, Caraco T. 1986. When foragers discount the future: constraint or adaptation? *Animal Behaviour* 34:271–283.
- Kammen D M, Hassenzahl D M. 1999. *Should We Risk It?: Exploring Environmental, Health, and Technological Problem Solving*. Princeton (NJ): Princeton University Press.
- Kaplan H S, Lancaster J B. 2000. The evolutionary economics and psychology of the demographic transition to low fertility. Pages 283–322 in *Adaptation and Human Behavior: An Anthropological Perspective*, edited by L Cronk, N Chagnon, and W Irons. New York: Aldine de Gruyter.
- Kaplan S. 1987. Aesthetics, affect, and cognition: environmental preference from an evolutionary perspective. *Environment and Behavior* 19:3–32.
- Kaplan S. 1992. Environmental preferences in a knowledge-seeking, knowledge-using organism. Pages 581–598 in *The Adapted Mind: Evolutionary and the Generation of Culture*, edited by J H Barkow, L Cosmides, and J Tooby. Oxford and New York: Oxford University Press.
- Kay C E. 1994. Aboriginal overkill: the role of the Native Americans in structuring western ecosystems. *Human Nature* 5:359–398.
- Kay C E. 1997. The ultimate tragedy of commons. *Conservation Biology* 11:1447–1448.
- Kellert S R, Wilson E O, editors. 1993. *The Biophilia Hypothesis*. Washington (DC): Island Press.
- Kirk D. 1996. Demographic transition theory. *Population Studies* 50:361–387.
- Kollock P. 1998. Social dilemmas: the anatomy of cooperation. *Annual Review of Sociology* 24:183–214.
- Konner M. 1990. *Why the Reckless Survive: And Other Secrets of Human Nature*. New York: Viking.
- Krech S, III. 1999. *The Ecological Indian: Myth and History*. New York: W. W. Norton.
- Leakey R, Lewin R. 1995. *The Sixth Extinction: Patterns of Life and the Future of Humankind*. New York: Doubleday.
- Leonard-Barton D. 1981. The diffusion of active-residential solar equipment in California. Pages 145–183 in *Marketing Solar Energy Innovations*, edited by A Shama. New York: Praeger.
- Lewis M W. 1992. *Green Delusions: An Environmentalist Critic of Radical Environmentalism*. Durham (NC): Duke University Press.
- Lewis M W. 1996. Radical environmental philosophy and the assault on reason. Pages 209–230 in *The Flight from Science and Reason*, edited by P R Gross, N Levitt, and M W Lewis. New York: New York Academy of Sciences.
- Low B S. 1993. Ecological demography: a synthetic focus in evolutionary anthropology. *Evolutionary Anthropology* 1:177–187.

- Low B S. 1996a. Behavioral ecology of conservation in traditional societies. *Human Nature* 7:353–379.
- Low B S. 1996b. Men, women, and sustainability. *Population and Environment* 18:111–141.
- Low B S, Heinen J T. 1993. Population, resources, and environment: implications of human behavioral ecology for conservation. *Population and Environment* 15:7–41.
- Low B S, Ridley M. 1993. Why we're not environmental altruists—and what we can do about it. *Human Ecology Review* 1(1):107–136.
- Lumsden C J, Wilson E O. 1981. *Genes, Mind, and Culture: The Coevolutionary Process*. Cambridge (MA): Harvard University Press.
- Lutz W, Sanderson W, Scherbov S. 2001. The end of world population growth. *Nature* 412:543–545.
- Mace R. 1998. The coevolution of human fertility and wealth inheritance strategies. *Philosophical Transactions of the Royal Society of London B* 353:389–397.
- Mace R. 1999. Dos and don'ts, whys and wherefores. Review of *Ever Since Adam and Eve: The Evolution of Human Sexuality*, by Malcolm Potts and Roger Short. *Nature* 400:131–132.
- Mace R. 2000. Evolutionary ecology of human life history. *Animal Behaviour* 59:1–10.
- Martin C. 1978. *Keepers of the Game*. Berkeley (CA): University of California Press.
- Martin P S, Klein R G, editors. 1984. *Quaternary Extinctions: A Prehistoric Revolution*. Tucson (AZ): University of Arizona Press.
- Mason K O. 1997. Explaining fertility transitions. *Demography* 33:443–454.
- McCay B J, Acheson J M, editors. 1987. *The Question of the Commons: The Culture and Ecology of Communal Resources*. Tucson (AZ): University of Arizona Press.
- McMichael A J. 1993. *Planetary Overload: Global Environmental Change and the Health of the Human Species*. Cambridge and New York: Cambridge University Press.
- Meadows D H, Meadows D L, Randers J. 1992. *Beyond the Limits: Global Collapse or a Sustainable Future*. London: Earthscan.
- Meffe G K, Carroll C R. 1994. *Principles of Conservation Biology*. Sunderland (MA): Sinauer Associates.
- Merchant C. 1980. *The Death of Nature: Women, Ecology and the Scientific Revolution*. San Francisco (CA): Harper & Row.
- Mies M, Shiva V. 1993. *Ecofeminism*. London: Zed Books.
- Milinski M, Semmann D, Krambeck H J. 2002. Reputation helps solve the 'tragedy of the commons'. *Nature* 415:424–426.
- Miller G F. 1999. Waste is good. *Prospect* February: 18–23.
- Miller G F. 2000. *The Mating Mind: How Sexual Choice Shaped the Evolution of Human Nature*. New York: Doubleday.
- Miller G H, Magee J W, Johnson B J, Fogel M L, Spooner N A, McCulloch M T, Ayliffe L K. 1999. Pleistocene extinction of *Genyornis newtoni*: human impact on Australian megafauna. *Science* 283:205–208.
- Miller R L, Brickman P, Bolen D. 1975. Attribution versus persuasion as a means for modifying behavior. *Journal of Personality and Social Psychology* 31:430–441.
- Morris D. 1994. *The Human Animal: A Personal View of the Human Species*. New York: Crown Publishers.
- Neiman F D. 1997. Conspicuous consumption as wasteful advertising: a Darwinian perspective on spatial patterns in classic Maya terminal monument dates. Pages 267–290 in *Rediscovering Darwin: Evolutionary Theory and Archeological Explanation*, edited by C M Barton and G A Clarke. Arlington (VA): American Anthropological Association.
- Nesse R M, Williams G C. 1994. *Why We Get Sick: The New Science of Darwinian Medicine*. New York: Times Books.
- Newport S. 2001. *Green Scissors 2001: Cutting Wasteful and Environmentally Harmful Spending*. Washington (DC): Friends of the Earth.
- Norton B G. 1991. *Toward Unity Among Environmentalists*. Oxford and New York: Oxford University Press.
- Nowak M A, Sigmund K. 1998. Evolution of indirect reciprocity by image scoring. *Nature* 393:573–577.
- Oelschlaeger M. 1994. *Caring for Creation: An Ecumenical Approach to the Environmental Crisis*. New Haven (CT): Yale University Press.
- Orians G H. 1986. An ecological and evolutionary approach to landscape aesthetics. Pages 3–25 in *Landscape Meanings and Values*, edited by E C Penning-Rowsell and D Lowenthal. London: Allen and Unwin.
- Orians G H. 1998. Human behavioral ecology: 140 years without Darwin is too long. *Bulletin of the Ecological Society of America* 79:15–28.
- Orians G H, Heerwagen J H. 1992. Evolved responses to landscapes. Pages 555–580 in *The Adapted Mind: Evolutionary Psychology and the Generation of Culture*, edited by J H Barkow, L Cosmides, and J Tooby. Oxford and New York: Oxford University Press.
- Ornstein R, Ehrlich P. 1989. *New World, New Mind: Moving Toward Conscious Evolution*. New York: Doubleday.
- Ostrom E. 1990. *Governing the Commons: The Evolution of Institutions for Collective Action*. Cambridge and New York: Cambridge University Press.
- Ostrom E. 1999. Coping with tragedies of the commons. *Annual Review of Political Science* 2:493–535.
- Ostrom E, Burger J, Field C B, Norgaard R B, Polican-

- sky D. 1999. Revisiting the commons: local lessons, global challenges. *Science* 284:278–282.
- Pallak M S, Cook D A. 1980. Commitment and energy conservation. Pages 235–253 in *Applied Social Psychology Annual*, edited by L Bickman. Beverly Hills (CA): Sage Publications.
- Palmer C T. 1991. Kin-selection, reciprocal altruism, and information sharing among Maine lobstermen. *Ethology and Sociobiology* 12:221–235.
- Palmer C T. 1993. Folk management, “soft evolutionism,” and fishers’ motives: implications for the regulation of the lobster fisheries of Maine and Newfoundland. *Human Organization* 52:414–420.
- Penn D. 1999. Explaining the human demographic transition. *Trends in Ecology & Evolution* 14:32.
- Ponting C. 1992. *A Green History of the World: The Environment and the Collapse of Great Civilizations*. New York: St. Martin’s Press.
- Pooley J A, O’Connor M. 2000. Environmental education and attitudes: emotions and beliefs are what is needed. *Environment and Behavior* 32:711–723.
- Porter G, Brown J W. 1996. *Global Environmental Politics*. Second Edition. Boulder (CO): Westview Press.
- Postel S L, Daily G G, Ehrlich P R. 1996. Human appropriation of renewable fresh water. *Science* 271:785–788.
- Pratkanis A R, Aronson E. 1992. *Age of Propaganda: The Everyday Use and Abuse of Persuasion*. New York: W. H. Freeman.
- Price M E, Cosmides L, Tooby J. 2002. Punitive sentiment as an anti-free rider psychological device. *Evolution and Human Behavior* 23:203–231.
- Raven P H. 2002. Science, sustainability, and the human prospect. *Science* 297:954–958.
- Redford K. 1991. The ecologically noble savage. *Cultural Survival Quarterly* 15:46–48.
- Redman C L. 1999. *Human Impact on Ancient Environments*. Tucson (AZ): University of Arizona Press.
- Richerson P J, Boyd R. 1992. Cultural inheritance and evolutionary ecology. Pages 61–92 in *Evolutionary Ecology and Human Behavior*, edited by E A Smithy and B Winterhalder. New York: Aldine de Gruyter.
- Ridley M. 1996. *The Origins of Virtue: Human Instincts and the Evolution of Cooperation*. New York: Viking.
- Ridley M, Low B S. 1993. Can selfishness save the environment? *Human Ecology Review* 1(1):1–13.
- Roberts R G, Flannery T F, Ayliffe L K, Yoshida H, Olley J M, Prideaux G J, Laslett G M, Baynes A, Smith M A, Jones R, Smith B L. 2001. New ages for the last Australian megafauna: continent-wide extinction about 46,000 years ago. *Science* 292:1888–1892.
- Rogers A R. 1994. Evolution of time preference by natural selection. *American Economic Review* 84:460–481.
- Rogers A R. 1995. For love or money: the evolution of reproductive and material motivations. Pages 76–95 in *Human Reproductive Decisions*, edited by R I M Dunbar. New York: St. Martin’s Press.
- Rogers A R. 1997. Evolution and human choice over time. Pages 231–252 in *Characterizing Human Psychological Adaptations*, edited by G R Bock and G Cardew. Chichester: Wiley.
- Rose M R. 1997. Toward an evolutionary demography. Pages 96–107 in *Between Zeus and the Salmon: The Biodemography of Longevity*, edited by K W Wachter and C E Finch. Washington (DC): National Academy Press.
- Ross E B. 1998. *The Malthus Factor: Population, Poverty and Politics in Capitalist Development*. London: Zed Books.
- Rozsak T, Gomes M E, Kanner A D. 1995. *Ecopsychology: Restoring the Earth, Healing the Mind*. San Francisco (CA): Sierra Club Books.
- Ruttan L M. 1998. Closing the commons: cooperation for gain or restraint? *Human Ecology* 26:43–66.
- Ruttan L M, Borgerhoff Mulder M. 1999. Are east African pastoralists truly conservationists? *Current Anthropology* 40:621–652.
- Sandvik H. 1999. On human population growth, natural selection, and the tragedy of the commons. *Conservation Biology* 13:447–449.
- Segerstråle U. 2000. *Defenders of the Truth: The Battle for Science in the Sociobiology Debate and Beyond*. Oxford and New York: Oxford University Press.
- Sessions G. 1995. *Deep Ecology for the Twenty-First Century*. Boston (MA): Shambhala.
- Singer P. 2000. *A Darwinian Left: Politics, Evolution, and Cooperation*. New Haven (CT): Yale University Press.
- Smith E A, Bliege Bird R L. 2000. Turtle hunting and tombstone opening: public generosity as costly signaling. *Evolution and Human Behavior* 21:245–261.
- Smith E A, Winterhalder B, editors. 1992. *Foundations of Human Behavior*, edited by S B Hrdy. New York: Aldine de Gruyter.
- Smith E A, Wishnie M. 2000. Conservation and subsistence in small-scale societies. *Annual Review of Anthropology* 29:493–524.
- Sober E, Wilson D S. 1998. *Unto Others: The Evolution and Psychology of Unselfish Behavior*. Cambridge (MA): Harvard University Press.
- Sosis R. 2000. Costly signaling and torch fishing on Ifaluk atoll. *Evolution and Human Behavior* 21:223–244.
- Steadman D W, Olson S L. 1985. Bird remains from an archaeological site on Henderson Island, South Pacific: man-caused extinctions on a uninhabited island. *Proceedings of the National Academy of Sciences* 82:6191–6195.
- Steadman D W, Pregill G K, Burley D V. 2002. Rapid prehistoric extinction of iguanas and birds in Polynesia. *Proceedings of the National Academy of Sciences* 99:3673–3677.

- Stearman A M. 1994. 'Only slaves climb trees': revisiting the myth of the ecologically noble savage in Amazonia. *Human Nature* 5:339–357.
- Strassmann B I, Gillespie B. 2002. Life-history theory, fertility and reproductive success in humans. *Proceedings of the Royal Society of London B* 269:553–562.
- Stuart D E. 2000. *Anasazi America*. Albuquerque (NM): University of New Mexico Press.
- Tinbergen N. 1976. Ethology in a changing world. Pages 507–536 in *Growing Points in Ethology*, edited by P P G Bateson and R A Hinde. Cambridge and New York: Cambridge University Press.
- Tooby J. 2001. Is human nature hidden in the genome? *Nature Genetics* 29:363.
- Tooby J, Cosmides L. 1992. The psychological foundations of culture. Pages 19–136 in *The Adapted Mind: Evolutionary and the Generation of Culture*, edited by J H Barkow, L Cosmides, and J Tooby. Oxford and New York: Oxford University Press.
- Trivers R. 1991. Deceit and self-deception: the relationship between communication and consciousness. Pages 175–191 in *Man & Beast Revisited*, edited by M H Robinson and L Tiger. Washington (DC): Smithsonian Institution Press.
- Turke P W. 1989. Evolution and the demand for children. *Population and Development Review* 15:61–90.
- Turke P W, Betzig L L. 1985. Those who can do: wealth, status, and reproductive success on Ifaluk. *Ethology and Sociobiology* 6:79–87.
- Ulrich R S. 1993. Biophilia, biophobia, and natural landscapes. Pages 73–137 in *The Biophilia Hypothesis*, edited by S R Kellert and E O Wilson. Washington (DC): Island Press.
- Veblen T. 1899. *The Theory of the Leisure Class: An Economic Study of Institutions*. New York: Macmillan.
- Vickers W T. 1994. From opportunism to nascent conservation: the case of the Siona-Secoya. *Human Nature* 5:307–337.
- Vining D R. 1986. Social versus reproductive success: the central theoretical problem of human sociobiology. *Behavioral and Brain Sciences* 9:167–187.
- Vitousek P M, Ehrlich P R, Ehrlich A H, Matson P A. 1986. Human appropriation of the products of photosynthesis. *BioScience* 36:368–373.
- Voland E. 1998. Evolutionary ecology of human reproduction. *Annual Review of Anthropology* 27:347–374.
- Waggoner P E, Ausubel J H. 2002. A framework for sustainability science: a renovated IPAT identity. *Proceedings of the National Academy of Sciences* 99:7860–7865.
- Warren B R. 1998. Reevaluating the tragedy of the commons. *Conservation Biology* 12:1168–1169.
- Wedekind C, Milinski M. 2000. Cooperation through image scoring in humans. *Science* 288:850–852.
- Whitehead B D. 1994. The failure of sex education. *Atlantic Monthly* 274:55–61.
- White L. 1967. The historical roots of our ecological crisis. *Science* 155:1203–1207.
- Williams G C. 1992. Gaia, nature worship and biocentric fallacies. *Quarterly Review of Biology* 67:479–486.
- Williams G C, Nesse R M. 1991. The dawn of Darwinian medicine. *Quarterly Review of Biology* 66:1–22.
- Wilson E O. 1984. *Biophilia: The Human Bond with Other Species*. Cambridge (MA): Harvard University Press.
- Wilson E O. 1992. *The Diversity of Life*. Cambridge (MA): Harvard University Press.
- Wilson E O. 1993. Biophilia and the conservation ethic. Pages 31–41 in *The Biophilia Hypothesis*, edited by S R Kellert and E O Wilson. Washington (DC): Island Press.
- Wilson E O. 1998a. *Consilience: The Unity of Knowledge*. New York: Alfred A. Knopf.
- Wilson E O. 1998b. Integrated science and the coming century of the environment. *Science* 279:2048–2049.
- Wilson E O. 2002. *The Future of Life*. New York: Alfred A. Knopf.
- Wilson M, Daly M, Gordon S. 1998. The evolved psychological apparatus of human decision-making is one source of environmental problems. Pages 501–528 in *Behavioral Ecology and Conservation Biology*, edited by T Caro. Oxford and New York: Oxford University Press.
- Wilson M, Daly M, Gordon S, Pratt A. 1996. Sex differences in valuations of the environment? *Population and Environment* 18:143–159.
- Winter D D. 1996. *Ecological Psychology: Healing the Split Between Planet and Self*. New York: Harper-Collins.
- Wong Y W. 1994. Impotence and intransigence: state behavior in the throes of deepening global crisis. *Politics and the Life Sciences* 13:3–14.
- World Commission on Environment and Development. 1987. *Our Common Future: World Commission on Environment and Development*. Oxford and New York: Oxford University Press.
- Wright R. 1994. *The Moral Animal: The New Science of Evolutionary Psychology*. New York: Pantheon Books.
- Wright R. 1995. The evolution of despair. *Time* August 28, 50–57.
- Wright R. 2000. *Non-Zero: The Logic of Human Destiny*. New York: Pantheon Books.
- Zahavi A. 1975. Mate selection—selection for a handicap. *Journal of Theoretical Biology* 53:205–214.
- Zahavi A, Zahavi A. 1997. *The Handicap Principle: A Missing Piece of Darwin's Puzzle*. Oxford and New York: Oxford University Press.

Copyright of Quarterly Review of Biology is the property of University of Chicago Press and its content may not be copied or emailed to multiple sites or posted to a listserv without the copyright holder's express written permission. However, users may print, download, or email articles for individual use.