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Theoretical Review

THE BEHAVIORAL ECOLOGY OF RESOURCE CONSUMPTION: WHY "BEING GREEN" IS SO HARD

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ABSTRACT

The life history and behavior of humans, like those of other species, are shaped by natural selection. Some life history traits that heighten our resource consumption arise from an unusual combination of high intelligence and extreme sociality; as humans evolved, we have become ever smarter and more efficient about obtaining resources for ourselves. We humans are doing what other species do, extracting resources from the environment to survive and reproduce—but we have become so good at it that we are having an ever-increasing impact on populations of other species. The reactions of other species depend in part on their life history, shaped by their evolutionary past: have they repeatedly confronted extremes? Changes? Or, if they have had a long history of relatively little change in important environmental variables, how can they cope? Further, their life histories and ecologies are strong determinants of the most efficient human extraction techniques. Understanding life histories, both of other species and of our own, is important for a sustainable future; in some important ways, our evolutionary past constrains our ecological future. Here I present an overview of what is known.

Keywords: *human behavioral ecology, life history evolution, resource ecology, sustainability*

INTRODUCTION

Scholars in many fields know the litany of environmental problems we face today: a changing climate, more severe floods and droughts, the extirpation of many species. Those of us who study human behavior in an evolutionary perspective—modern ethologists, behavioral ecologists, and evolutionary anthropologists and psychologists—may have something to offer about what kinds of conservation strategies are more, and less, likely to convince ourselves to behave sustainably in particular cases. Here I examine some of the past selective forces that have shaped our (extraordinarily high) resource consumption patterns, by examining human life histories, patterns of resource consumption in traditional societies, and how both our intelligence and sociality contribute to our patterns of resource consumption and management. Appeals to "be green"—to consume resources in a more sustainable manner—might profit from some of the information evolutionary anthropologists and psychologists can provide, which I review here.

Human Life Histories: Why Are We Such Expensive Animals?

Behavioral ecology, one of the disciplines analyzing behavior through an evolutionary lens, argues that environmental conditions shape the lifetimes and behavior of organisms, and that by crafting testable hypotheses and making the right observations, we can understand the basic rules that drive a species' behavior as shaped by ecological conditions. Darwin understood this; that is why he began his *Origin of Species* (1859) with the observation that organisms are generally well-suited to their environments. The basic rules of behavioral ecology apply to humans as well as to other animals (e.g., Cronk, 1991; Borgerhoff Mulder, 1991; review in Low, 2000). Because we often try to explain human behavior through social and cultural factors alone, however, we can easily forget that humans must solve the same fundamental problems as all other species: eating and growing, learning life's skills, finding mates, and raising offspring. Biological fitness requires resources to solve these problems; but great complexity arises because not only ecological, but also social and cultural, factors, can strongly influence human behavior (e.g., Richerson & Boyd, 2005; Henrich et al., 2004).

Human behavioral ecology, like that of other species, is largely about getting and using resources to survive and to reproduce. True, we are a complex and highly social species, but the starting point of *why* humans behave as they do is behavioral ecology. Human life histories and behavior are shaped by environmental (including social) pressures, just as they are for other species. Today we find ourselves in situations in which our evolved predispositions toward maximizing our individual success (along with the success of our kin and those who reciprocate), coupled with our advanced technology, cause us to seek and use more resources than ever before. We publicly challenge ourselves for restraint, to behave for the good of strangers we may never meet, but this turns out to be a very difficult proposition.

Important questions arise: Can understanding the principles of behavioral ecology help humans live more sustainably? How does human behavioral ecology influence the life histories of other species?

Humans as Mammals and Primates

In some ways, humans are a typical primate, with omnivorous diets, large brains, stereoscopic vision, and, importantly, flexible behavior. In other ways, our life history is odd—and it is odd in ways that make us super-consumers compared to most other organisms. It is likely that we are one of the most expensive organisms alive today.

Some of our strategies are constrained by phylogeny. We are mammals, primates, and in the sub-family Homininae. Other constraints arise from our size, because size drives much of the pace of life history; because of that, we can predict when many life history event "should" occur (e.g., Low, 2013a). We have our first offspring just slightly later than predicted from size (Figure 1). Across most traditional societies, girls in their early teens are sub-fecund: they may be able to conceive, but a full-term healthy birth is rare, and the help of others can be significant (Lancaster, 1986, 1991; Kramer & Lancaster, 2010). Another indication that nutrition affects fecundability, and thus fertility, is clear in comparing the total fertility rate (TFR: the number of children a woman would have if she lived the maximum number of years, and at each age had the average number of children) across traditional hunter-gatherer societies versus traditional agriculturalists: agriculturalists, who can produce and eat more calories, typically have higher fertility than hunter-gatherers (Bentley, Goldberg, & Jasienska 1993; note, however, that agriculturalists have more health problems, such as parasite loads). However, the real outliers are women in first-world countries, who delay fertility, often into their thirties (Low, Hazel, Parker, & Welch, 2008).

In some ways, we are rather odd—and very expensive—primates, and this mediates our impact on other species. Again, working from predictions based on adult female size, we are really long-lived (life expectancy at birth is longer than expected for a primate of our size; Figure 1). This varies across populations (see Kaplan & Gurven, 2007, Low, Hazel, Parker, and Welch 2013), but the main point is clear. This discrepancy may relate to our exceptionally large brains and our cooperative social approaches to many problems, which allowed us to avoid predation and numerous other environmental hazards, including other humans. Similarly, babies' brains are much larger (more expensive) at birth than we would predict—and while the brain growth of other primate infants slows dramatically after birth, in human infants the post-natal brain growth rate continues to be quite rapid for about a year. Adult brains are more than two standard deviations larger than expected. This may relate to the fact that we are extreme in our use of learning and cultural transmission of traits, and again, this affects our resource needs.

We know (e.g., van Schaik & Isler, 2013) that wild non-human primates can differ greatly in life-history timing across populations, and that captive and wild populations typically differ greatly. Graphs such as Figure 1 make two important assumptions: that any population will adequately represent the species, and that conditions are relatively stable, so that one can use the phenotypic gambit. As Low et al. (2008, 2013) have shown, neither is true for modern humans, and Kaplan and Gurven (2007) have shown variation in traditional societies (for example their Figure 1 and Table 4 on variation in survivorship and mortality). Such approaches cannot show either the variation within species (see, e.g., Kaplan & Gurven, 2007; Low, Hazel, Parker, & Welch, 2013), or some of the ways in which growth differs across species (e.g. human growth after weaning tends to be slow compared to chimpanzees: Walker, Hill, Burger, & Hurtado, 2006).

Perhaps in response to the relatively long dependency and high expense of children, humans are, by and large, "cooperative breeders": others besides the mother contribute food and care for offspring). Who helps mother and child can vary (e.g., Hames & Draper, 2004; Whiting & Whiting, 1975; Hawkes, O'Connell, Blurton Jones, Alvarez, and Charnov, 1999). And whether "help" actually increases or decreases survivorship can vary, and there remains considerable debate. Probably because of the weak selection on relatively few women toward the end of life, models suggest little impact of grandmothering (Kachel, Premo, & Hublin, 2011). Some authors find very small relationships (Hill & Hurtado, 1991, 1996, working with the Ache). Because the value of a grandmother may vary with age-specific fertility and mortality patterns, we expect variation across societies. Studies in The Gambia have found that maternal grandmothers improve the survivorship of their grandchildren (Sear, Mace & McGregor, 2000); and that the presence of a woman's in-laws increases her fertility (Sear, Mace, & McGregor, 2002). In contrast, no such effects existed in Malawi (Sear, 2008). Conflicting results arise from cross-cultural reviews (Hill & Hurtado, 1991, 2009; Sear & Mace, 2008; Shanley, Sear, Mace, & Kirkwood, 2007). In a metanalysis, Strassmann & Garrard (2011) found that living maternal, but not paternal, grandparents, decreased infant mortality. In different societies, various relatives may or may not affect women's fertility and children's survival. The issue remains unsolved so far. Whoever helps, some aspects of human resource consumption are driven by this cooperative breeding.

Cooperative breeding has had a great impact on human demographic success (Kramer, 2010): The length of human pregnancy is just what we would predict from our size. Human newborns, however, are relatively large: almost a half standard deviation larger at birth than one would predict from adult human size (Figure 1). For the occasional set of twins, the "litter weight" is almost twice that. Yet our infants spend relatively much less time between conception and weaning (Figure 1) other primates, and they are 10% lighter at weaning than we would expect.

Why do we see such oddities: large newborns, but early weaning of light infants? Here, the importance of cooperative breeding as a response to having expensive offspring is clear. Whereas a mother gorilla or chimpanzee forages and nurses her infant alone, in humans, others besides the mother bring food and give care, not only during pregnancy, but also while the mother is nursing and after infants are weaned (e.g., Reiches, Ellison, Lipson, Sharrock, Gardiner, & Duncan, 2009; Hill & Hurtado, 2009; Kramer 2010).

This cooperative breeding—help to mother and child by others in the family or group—allows women to give birth to large babies and to wean them early; it also contributes to the fact that human interbirth intervals are shorter than we would predict, although there is more to that story (Low, 2013a). These factors also affect our rates of resource consumption. Humans, then, are expensive: they have evolved as intense consumers of resources.

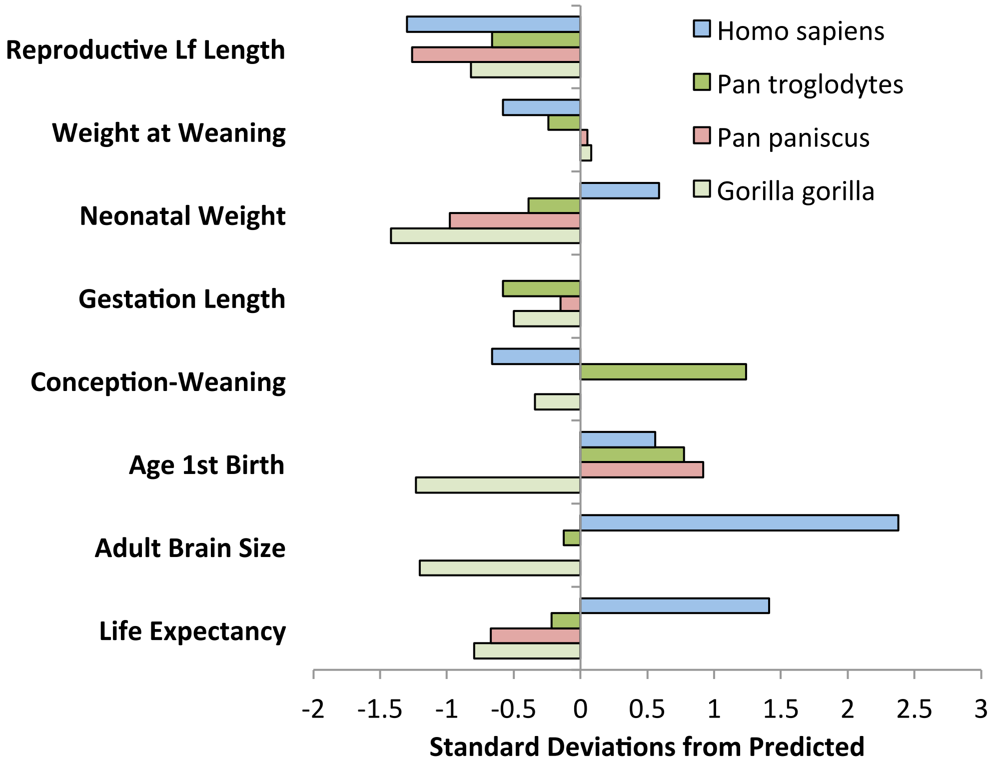

Figure 1. Several important female human life history traits differ from values expected from our size (Low 2013a; non-captive data from Rowe 1996, Lindenfors 2002). Earlier estimates (Harvey, Martin, & Clutton-Brock, 1986) overestimated human deviation from expected patterns.

THE BEHAVIORAL ECOLOGY OF RESOURCE ACQUISITION AND CONTROL

There are excellent general treatises on human behavioral ecology (e.g., Cronk, 1991; Borgerhoff Mulder, 1991), but I have a specific focus here (cf. Low, 1996 a, b, 2004; Low & Heinen, 1993; Penn, 2003; Ridley & Low, 1993; Low, 2013b). If natural selection has shaped human behavior and life histories, as well as those of other species, just how has it shaped the ways humans seek and use resources? Further, how does human resource striving affect the lifetimes and behavior of other species? Basic human behavioral ecology shapes our impacts on other species (interacting with those species' life histories and ecology); this suggests that behavioral ecology can help us predict not only the vulnerability of other species, but also something about our own behavior and its results. Today we smart and social hominins introduce rapid environmental changes, resulting in evolutionary novelty and often evolutionary mismatches (ecological and evolutionary traps; e.g., Cross & Guyer, 1980; Costanza, 1987). Currently, much conservation effort is prescriptive ("Just Save It"), without taking into account the evolutionary history of human behavior—this is why, even when we understand intellectually what will help us be "green," we may have trouble convincing ourselves to do it. Perhaps behavioral ecology can offer us guidance in shaping our conservation efforts. To what pleas will we respond?

The Resource Ecology of Our Past: Traditional and Historical Societies

Ancient *Homo*, and even pre-*Homo*, affected other species. We know something of the evolution of primates, including humans, but mostly we rely on physical remains: seeds, skeletal remains, pot-shards, arrowheads. These tell us, for example, where and when people lived, how large and fast they grew, how big and complicated their populations became. They tell us how people made a living—did they hunt and gather, fish, depend on agriculture?

Though we have relatively little information on our ancient interactions with other species, we do know that ancient and traditional societies have sometimes over-exploited resources (e.g., Clay, 1988; Bodley, 1990) to the point of causing extinction. There are documented human-caused extinctions from the Quaternary (Martin & Klein, 1984). In Pleistocene North America, we humans extirpated some large mammals and large birds, and some small mammals. Less well-known, Late Pleistocene (which ended about 10,000 years ago) extinctions in South America, Australia and New Zealand followed a similar pattern. As Polynesians spread across the islands of the Pacific, they extinguished all of the giant flightless birds, a number of other flightless and flying birds, many marine mammals, frogs, lizards, and flightless insects—not to mention a number of plant species (e.g., Anderson, 1984; Cassels, 1984; Trotter & McCullough, 1984; Crosby, 1986). The arrival of Polynesians on the Hawaiian Islands , for example, appears to have wiped out more than half (54%) of the endemic bird species.

Humans caused harm in several ways: unintended fellow-travelers like rats, whose competitors and predators were left behind; intentional introduction of agriculture, of animals we husbanded (goats, sheep, cattle, pigs), and of carnivorous pets like cats and dogs; weapons that made hunting efficient; and more.

To learn more in depth about earlier people's attitudes and behavior about resource use, and about their impact on other species, typically we look at contemporary traditional societies: hunter-gatherers and slash-and-burn agriculturalists, for example. When we do look, several facts emerge. First, for these populations, resources, status, and reproductive success are intimately tied together, just as they are for other species (reviews by Borgerhoff Mulder, 1991; Cronk, 1991; Low, 2000).

Across societies, resource consumption is essentially always positively related to family (lineage) success, most dramatically for men. Usually, this happens because men with more resources can marry more, and younger, wives, who then produce more children than women first married at older ages. The wealth-fertility associations for women often show similar patterns to those for men, but typically are non- or only marginally significant. So throughout our evolutionary past, resources have contributed to reproductive success, as studies of traditional societies show (Low 2000, chapter 7). The basics seem clear: consider people's resource behavior in a few well-studied societies (for more in-depth treatment of how people in traditional societies conserve (or not) resources, see Borgerhoff Mulder & Coppolillo 2004).

The Amazonian Piro. The Piro of Amazonian Peru are hunters and gatherers. Anthropologist Michael Alvard (1993, 1994, 1995, 1998, 2000), who worked among the Piro, is one of the few scholars to ask specifically, and in a testable way, about conservation strategies of people in a traditional society. The idea of the "Noble Savage" is that people in traditional societies are intrinsic conservators. The phrase is often used in the sense of morally superior human, uncorrupted by civilization, and ever concerned with sustainability of resources. This concept was strong in Western thought from the 16th through 19th centuries, and occasionally pops up even today. In the popular imagination, indigenous peoples showed far-sighted ecological concern; they were "Noble Savages." Ray Hames (2007) has an excellent review of the flaws in this approach.

Alvard's data allow real testing between these two hypotheses: that hunters are conservationists ("Noble Savages"), versus that they are simply trying to maximize their rate of return from hunting—that they are optimal foragers, just like other species. What does it mean: "to conserve"? Some species hunted by the Piro are endangered. Suppose a Piro hunter encounters a prime reproductive-age female of an endangered species: do we imagine he will kill her? There is no doubt that hunters in traditional societies know quite well which species are common, which are rare, and which are extremely rare. If a Piro man is an optimal-returns hunter, he will kill her: she is excellent caloric return for his hunting investment. On the other hand, if he is a deliberate conservator, he will pass her by. You probably already suspect that he will kill her, and he does. In fact, the Piro are extremely good at maximizing their caloric returns—young (too small) individuals are passed up, and prime animals are always taken, even if they are an endangered species.

This example suggests an important set of criteria for assessing actual conservation*: low impact is insufficient to infer "conservation"* (Figure 2). To infer conservation, we must see lower-than-expected impact (Figure 2), given population size, technological efficiency, and potential profit. I will return to this topic below.

Why don't rare species always disappear? There can be ecological reasons (rarity because very dispersed; e.g., Rabinowitz, 1981), but there are also human behavioral reasons. When hunters try to maximize their caloric return, it does not necessarily lead to overhunting or real depredation. With their population densities (typically low), and relatively inefficient available technology, people in most traditional societies simply are usually unable to devastate local game populations (Figure 2). When hunters in traditional societies do overhunt, they typically affect only some species: those most visible or frequently encountered.

The Ache. The Ache hunter-gatherers of Paraguay tell us other things about the importance of resources in our past. They live in small bands of 15 to 70 individuals, moving throughout the forest. Their demography and issues of conservation have been well studied by anthropologists Kim Hill & Magdalena Hurtado (1996). Bands comprise closely related kin and some long-term friends. Daily life centers on hunting and gathering. Women spend about two hours a day gathering; they collect fruits and insect larvae, and extract the fiber from palm trees. Their care of children and possessions constrains women's ability to forage. Men usually set off in small groups to search for game, spending about seven hours per day hunting white-lipped and collared peccaries, tapir, deer, pacas, agoutis, armadillos, capuchin monkeys, capybara, and coatis. Men also collect honey. Food serves not only nutritional needs, but can be shared or traded for other reasons: in particular, men can trade meat for sexual access and political alliances (Hurtado, Hawkes, & Hill, 1985; Hawkes, 1993; Hill & Hurtado, 1996; Winterhalder, 1997).

Ache hunters rarely eat from their own kills, and much food is shared; this led early observers to argue that the society was completely egalitarian. But in fact hunting success and mating success—resources and reproduction—are closely related in the Ache, as in many traditional societies, though there may be no single mechanism (e.g., Smith, 2004). Men often hunt in ways that look inefficient from standard optimal foraging perspectives, but when you look closely, such men may actually be pursuing a high-risk-high-gain "showoff" strategy, just as in many cases of sexual selection in other species (e.g., Hawkes, 1993). Perhaps an even more generalizable argument is about risk in the economic sense: hunt to minimize failure, or seek high variance (some big payoffs), thereby typically raising the mean return (Gurven, Jacugli, & Michael, 2004). Many men who attempt such high-risk, high-gain strategies fail, but the men who succeed produce big, flashy hunting successes—and, with success, high sexual access to women. Men share meat relatively evenly in many circumstances, but share with each other as a sort of political favor-trading, and with women for sexual access. Plants gathered by women are not shared evenly; they remain in the family.

Meat resources matter demographically in additional ways. Despite the fact that the Ache have little in the way of heritable wealth, they keep track of likely paternity, and a man's status as a hunter matters (Kaplan & Hill, 1985; Hill & Hurtado, 1996). The importance of a father in the family is stark: when a man dies, his young dependent children (<10 years) are far more likely to die than if he had lived. When a man has died he can no longer reciprocate in men's political meat-trading, and other men do not share meat with his widow and children (though men may still offer meat for sexual favors). This means that small children whose father dies are also likely to die (Hill & Hurtado, 1996; Hawkes, 1993). Resources and family success are strongly linked.

Indigenous Americans. The resource ecology of Native Americans tells us some other important things: the interplay of technological efficiency and profitable markets makes a big difference to a population's impact on any resource (Figure 2). Two resource mainstays for several Native American groups were beaver and bison. In North America, Great Lakes Indian societies had efficient technology for trapping beaver (*Castor canidensis*) well before recorded times. Northern Algonquians, for example, used beaver for food and clothing, and used the incisors as cutting and sharpening tools. But the local indigenous markets became relatively saturated by the eighteenth century: what can one do with the 25th beaver hide?

As a result, beaver populations remained relatively stable until the Hudson's Bay Company entered eastern North America in the late 18th century. Hudson's Bay introduced a growing market economy, and the value of beaver pelts soared. A male beaver pelt, according to company records in Albany Fort (1773), was worth a brass kettle, or twenty steel fishhooks, or two pounds of Brazilian tobacco. "Mountain men" arrived to trap beaver, and indigenous groups increased their harvests. Beaver declined. By the beginning of the nineteenth century, beaver harvests had first increased, and then fallen to one tenth of their level a century before (e.g., Krech, 1999), and beaver were nearly extirpated.

Indigenous technology was always sufficient to take far more beavers than people did. But there was no point, no advantage, to intense trapping (Figure 2). It was the market, and thus the profit, that changed, driving intensified harvesting and beaver decline. Many cases of anthropologists' "post-contact" extinction and ecological degradation relate, as in this example, simply to changes in profit and/or technological efficiency.

To infer "conservation ethic" simply from low impact is specious: if the human population is small, the technology ineffective, and/or no good market exists, impact will necessarily be low. Only when high consumption is possible and profitable, yet remains low, can one infer deliberate conservation (Figure 2).

This is exactly what behavioral ecology would predict: that people would take as many useful resources as they could from the environment (and if extraction technology increases faster than the resource, extinction may follow). Because people in traditional societies seldom were sufficiently numerous or efficient to create problems for themselves in the short term, there was no selective advantage to doing otherwise.

Plains societies displayed another common outcome related to technology. Bison (*Bison bison*) were once plentiful on the North American plains; it was hard for people in the 19th century to imagine anything but abundant bison. Although no accurate counts were made when bison were plentiful, historical sources from the seventeenth and eighteenth centuries provide dramatic testimony to their large populations (e.g., Peter Fidler, cited by Krech, 1999). Bison ranged from the Northwest Territories to Mexico, from Georgia and South Carolina to Washington, Oregon, and Nevada. It was unimaginable that bison would ever become rare. Yet by 1884, bison were almost extinct.

Why and how did we almost lose the bison? Believers in the Noble Savage think that indigenous peoples, in contrast to European settlers, husbanded bison populations as they did most or all other resources. The rhetoric goes: indigenous peoples were skillful, ecologically-sensitive conservationists, but White settlers wasted bison, causing their extermination. This makes a nice story, but one belied by the evidence. Indeed, white hunters, often hunting from trains, did kill bison wastefully. But as indigenous peoples' extraction techniques became more efficient—from the use of horses on—their harvests increased. In the early 1800s, Indians took approximately 60 million bison; in the mid-1840s, they sold 100,000 bison hides to the American Fur Company (Krech, 1999).

Perhaps the most (inadvertently) wasteful indigenous technique was the "cliff jump". When topography allowed, Plains hunters on horseback could drive the bison up a small rise—which ended in a cliff, not obvious until the animals were too close to turn. Bison would charge off the cliff, to be butchered below. Plains Indians who hunted bison using cliff jumps were highly selective in their use of meat, hides, and other by-products of the hunt, seeking particularly fat and fatty meat (and fetuses), and leaving heavy, less nutritious parts at the kill. Cliff jumps were too efficient in production; they produced far more meat for less effort than competing technologies. However, huge amounts of meat rotted at the base of cliffs, because hunters took only the choicest meat. The extraction technology was highly efficient, but the storage technology lagged behind (e.g., Hames, 1990, 2007; Speth, 1990; Krech, 1999).

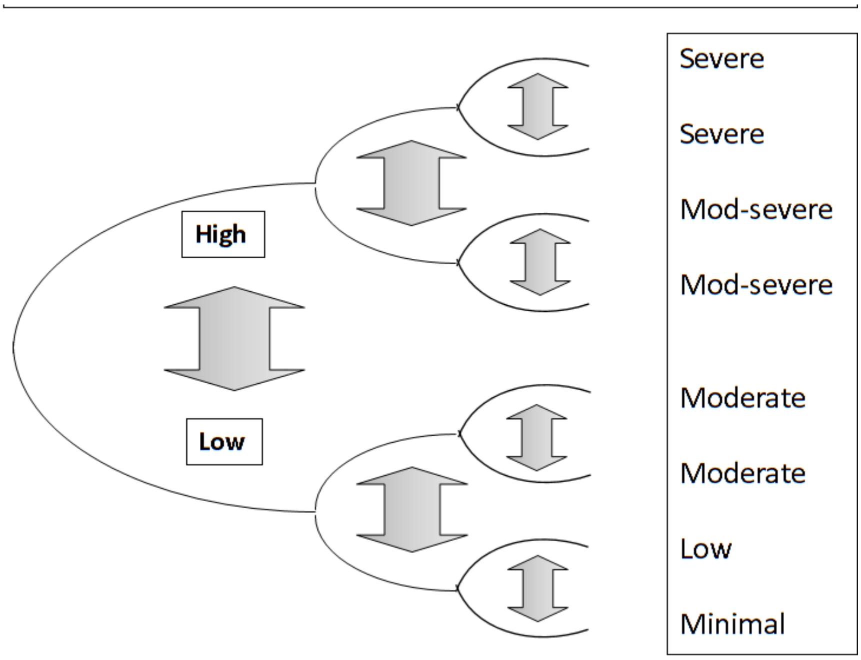

Figure 2. Human impact on resources in traditional societies depends on several things: their population size and density, technological efficiency, profitability. Importantly, low impact does not imply restraint. You can only imply a conservation ethic if you find a combination of high population density, efficient resource extraction techniques, and profitable markets—but low impact (modified from Low, 1993).

Cross-cultural Generalizations. These cases reflect broad generalizations (Figure 2): people strive to get resources and are quite clever at doing so, but how much impact they have on a species depends on their population size or density, the effectiveness of their extraction technology, and whether there is anything to be gained from further hunting or extraction (the marginal value of continued hunting, for example). In the case of the beaver, technology was well up to the job of harvesting far more beaver than were actually taken—however, the market was missing; in some other cases effective markets existed, but old technologies could not produce sufficient supply. For example, when steel axes were introduced in New Guinea, with a market available for wood exports, serious ecological degradation followed (Salisbury, 1962). On the other hand, among the Ye'kwana, enhanced technology increased hunting efficiency, but did not increase exploitation (Hames, 1979): game could neither be stored nor traded regardless of the presence of a market economy.

Are there general patterns? A cross-cultural study (Low, 1996b) of societies in the Standard Cross-Cultural Sample found that in about a third of societies (39/122) for which there were data, severe environmental degradation existed. Degradation was strongly positively correlated with recent population growth and recent technological improvements ($p \leq 0.0005$ in both cases), although neither was universally present as a driver of degradation. These crude cross-cultural data are consistent with the more detailed ethnographic data on the societies above, suggesting that resource acquisition is a primary goal for most peoples.

Other Ancient and Historical Societies. Hunter-gatherer societies tend to be small, and to lack complex political hierarchies. What about more complex societies? Jared Diamond (2005) reviewed several major societies that had thrived and then collapsed: Easter and Pitcairn Islands, the Anasazi, the Mayans, and Norse Greenland. In some cases (Anasazi, Mayans, Greenland) climate change interacted with population growth; hostile neighbors were a factor in the Mayan and Norse Greenland cases, and weakened trading mattered in Pitcairn and Greenland. Two things were present in every case: first, population growth combined with human environmental damage, and (perhaps partly as a result) failure to solve large-scale societal problems. As we look at the simpler societies above, it seems likely that individual striving and competition, largely hidden from view in large complex societies, may nonetheless matter as much there as in simpler societies—just as recent financial near-collapses of several large nation states may have been driven by the behavior of a relatively small group of powerful individuals.

The Bottom Line: Impacts of Past Selection

Everything we learn from traditional and historical societies reflects the fact that humans are not exempt from selection on our resource consumption: what we do reflects how past natural selection on our resource use influences our decision-making daily, even today. And there is, so far as we can find, no evidence of a highly successful society that deliberately short-changes itself in the near term to husband resources for the distant future. Among traditional societies we see good short- to mid-term management, mostly in rather local, stable-membership, somewhat isolated, groups—groups in which social currencies are important, and "take the money and run" is not a viable option. This is why common-property regimes tend to be relatively small, with stable membership, isolated from highly profitable markets and why there are still so few successful commons today (e.g., Ostrom, 1990; Costanza, Low, Ostrom, and Wilson 2001).

In our evolutionary past, crucial resources were hard to get. Our main problems were getting enough resources from the environment for our needs, maintaining satisfactory and stable friendships, finding mates, and raising families. Improving technology was always good. Predicting the effect of our actions decades in the future was never a priority, and in fact, inability to predict future environmental conditions made such long-term planning futile. Getting rewards now was more profitable. (There are large literatures in psychology, child development, economics, and environment, for example, on future discounting.) Most of the time, our populations and technology were sufficiently limited that even with our fiercest striving, we did only local damage to our environment.

The result was that we evolved to strive for resources, and seldom—if ever—found ourselves evolutionarily "rewarded" for conscious current restraint in the service of future gains—especially future gains for strangers. We evolved to be efficient short- and medium-term local environmental managers, not long-term global conservationists.

RESOURCE CONSUMPTION PATTERNS TODAY

Now we are so numerous, with such effective technology, that our short-sighted, self-centered tendencies, which have served us well in the past, can cause us difficulties today. Today we have far more technological effectiveness than the Maya or the Anasazi. We can harvest more resources for less human effort. But efficient technology can sometimes mean that we destroy too much "natural capital" (i.e., the biomass of the species we are hunting or fishing). When that happens recovery is likely to be neither quick nor easy—and sometimes impossible (e.g., Myers & Worm, 2003; and the discussions engendered by that paper).

For some years, the Global Footprint Network (www.footprintnetwork.org) has been estimating, at national and regional levels, the per capita consumption of categories of resources: cropland, grazing land, forests, fishing grounds, and built-up land, as well as the resulting carbon footprint. Figure 3 shows the global trend in consumption since 1961 (latest data from their 2010 report, using data collected through 2007). Per capita consumption has increased from 2.4 he/capita in 1961 to 2.7 in 2007; global population has increased during that period from 3.1 billion to 6.7 billion. The Global Footprint Network now calculates an "Earth Overshoot Day": the date on which consumption for that year exceeds global biocapacity. In 2013, that was 20 August.

But population is only part of the problem; our human impact is a function of both consumption and population. As Ehrlich and Holdren (1972) first pointed out, Impact=Population*Affluence*Technology. The impacts of humans on resources arises from very different causes in least-developed (population numbers) and developed (per capita consumption) (e.g., Low, 2013b). North Americans, and members of the European Union enjoy consumption levels that are utterly luxurious compared to the rest of the world. And it is worth noting that the US per capita consumption figures are three times those of Canada in this analysis, and about four times as high as the Asian Pacific (though China will soon catch up).

Failure to grasp this concept is not surprising, given our evolutionary past, but it means that well-meaning people, including scholars, have been, at least since the Rio Conference of 1992, talking past each other. Underneath the polite rhetoric, first-world nations complain about population growth in developing nations, and developing nations respond that they could afford such growth if first-world nations were not such super-consumers. In developed nations, we have broken the link between resources and number of children, but we invest enormously in our fewer super-children (e.g., Low, Simon, & Anderson, 2002; Low 2013a). The result is that we consume somewhere between 7 and 12 times the resources per capita as in least-developed nations. This is why biologist Joel Cohen (1995) answered the question "How many people can the earth support?" with a resounding "It depends"—on the degree of equity and the living standard you seek.

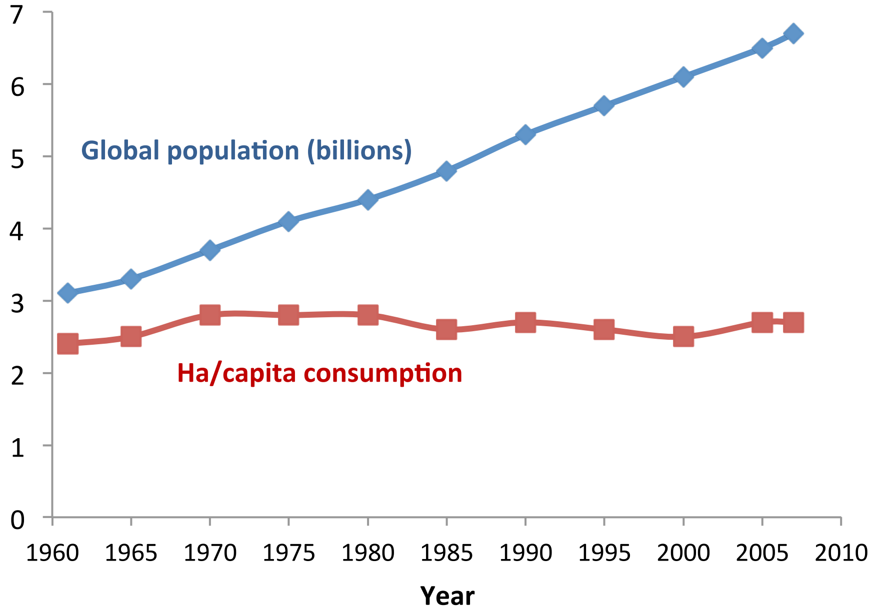

Figure 3. Human consumption certainly can vary across nations, and locally within nations. Nonetheless, Ehrlich and Holdren's (1972) general statement holds: that human impact on the environment is a function of population numbers, affluence (consumption rate), and technology (the source of various pollutants). Globally, both population numbers and per capita consumption have increased since first measured in 1961 (Global Footprint Network).

Human Behavioral Ecology and Our Resource Behavior

We have striking impacts on other species. We know some species are far more vulnerable to human actions than others; we need to understand better the pattern behind what makes cockroaches almost invincible, and condors quite vulnerable, to our actions (e.g., Boyer, 2009; Collen, McRae, Deinet, De Palma, Carranza, Cooper, & Loh, 2011). Here again, the life history arising from an organism's evolutionary past can help us predict its future: whether it will be easy or difficult to manage, whether it will thrive or disappear with ever-more-rapid human changes to the environment. We need good information on other species' ecology, life history, and behavior, and we will have to find the right matches for good strategies. Important are past exposure to, and survival through extreme, highly variable, spatially patchy, and temporally unpredictable conditions (e.g., Low, 2013b).

Today, as in the past, we affect other species in several major ways. Sometimes (hunting, the bushmeat trade, fishing) we consume them directly. We also, as noted above, have introduced species, both deliberately (cattle, camels, goats) and accidentally (rats, some snakes), that wreaked havoc with native species. We may also manage populations to increase them, perhaps by putting out nest boxes for certain birds, or regulating hunting or fishing. When we know too little of the species' life history and ecology, the results can be counter to our intent. Our indirect impacts can create another of the most difficult problems to solve: those in which we have changed one of the environmental aspects that are so important in shaping life history: extremeness, range of variation, spatial patchiness, and temporal predictability. For example, when we change climate (for reasons unrelated to any aspect of species management), we can disrupt a co-evolved system in which different species evolved to use different cues for when to initiate important activities like egg-laying—except, because they were correlated before disruption, we never understood that (e.g., Grossman, 2004).

Our actions have modified all of these factors—extremeness, range of variation, spatial patchiness, and temporal predictability—in various cases, in ways mundane to extraordinary. Cities, for example, are "urban heat islands": the temperature in cities is both warmer (more extreme) and less variable than the surrounding countryside. The soil in cities is more compacted, and the air is dustier (more extremeness) than in surrounding areas. No wonder horticulturalists and landscape architects selectively breed plants that can tolerate compact soil, dusty leaves, and specific temperature ranges. Human habitation displaces some vertebrate species (e.g., bobcats, wolves), and other species can become pests (raccoons, deer).

We further will have to deal, in making specific decisions, with the fact that there are many "actors" with varying interests and differential power; decisions can be made, or discarded, at many levels. When the problem is large-scale, indirect, and long term (as in the case of global climate change), solutions can be particularly elusive. For some time, we were unaware of many secondary impacts of our use of fossil fuels to power societal expansion, for example. But climate change has multiple impacts, some of which are only now surfacing. Understanding both organism life history and our own predilections is important to solving these problems.

Solving Unintended Management Mismatches

We work at managing populations of other many species: controlling (or trying to eliminate) pests, trying to increase numbers of other species. But sometimes well-intentioned management efforts fail, if we don't know enough about the behavior and life history of the species we want to "help." Consider wood ducks (*Aix sponsa*), in which males are one of the most dramatically colored ducks in existence.

Wood ducks nest in tree cavities near open water; they were almost extinguished in the early 20th century, as logging destroyed their nesting habitat. Nest boxes became a popular management tool, and remain so to this day. It probably seemed reasonable that "the more nest boxes the better," but young wood duck females, like those in a number of bird species, practice what is called "dump-nesting" (intraspecific brood parasitism): they may sneak in to other females' nests, lay eggs, and leave quickly. In places where nest boxes are concentrated, such a free-riding female can make many "dumps"; parasitism occurs even when there are suitable, previously successful, unused nest sites. Wildlife biologist Brad Semel and behavioral ecologist Paul Sherman found nest parasitism rates as high as 95% in one locality. Occasionally a “host” female would be trying to incubate as many as 37 eggs, with the outcome that many eggs got broken, and many (often laid by a parasite after incubation had started) never hatched (Semel & Sherman, 1986; Semel, Sherman, & Byers, 1988).

The artificially increased concentration of nest boxes in this case, far from enhancing nesting success in Wood Ducks, created easily-found concentrations of nests, and increased nest parasitism and failure. This initial failure arose because people focused only on part of the problem, and failed to account for the life-history dump-nesting phase. Fortunately, this example had a straightforward solution: space nest boxes farther apart, and place them in the woods, where they are less visible than on the shoreline (Semel & Sherman, 1986; Semel et al., 1988; Eadie, Sherman, and Semel, 1998). This is only one of a variety of similar hopeful examples.

How Human and Non-Human Life Histories Interact in Conservation

Among the important complexities affecting human resource acquisition are how the ecology, behavior, and life history affect how profitable it is for humans to cooperate and/or compete in, for example, hunting or fishing. Successful management requires considerable information and judgment: understanding a species’ life history (and its vulnerabilities), its population dynamics and geographic range, and more, as in the wood duck example above. Life history dynamics are perhaps the most central, and certainly the least well understood, of these.

But human behavior also matters significantly in successful management. The importance of cooperation and successful collective action differ, perhaps surprisingly, with a managed species’ ecology, which can influence (along with other factors) our choice of how to acquire useful knowledge; this in turn can determine how individuals compete and cooperate (Wilson, Acheson & Johnson, 2013; Wilson, et al., 2013).

Compare the management difficulties for lobster, groundfish (e.g., cod, haddock) and sea urchin fisheries. The species’ behavior in these fisheries differs greatly, leading fishermen to adopt very different ways of searching for knowledge about their current location, and presenting them with different problems. Groundfish range most widely, and sometimes (as in some cod populations) exist in what are called structured metapopulations: if a sub-population is fished out, it is not replaced by in-movement of neighboring cod. Groundfishermen must range widely to fish, and their knowledge of local conditions is not easily transferred from location to location. Asking competitors for helpful information is not typically a viable strategy. Sea urchins are local, moving only meters to feed. They are strongly associated with kelp beds, and are prolific “broadcast” spawners. You might imagine that local knowledge, and its sharing, would be relatively easy. But local overfishing, and vagaries of tide and winds, create ever-changing distributions. Both of these fisheries, superficially so different, are alike in failing to lead to cooperative collective management.

In contrast, Atlantic lobsters, though they move across depths throughout their lives, only migrate over a significant distance at one limited life history stage. Lobstermen are territorial, and in some cases, lobstering is a familial pursuit. There is considerable skill in being able to “read” the locations and understand where the most likely catches will be.

Fishing, which is done with traps, tends to take place over a relatively limited, but ecologically complex, area. It is easy for fishermen to destroy or disable their competitors' traps, but doing so would quickly lead to a 'trap war' in which everyone loses. As a result, because the ecology forces fishing in close proximity, lobstermen have learned to restrain their behavior. Groups of older, experienced lobstermen ("lobster gangs") have for some years set rules, influenced by success rates and market prices (Acheson, 1988). To become a lobster fisherman, one must gain their acceptance. Thus, the mutual restraint common in the fishery makes collective action feasible, and the senior lobstermen of the lobster gangs can be highly effective in constraining behavior. The lobster industry is thriving, but that is definitely not true for groundfish and sea urchin fisheries.

These three fisheries, in the same geographical area, operate quite differently because the best human fishing strategies—and the cost of knowledge and of collective action—depend on the ecology and life history of the fished species (Wilson et al., 2013; Wilson, Acheson, and Johnson 2013).

Other factors also matter: the demography of a population (distribution of ages and sexes), mating system, and more. This is true particularly in release programs, which have a spotty record of success: imagine releasing gray wolves as a group of pups. The probability that any would reach breeding age is miniscule. The successful releases have breeding-age adults, and younger individuals as well.

WHAT CAN BEHAVIORAL ECOLOGY DO?

The behavioral ecology and life history strategies of non-human species are critical in management; fortunately we learn more every day. As the last three examples illustrate, it is human behavioral ecology, of which many have remained largely ignorant, that might make significant contributions to future human wellbeing, and it is evolutionary anthropologists, human behavioral ecologists, ethologists, and evolutionary psychologists who can contribute the most knowledge.

The lobster fishery above works as a common property regime: only certain lobstermen can work in a particular area, each has a defined "area, the groups are small, and cheaters can be discovered and punished. The most difficult resource issues to solve, from our perspective, are those in which some actors are able to externalize their costs, making others pay: where there are no well-defined property rights, when it is impossible to monitor, detect, and punish cheaters, and when "solutions" are either ignorant of life history realities, or fail to match the scale of the problem (e.g., Ostrom, 1990, 1998, 2009; Costanza, et al., 2001). As in the examples above, our evolutionary past can significantly influence what strategies will help change these difficulties. I am convinced that the most effective strategies will involve: (1) understanding the life history and ecology both of humans and of affected species, (2) designing conservation programs that work with, not against, our evolved human tendencies as a very smart, long-lived, and highly social mammal, and (3) matching the scale of the problem and the solution—and avoiding separation of costs and benefits.

There is the further difficulty that many centralized approaches to issues such as species and natural area conservation, and pollution abatement, develop into common-property regime dilemmas, often by inadvertently separating "who pays" and "who benefits" from people's actions. If strategies produce inherent benefits for society at large, but also produce local or regional costs, they become one kind of commons: widely dispersed benefits, concentrated costs (e.g., spotted owl management). Or they can become another major kind of commons (with concentrated benefits and dispersed costs: e.g., cattle leases by the Bureau of Land Management), first highlighted by Garrett Hardin in the 1960s (Hardin, 1968). Not surprisingly, even when such programs have a general public support, implementing them can be difficult: there are frequently free-rider problems and strong local dissent. Further, the issues are typically scientifically complex as well as highly emotional; as a result, definitions of, and opinions about, "success" vary greatly.

Finally, I am not sanguine about urging ourselves to be "global altruists." People—you, I—are unlikely to give up short-term individual or familial benefits happily for long-term societal or global gains. As I have argued here, this is not a new phenomenon associated with technological innovation. And it shouldn't surprise any of us that human behavior reflects benefit-cost relationships, just like the behavior of other species. We have evolved to maximize short-term rewards that, in our past, correlated with reproductive success. What makes us proud, what makes us feel good, is also generally what gives us status among our group, and makes us attractive to others. In novel evolutionary environments, these strategies may be harmful ecological traps—but of course, that was never something that mattered in our evolutionary past!

Even the crucial problems of population numbers and per capita consumption arise in part from us as individuals satisfying our (evolved) proximate desires to have children and invest in them to give them a good start in life (e.g., Low, 2013a). We have, I suggest, simply become ever more efficient, better and better at doing exactly what we evolved to do, until today we literally could destroy the earth to satisfy our proximate goals. Appeals to people to make relatively small individual sacrifices for the ultimate good of all people everywhere have had limited success; we have not evolved to consider the global population our family.

LOOKING TO THE FUTURE

Can we design better strategies by taking our evolution into account? The most difficult resource-use problems have the following characteristics: *inadequately-known resource base, slow feedback; externalized costs; and use by many, unrelated, non-interacting individuals*. Like the groundfish and urchin examples above, we can't fix our negative impacts if we can't yet perceive them. This is also a problem with some evolutionarily novel dangers (e.g., chemicals we cannot see or taste); most of us are far more averse to mammal excrement than to something like chemical spills we cannot smell or see.

Successful approaches for convincing people to shift their resource use to more "conserving" patterns must often, I suspect, appeal to people's perceived short-term, familial and local, interests (Low, 1989, 2004; Low & Heinen, 1993; Low & Ridley, 1994; Low, 1996a, b, 2013b; Wilson et al., 2013; cf. Griskevicius, Cantu, & van Vogt 2012). If perceived benefits of conservation can be made to outweigh perceived costs for people, then conservation strategies are likely to persist and spread. In most nations today, these are likely to involve economic or other incentives that confer immediate or short-term benefits to individuals and/or their families and potential reciprocators.

The more costs and benefits are separated (across individuals, across space, or across time), the more difficult the problem will be to solve (Low, 2013b). This is why household recycling (a relatively local issue, in which the same individuals pay the costs and reap the benefits) has been fairly easy to tackle in quite varied situations. In contrast, to ask ourselves for possibly-expensive changes in policy and behavior now, to avoid eventual harmful impacts of climate change—especially when we may not know for 50 years whether we are successful—meets with resistance.

The relative scales of environmental issues and solutions interact in another way with our evolutionary past. We had little control over our environment for much of our existence: hurricanes, droughts, many phenomena were beyond our control (although note that we do not control them perfectly now). It never made sense to worry about the world your grandchildren would see, or the fate of people you would never actually see who lived far away (mostly we didn't even know they were there).

The sum of approaches we use in the face of management and conservation problems is still rather limited, and our most-used strategies are arguably not the most effective. *Information* is obviously necessary, but not sufficient. *Teaching*, or inculcation, and exhortation (e.g., to do the right thing) may sometimes be effective, but the data tend to be sparse and anecdotal. *Social incentives* may have an influence when your reputation matters more to you than profit, typically in small, stable-membership groups—a situation not really common in today's western world, at least. Nonetheless, these strategies play on our highly developed cultural transmission. *Economic incentives* of various sorts are perhaps the most widely used strategies today, from regulations to tradable permits to voluntary agreements. No one type of solution is applicable in all situations; clearly we have a large task, an uphill battle

Because we are such a social species, social incentives and disincentives, rather than monetary rewards, may still work in some modern cases—as they did and do in many traditional societies. It may be productive to devise policies that create real, personal incentives to conserve: the more immediate the benefit, the more successful should be the response. Griskevicius et al. (2012) have a thoughtful paper on problems and strategies for sustainable behavior. In a table, they name common strategies to promote conservation—all of which are indeed common, but also largely ineffective. They make suggestions a behavioral ecologist would make. And political scientists, such as Elinor Ostrom in her presidential address to the American Political Science Association (Ostrom, 1998), have strikingly convergent ideas about how such incentives work (see also Ostrom, 2009). Even in large modern societies, perhaps we can make use of social incentives; consider that many household recycling efforts use highly visible signals to advertise cooperation.

In sum, if we can devise strategies that work *with* our evolved tendencies (Ridley & Low, 1993; Penn, 2003; Low, 2000: chapter 15), perhaps we can become more conserving. But time is short for many problems.

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