Journal of World Prehistory, Vol. 15, No. 1, 2001

The Archaeological Record of Human Impacts on Animal Populations

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Recent archaeological research has fundamentally altered our understanding of the scope of past human impacts on nondomesticated animal populations. Predictions derived from foraging theory concerning the abundance histories of high-return human prey and diet breadth have been met in many parts of the world. People are known to have introduced a broad variety of nondomesticated animals, from sponges to agoutis and rats, to a remarkably broad set of contexts, in turn causing a wide variety of secondary impacts. By increasing the incidence of fire, human colonists have in some cases transformed the nature of the vegetation on the colonized landscape, in turn dramatically affecting animal populations on those landscapes. In island settings, these triple threats—predation, biotic introductions, and vegetation alteration—routinely led to extinctions but there is no archaeological evidence that small-scale societies caused extinction by predation alone on islands or continents. Indeed, the recent history of this famous argument suggests that it is better seen as a statement of faith about the past rather than as an appeal to reason. Perhaps most importantly, our burgeoning knowledge of past human impacts on animals has important implications for the conservation biology of the future.

KEY WORDS: prehistoric human impacts; biogeography; extinction; translocation; conservation.

INTRODUCTION

There is an interesting debate going on among those interested in conservation biology, one that would be surprising to many, and perhaps most,

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archaeologists. On one side of this debate are those who believe that people organized into small-scale societies—those who make their living by some combination of hunting, gathering, and horticulture, and, at times, as pastoralists—are by their very nature conservationists (e.g., Alcorn, 1993, 1996; Hunter-Anderson, 1998). On the other are those who find very little evidence for conservation among such groups (e.g., Alvard, 1994, 1995, 1998a,b; Smith and Wishnie, 2000).

At times, parties to this debate stress different aspects of "conservation." Alcorn (1996, p. 234), for instance, focuses on the endpoint, on the "maintenance of viable populations of native species representing wide genetic diversity, local habitats and ecosystems." Smith and Wishnie (2000, p. 515), on the other hand, focus on the processes involved, on "practices designed to prevent or mitigate species depletion or habitat degradation."

These differences are significant. As Smith and Wishnie (2000) and Alvard (1998a) discuss, the lack of detectable anthropogenic impacts on any given biotic community does not necessarily mean that the people involved were conserving anything. For instance, population numbers may have been too low or technology too limited to have produced a detectable biotic impact—what Hunn (1982) has appropriately called epiphenomenal conservation. In this situation, determining whether or not the people involved were conservationists would require that we determine that they had behaviors designed to achieve conservation goals. Such ideational matters, however, largely remain beyond the reach of archaeological research. At least, though, we can ask a question that is relatively easy to address archaeologically. Is there widespread evidence from the archaeological past that modern peoples (*Homo sapiens sapiens*) organized into small-scale societies caused habitat degradation, including resource depletion and species loss?

It is because this is the key question that archaeologists are likely to be surprised, if not astonished, that this debate exists at all. As Kirch (1997c) has noted, archaeologists are generally fully aware of the impacts that prehistoric small-scale societies had on their environments, even if others are not, and entire books dealing in whole or in part with human impacts on ancient environments are now appearing (e.g., Krech, 1999; Redman, 1999). These works, and others like them (e.g., Burney, 1997b), make strong use of one of the greatest contributions archaeologists and their colleagues have made to our understanding of the modern world during the past two decades or so: that almost no matter where we look, the environments first encountered by Europeans as they expanded across the globe were to one degree or another anthropogenic. In those few instances where they might not have been, they rapidly became so. The Scandinavian colonization of Iceland by A.D. 874 quickly "created a cultural landscape from wilderness" (Amorosi *et al.*, 1997, p. 501), making it "perhaps not a little ironic that tourism in Iceland focuses on what is regarded as the natural landscape and yet the bulk of that visited is the result of human management over the last 1100 years" (Buckland *et al.*, 1991a, p. 130). Few archaeologists can be unaware of the fact that, if we replace this specific date with "archaeological time" and "management" by "impact," it is a rare place indeed for which the same cannot be said.

The literature on human impacts on the environment is vast, extending back into the nineteenth century (see, for instance, the discussion in Grayson, 1984b). Archaeological research conducted during the past two decades, however, has fundamentally altered our understanding of the nature and scope of these impacts. Here, it is my goal to synthesize and discuss what this recent archaeological work seems to have taught us about human impacts on nondomesticated animals, and what this knowledge implies for conservation biology.

PREDICTED IMPACTS: PREDATION-BASED RESOURCE DEPLETION

A Conceptual Introduction

In 1973, a small group of Siona–Secoya Indians established the community of San Pablo on the Aguarico River near the Colombia border in northeastern Ecuador. Occupying land that had seen only light hunting pressure during the previous two decades or so and surrounded by wet tropical forest, these people made their living primarily by hunting, fishing, and small-scale farming. With them was anthropologist W. T. Vickers who, among other things, gathered precise data on the kinds of animals the Siona–Secoya hunted and on their success rates in hunting them. Vickers continued his work here through 1975, then returned in the late 1970s and early 1980s (Hames and Vickers, 1983; Vickers, 1988, 1989, 1991, 1994). Vickers' data on changing hunting success rates through time presaged what archaeologists have now documented multiple times in the deeper past.

Figure 1 plots the changes in Siona–Secoya mammal kill probabilities between 1973–75 on the one hand, and 1979 on the other, against the size of the mammal involved (see Table I). After a period of only 5 years, these hunters had clearly found it increasingly difficult to secure large mammals and had turned instead to smaller ones. The same effect is seen for birds (Fig. 2).

To some extent, what happened here is intuitively obvious. A colonization event, in this case involving the movement of a relatively small number of people onto a landscape that had not been extensively utilized for some

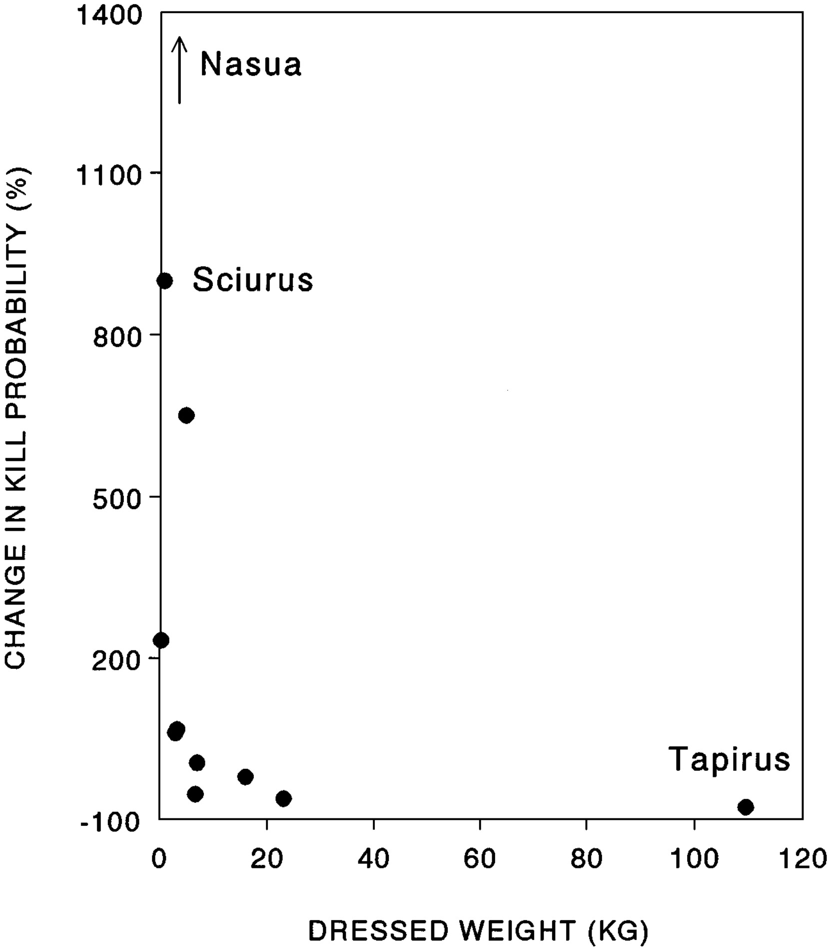

Fig. 1. The relationship between dressed weight and change in kill probability for a Siona–Secoya community: mammals (data from Hames and Vickers, 1983).

20 years led, through hunting, to the depletion of larger vertebrates on that landscape.

A series of concepts drawn from evolutionary ecology allows us to turn the intuitively obvious into a set of statements about the nature of human impacts on the faunal landscape that have quantitative predictive power and that can be, and have been, applied archaeologically. These statements can then be used to better understand the potential impact of small-scale human societies on sympatric vertebrate populations in the deeper past.

Table I. Changing Mammal Hunt Success Probabilities for the San Pablo Siona–Secoya

	Kill probability			
	Dressed weight (kg)	1973–1975	1979	% Change
Tapirus terrestris (South American tapir)	109.5	4.5	1.0	−78
Tayassu pecari (white-lipped peccary)	23.1	31.8	12.1	−62
Pecari tajacu (collared peccary)	16.0	28.7	22.7	−21
Alouetta seniculus (red howler monkey)	7.0	3.8	4.0	+5
Lagothrix spp. (woolly monkey)	6.7	49.7	23.2	−53
Agouti paca (paca)	4.8	0.6	4.5	+650
Dasypus spp. (armadillo)	3.3	2.1	3.5	+67
Dasyprocta punctata (Central American agouti)	3.0	3.8	6.1	+60
Nasua spp. (coatimundi)	1.2	0.0	2.5	—
Sciurus sp. (squirrel)	0.7	0.3	3.0	+900
Myoprocta sp. (acouchi)	0.3	0.3	1.0	+233

Note. Data from Hames and Vickers, 1982; nomenclature follows Wilson and Cole, 2000.

I begin with the concept of resource depression, the situation in which the activities of a predator lead to reduced capture rates of prey by that predator (Charnov *et al.*, 1976). These reduced capture rates may result from "behavioral depression," in which prey adopt behaviors—for instance, increased vigilance or altered periods of activity—that decrease the likelihood that they will be preyed upon. They may also result from "microhabitat depression," in which prey decrease their vulnerability by moving out of geographic reach of their predators (see Hill *et al.*, 1997), or from "exploitation depression," in which numbers of prey individuals decrease because harvest rates exceed both reproductive rates and rates of in-migration. From the point of view of the predator, all have the same impact – reduced prey availability.

Foraging theory not only predicts that resource depression may occur on a hunted landscape, and under what conditions it will occur (e.g., Winterhalder *et al.*, 1988; Winterhalder and Lu, 1997), but also predicts which species are most likely to undergo such depression. The fine-grained prey choice model (Charnov, 1976; Kaplan and Hill, 1992; Stephens and Krebs, 1986) demonstrates that, given certain conditions, the most efficient dietary strategy for a forager to pursue is to take higher return prey items – those resources that return greater amounts of calories (though some other currency may be used to calibrate the model) per unit of energy expended in pursuing, capturing, and processing those resources. The use of lower return resources depends, in turn, on encounter rates with higher return ones. Since encounter rates depend on prey abundances, lower return prey

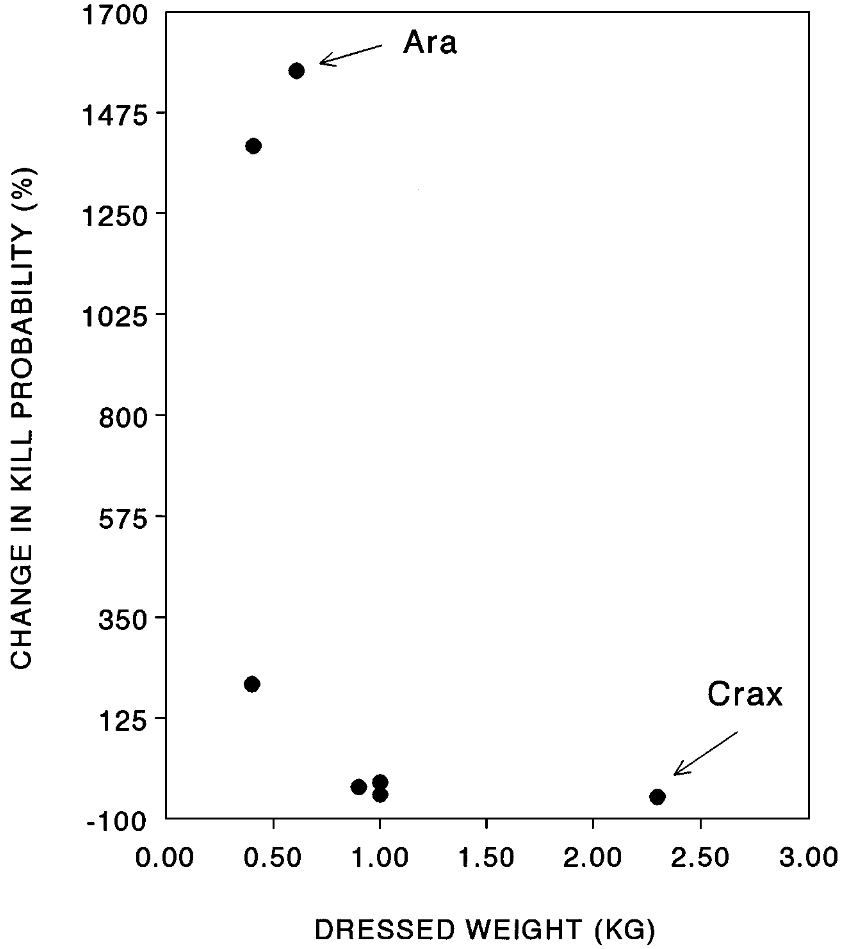

Fig. 2. The relationship between dressed weight and change in kill probability for a Siona–Secoya community: birds (data from Hames and Vickers, 1983).

species will enter the diet as the abundance of higher return prey types declines.

As higher return resources decline in abundance on a given part of the landscape (or "patch"), fewer calories are returned to the forager for a given expenditure of effort and, by definition, foraging efficiency declines. Mobile foragers might avoid this reduction in foraging efficiency by using more distant resource patches, and thus incur added travel costs. Central-based foragers can accomplish the same goal by relocating on a more permanent basis, thus incurring relocation costs. If travel or relocation costs are too high—as might occur, for instance, if appropriate target areas are spatially too far removed or are defended (e.g., Dyson-Hudson and Smith, 1978)—resource depression in hunted and gathered resources should result in resource intensification unless practices designed to conserve resources are introduced. Such intensification can be evidenced in a number of ways: an increase in the abundance of lower return resources in the diet (e.g., Broughton, 1994a,b, 1997, 1999), more intensive use of those prey items that are taken (e.g., Gould, 1996), and an increase in the number of prey types utilized (discussed later).

Often (e.g., Alvard, 1994, 1995; Fa *et al.*, 1995; Peres, 2000), but not always (e.g., Bodmer *et al.*, 1997; FitzGibbon *et al.*, 1995), higher return vertebrate prey are larger vertebrate prey (see the discussions in Broughton, 1994a,b, 1999; Grayson and Cannon, 1999; Hawkes *et al.*, 1982; Madsen and Schmitt, 1998; Smith, 1991). This relationship also follows from the fact that very large and very small body sizes in many vertebrates have evolved at least in part as predator defense mechanisms (e.g., Maiorana, 1990), and that humans, as predators, are not immune to these evolved defenses.

Foraging theory thus predicts that, in the face of heavy human hunting pressure and in the absence of conservation practices, larger vertebrates will in general decline in abundance more rapidly than smaller ones, and that as this occurs, greater numbers of smaller vertebrates will enter the diet. This, of course, is exactly what occurred in the Siona–Secoya example between 1973 (when the area was colonized) and 1979. Interestingly enough, this trend was partially reversed after 1979–by 1982, the abundances of some larger vertebrates had begun to increase in the San Pablo Siona–Secoya diet. It is unlikely to be coincidental that, as Vickers (1988, p. 1521) has observed—though he interprets the dietary results in a very different way—"by 1980, the settlement was considered 'old' and declined as some households relocated." It would appear that, as foraging theory predicts, a reduction in human predation pressure allowed larger vertebrates to increase in number.

We can, as a result, expect that increasing predation pressure by human hunters will result in the decline in abundances of higher return, and thus usually larger, prey species on the landscape and in the diet. Likewise, we can expect that the abundances of lower return, and thus usually smaller, prey species will increase in the diet. We can also expect that, at times, greater numbers of species will be incorporated into the diet—that is, that "diet breadth" will expand—and that those species that are taken may be more intensively utilized. We can expect the people involved to respond to this situation by increasing the distances they travel across the landscape or by relocating if those options are possible. We may also expect technological innovation directed toward increased extractive efficiency (e.g., Grayson *et al.*, 2001; Hawkes and O'Connell, 1992). In general, the only situation in which some combination of these results is not to be expected are those in which human population densities are so low, or technology so ineffective, that resource depression in any of its forms does not occur. And, because of all this, we can also expect that the impact of human colonizers on islands—landscapes that have the potential of quickly filling with people who cannot readily relocate in number—will be particularly striking.

The quantitative archaeological application of these concepts was pioneered by Bayham (1979) in a continental setting and by Keegan (1989) in island contexts. It was, however, Broughton (1994a,b, 1997, 1999), building partly on Bayham's work, who more fully demonstrated the power that quantitative applications of foraging theory models can have in elucidating the nature of the past.

Broughton became intrigued by the stark contrast between the dramatic descriptions of the abundance of western Californian wildlife left by early European explorers and the comparative faunal poverty of the late prehistoric archaeological record of this area. The contrast, he showed, was a function of human-induced resource depression during late prehistoric times on the one hand, and, on the other, the subsequent rebound of prey species after native human hunting pressure had been removed. The European explorers, it now seems, traversed an Edenic blip on the California landscape, something that would not have been seen a century earlier and was not to be seen a century later. It is now becoming quite clear that the process that Broughton's work uncovered was a common one.

Human Colonization and New Zealand Vertebrates

Just prior to the human colonization of New Zealand, these islands supported some 11 species of moas – large, flightless birds that ranged in weight from about 20 kg to over 200 kg. Although there is debate over the timing of the first human contact here (Anderson, 1996, 2000; Brook, 2000; Higham and Petchey, 2000; Holdaway, 1996, 1999a; Holdaway and Beaven, 1999; Holdaway and Jacomb, 2000; Lowe *et al.*, 2000; Smith and Anderson, 1998), ephemeral visits may have begun around 2,000 years ago, with permanent settlement underway by about 900 years ago or soon thereafter. A few hundred years later, the moas were gone (Anderson, 1989; Holdaway and Jacomb, 2000; Worthy 1999 unless otherwise indicated, all archaeological ages in this paper are in radiocarbon years).

These extinctions seem to have had multiple causes, all related to human activities. The human colonizers brought with them both Polynesian rats (*Rattus exulans*) and domestic dogs. Indeed, Polynesian rats may have been present in New Zealand by some 2,000 years ago, suggesting, as I discuss later, that ephemeral human visits had begun by this time (Holdaway, 1996, 1999a; Holdaway and Beavan, 1999; Matisoo-Smith *et al.*, 1998; McGlone and Wilmshurst, 1999).

Holdaway (1999b) thinks it unlikely that Polynesian rats or domestic dogs played an important role in reducing moa numbers, but others disagree (Fleming, 1969; Anderson and McGlone, 1992; Towns and Daugherty, 1994; Worthy, 1999; for an interesting discussion of prehistoric New Zealand dogs, see Clark, 1997). Even if, as Holdaway (1999b; see also McGlone, 1989) argues, direct predation by Polynesian rats on moa eggs was not significant, rats would nonetheless have both competed with moas for food resources and have impacted the vegetation on which those birds depended, as I discuss later.

A role for human predation in moa extinction, on the other hand, is not doubted. Such a role is clearly indicated by the fact that there are some 300 archaeological sites in New Zealand that have been interpreted as related to moa hunting (Anderson, 1989), and Worthy (1999) reports 103 sites with published avifaunal lists that contain moa remains. As a result, there has been no debate over the potential role that human hunting may have played in causing these extinctions, quite unlike some other cases of prehistoric vertebrate losses discussed later.

The precise role that human predation played in causing moa extinction, however, is not known. This is the case not simply because we do not know what role may have been played by rats and dogs, but because the human colonization of New Zealand was rapidly followed by massive, fire-caused deforestation. Within a few hundred years of human settlement, almost all of the lowland forest of both North and South Islands had been destroyed by fire, with higher, wetter sites affected as well (Horrocks and Ogden, 1998, 2000; McGlone, 1983, 1989; McGlone *et al.*, 1994, 1996; McGlone and Wilmshurst, 1999; Newnham *et al.*, 1998a,b; Wilmshurst, 1997; Wilmshurst *et al.*, 1997, 1999). McGlone (1989) has estimated that roughly 85–90% of New Zealand was forested 3,000 years ago. By the time widespread European settlement was underway in the mid-nineteenth century, half of that forest was gone.

The human colonization of New Zealand was thus followed by massive environmental change, involving the introduction of rats and dogs, fire-driven deforestation, and vertebrate extinctions (among other things: see, for instance, McGlone, 1989 and Wilmshurst *et al.*, 1999 on erosion). Moas did not go alone in this prehistoric extinctions episode. At least 21 other species of landbirds became extinct on New Zealand, along with at least one species of bat, three species of frogs, and an unknown number of lizards (Holdaway, 1989, 1999b; Towns and Daugherty, 1994; Worthy, 1999, Appendix 2).

Anderson (1983; Anderson and McGlone, 1992) has observed that the general prehistoric dietary sequence in New Zealand shows a shift from an earlier reliance on larger terrestrial vertebrates, including moas, to much smaller prey species. He has argued that human hunting played the pivotal role in reducing the abundances of these larger vertebrates, and that the later focus on much smaller prey species is a direct result of this predation-driven resource decline. The resultant resource intensification, he has argued, also played an important role in the development of mass-capture technologies and associated behavior (see, for instance, Anderson and McGlone, 1992, p. 233–235). Nagaoka (2000, 2001) has now provided quantitative details on the nature of the processes involved, applying concepts derived from foraging theory to the vertebrate faunal remains from New Zealand's Shag River Mouth archaeological site and building on the work by Broughton (1994a,b, 1997, 1999).

This site, located on the east coast of South Island, was occupied for at most a century or two beginning at about 650 B.P. (Anderson *et al.*, 1996), a period of time that saw a dramatic decline in the abundance of at least locally available moas. Focusing on the vertebrates that must have come from South Island's interior, Nagaoka showed that the six oldest Shag River Mouth assemblages (strata 6–11) were composed of at least 95% moa bones. After this point, moas dwindled significantly in abundance. As this occurred, the number of inland species incorporated into the diet increased substantially (Fig. 3). As predicted from foraging theory, diet breadth increased in parallel with decreases in the abundance of larger vertebrates in the diet.

At the same time, the number of moa tracheal rings – bony elements from the neck, a relatively meat-free part of the skeleton – decreased sharply in the Shag River Mouth faunal assemblages (Fig. 4(A)), and the proportion of skeletal elements associated with meat-rich parts increased (Fig. 4(B)). Earlier, I noted that one possible response to local resource depression involves traveling greater distances to obtain higher return resources from areas in which they still exist. Nagaoka's analysis suggests that this is exactly what happened at Shag River Mouth. As the distance between hunting locale and central base increased, transport costs would have increased as well. In response, the body parts retrieved tended to become restricted to those of greater economic value (for discussions of offsite processing in central-based contexts, see Bartram, 1993; Bettinger *et al.*, 1997; Metcalfe and Barlow, 1992; O'Connell *et al.*, 1990). The clear implication is that local populations of moas had been exhausted or nearly so, and that those individuals that continued to be taken were coming from further and further afield.

Correlated with all of this was a marked increase in the use of more expensive offshore resources (Fig. 5). It also appears very possible that as offshore resources came under increasing predation pressure by the occupants of Shag River Mouth, that pressure drove the size of one of these

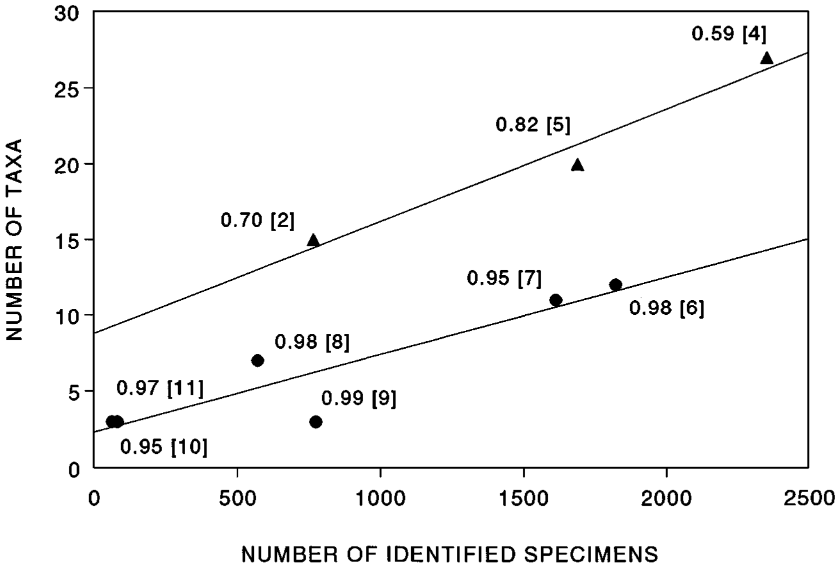

Fig. 3. The changing numbers of inland taxa incorporated into the Shag River Mouth diet through time (after Nagaoka, 2000). Because numbers of identified taxa are routinely strongly correlated with numbers of identified specimens, taxon counts are arrayed against sample sizes. The numbers on the plot provide the percentage of moa specimens in the inland fauna from each stratum, followed by the stratum number in brackets.

species – barracouta (*Thyristes atun*) – downwards (Leach *et al.*, 1999), although, as the authors of this study carefully note, the small numbers of measurable specimens involved in this analysis make this conclusion somewhat ambiguous.

Nagaoka's work, only a small part of which I have reviewed here, thus provides a detailed view of the effects of human colonization on the vertebrate faunal landscape of New Zealand, and of the impacts that these effects had on the people themselves, as seen from one particular spot on the ground. In many ways, the results she obtained are similar to those provided by the Siona–Secoya ethnographic example I discussed earlier. But because her analysis is grounded in a single site, it cannot show what was happening throughout New Zealand as a result of the human arrival. In addition to postcolonization deforestation and the bird, reptile, and amphibian extinctions that I have noted, marine mammals were also affected. At 1200 B.P., for instance, fur seals (*Arctocephalus forsteri*) bred along the coasts of both North and South Islands. By the time of European contact (A.D. 1769), fur seal rookeries were restricted to the southern tip of South Island, a retreat that is clearly related to human predation and, perhaps, to the impact of introduced domestic dogs (Anderson and McGlone, 1992).

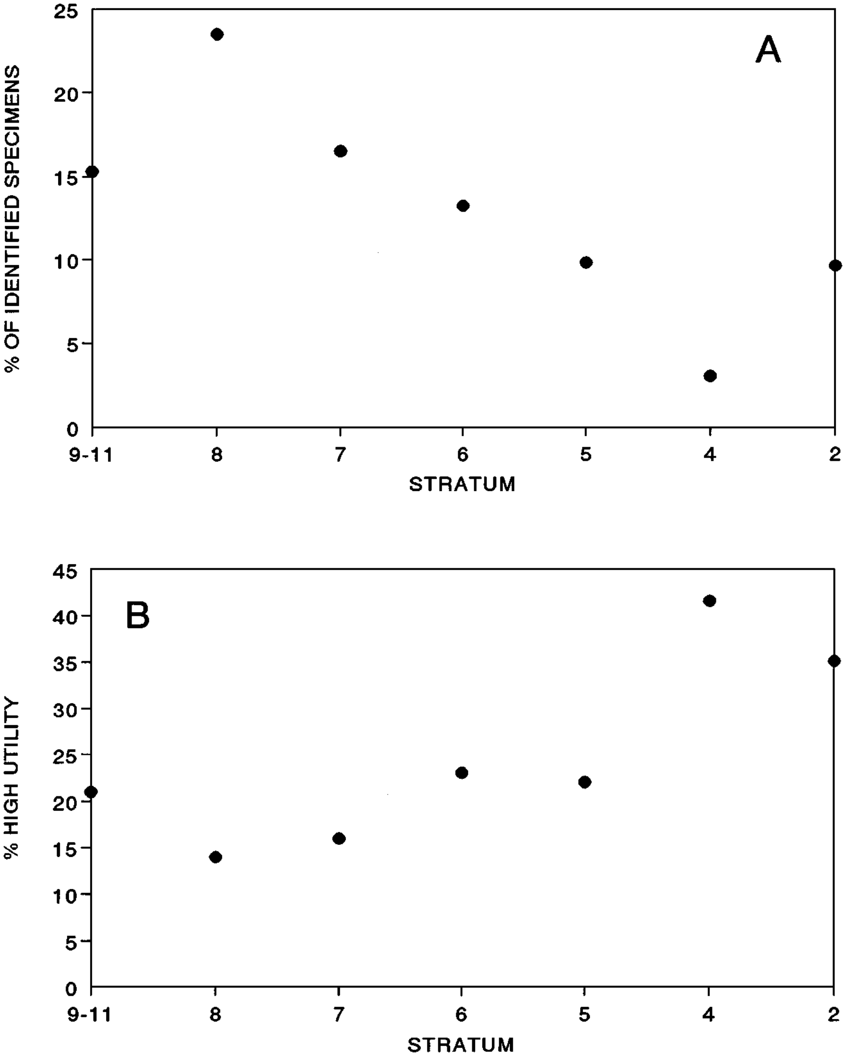

Fig. 4. (A) The changing relative abundances of moa tracheal rings in the inland faunal component at Shag River Mouth; (B) The changing proportions of meat-rich skeletal elements at Shag River Mouth; % High Utility = the percentage of the moa component of the fauna in each stratum that is provided by meat-rich skeletal parts (after Nagaoka, 2000).

The White Mountains, California (USA)

Archaeological evidence resulting from human colonization events is not confined to oceanic islands. For instance, a vertebrate response to human

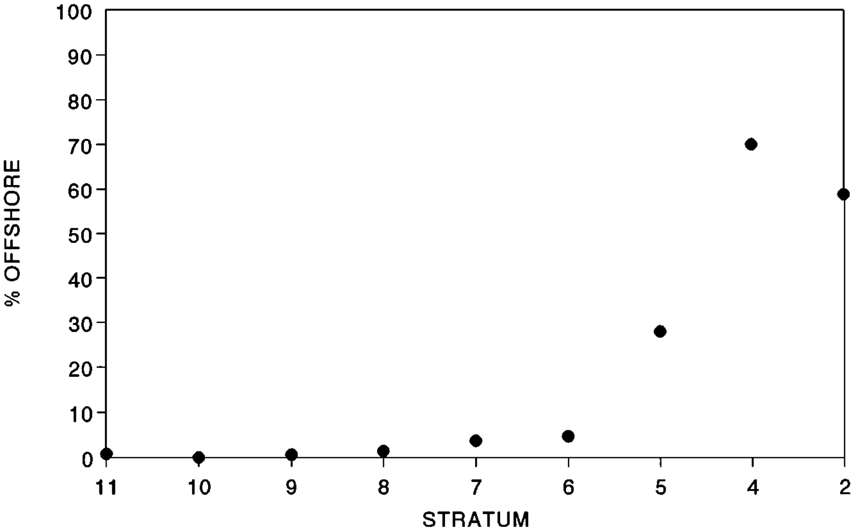

Fig. 5. The changing importance of offshore resources at Shag River Mouth (after Nagaoka, 2000); "% Offshore" provides the percentage of the entire set of identified specimens from each level that came from offshore settings.

predation similar in many ways to that found by Nagaoka (2000, 2001) is shown by faunal sequences from very high elevation (3,170–3,850 m) archaeological sites in the White Mountains of southeastern California, just east of the Sierra Nevada (Grayson, unpublished data).

The relevant archaeological sequence in this above-treeline alpine setting begins at an estimated 3,500 years ago and continues into early historic times. Early in the sequence, the record suggests that the alpine tundra of this region was being used primarily for sporadic hunting, presumably by male hunting parties (Brown, 1970; Hawkes, 1990). Later in the sequence, small villages, marked by houses with substantial circular stone footings, began to be used, with both hunting and gathering, and thus presumably family groups, represented (Bettinger, 1991, 1994).

It is not clear that the 3,500-year-old onset of the archaeological record here can be taken as the first significant use of this area by human foragers. That there is no earlier archaeology known from the area may simply mean that more ancient vestiges of human occupation have yet to be found. However, it is unlikely that dramatically older archaeological material will be found, since there is no evidence that such high elevation areas were used anywhere within the Great Basin prior to about 5,000 years ago, and evidence for the timing of such use elsewhere in this region matches the White Mountains record quite well (Canaday, 1997; Thomas, 1988). If the known archaeological record here does not catch the onset of human use of these uplands, it likely comes fairly close to doing so (see Grayson, 1993, 2000a, and Kelly, 1997, for a discussion of the general Great Basin archaeological record during this period of time).

Throughout the sequence here, the two most abundant mammals in the archaeological faunas are mountain sheep (*Ovis canadensis*) and yellow-bellied marmots (*Marmota flaviventris*); smaller numbers of other artiodactyls, small rodents, and lagomorphs are also present (Grayson, 1991a). The relative abundances of these animals in the White Mountains faunal assemblages, however, vary substantially through time. The early assemblages are marked by relatively high percentages of artiodactyls, animals that are presumed, because of their large size, to be high-return prey items. Through time, these percentages decline steadily and, by the very late prehistoric, the vertebrate portion of the diet was being contributed almost entirely by mammals whose body-weight does not exceed a few kg, among which marmots were by far the most important (Fig. 6).

Although some of the skeletal results of the hunting that took place in this alpine setting may have been transported downslope, and thus be archaeologically invisible in the high elevation sites, it is highly unlikely that this mechanism has produced the pattern shown in Fig. 6. First, the transport costs involved in moving significant portions of artiodactyl skeletons to consumers located far downslope would be substantial, and it is far more likely that meat alone would be moved (e.g., Bartram, 1993; O'Connell *et al.*, 1990). Second, even if entire artiodactyls were carried downslope, any such movement would have been far more likely to have occurred early in the sequence, when a smaller set of consumers was apparently present, than later, when entire family groups were apparently present. There is also no evidence for the differential removal of marmot skeletal parts between the earliest and latest White Mountains assemblages. While butchering marks make it quite clear that skins were being removed from these animals (Grayson, 1991a), the ratio of more peripheral elements (for instance, tarsals), which were demonstrably removed during the skinning process, to more central skeletal elements (for instance, humeri), which were not, is virtually constant across the earliest and latest assemblages.

Patterns of the sort seen in Fig. 6 can also be driven by climate change that alters the underlying abundances of the species involved. However, while this period did see marked changes in climate—perhaps most notably the Medieval Warm Period, ca. A.D. 900–1300 (Crowley and Lowery, 2000; Jones *et al.*, 1999)—there are no unilinear changes in climate in this region that are correlated with the nearly unilinear decline in the abundances of large mammals in the White Mountains faunal assemblages.

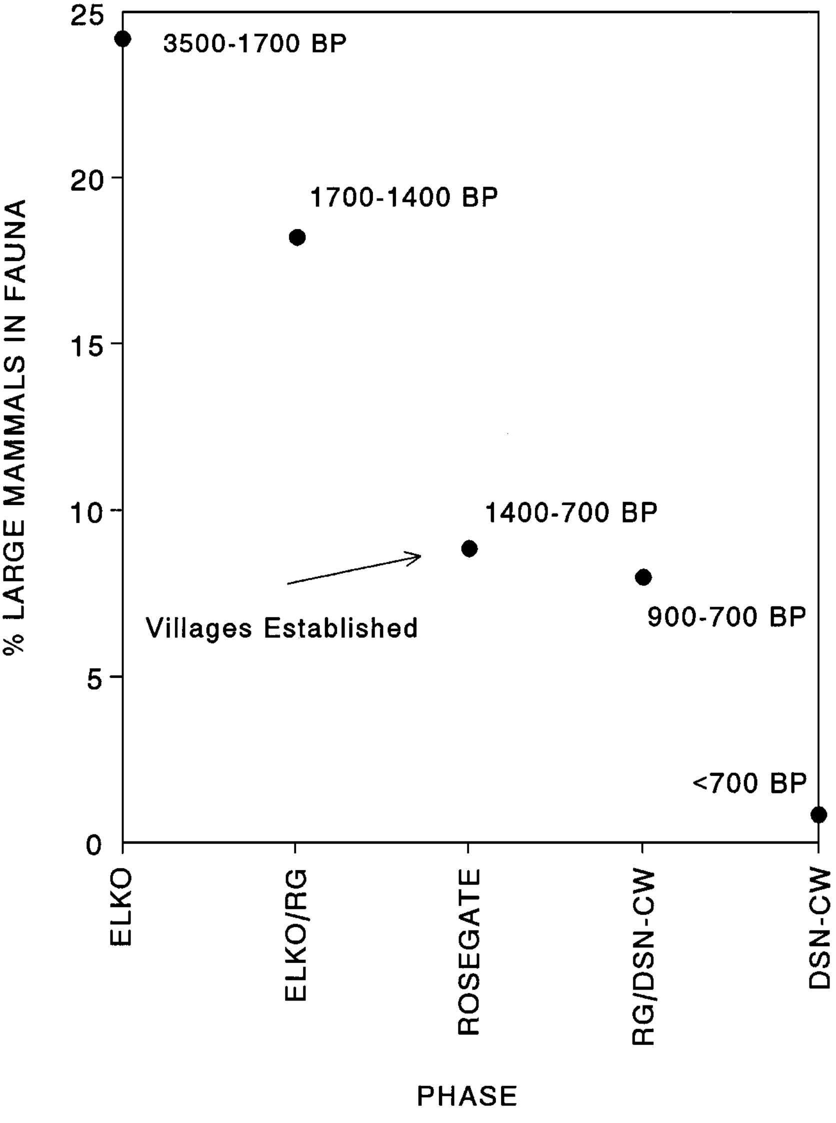

Fig. 6. The declining importance of artiodactyls in the high elevation sites of the White Mountains (Grayson, unpublished data). B.P. = years before the present; "phase" refers to archaeological sites grouped on the basis of chronologically sensitive projectile point styles, named on the X axis (RG = Rosegate; DSN = Desert Side-notched; CW = Cottonwood).

It is, as a result, fairly clear that several thousand years of sporadic hunting in the upper elevations of the White Mountains led to substantial reductions in mountain sheep numbers, with those reductions beginning as a result of the first human hunting documented in this region. There is also some evidence that diet breadth was greater later in the sequence than it was earlier (Broughton and Grayson, 1993; Grayson, 1991a). These changes occurred even though human population densities in this region were undoubtedly low and the hunting likely to have been sporadic. It is even possible that the alpine villages were ultimately abandoned as a result of the loss of higher return resources, though other explanations of this abandonment are perhaps more likely (Bettinger, 1991; Grayson, 1993). As I have already noted, large mammal history in the alpine tundra of the White Mountains provides a striking parallel, across a much greater period of time, to what we have already seen among the Siona–Secoya.

The Apparent Universality of Resource Depression

The analyses of resource depression that I have described have not been selected from a larger variety of analyses that have tried and failed to detect prehistoric human impacts on prey species. Indeed, virtually wherever archaeologists have sought such effects, they have found them-among, for instance, pinnipeds along the west coast of North America (Hildbrandt and Jones, 1992; Jones and Hildebrandt, 1995; see also Lyman, 1995); mammals and fish along the lower Columbia River of Oregon during the last 2,200 years (Butler, 2000), artiodactyls in the eastern Great Basin and northern Plateau of Utah between 1400 and 600 B.P. (Janetski, 1997), fish between 1000 and 300 B.P. on Mangaia, Cook Islands (Butler, 2001), and land crabs in the West Indies (de France *et al.*, 1996; Keegan, 1989, 1995; Keegan and DeNiro, 1998). As Rolett (1998) has observed, much the same can be said for the declining abundances of turtles between ca. 1600 and 150 B.P. on the Marquesas Islands (Kirch, 1973; Rolett, 1998), between 2100 and 200 B.P. on Rennell Island, southern Solomon Islands (Chikamori, 1986), and beginning at about 2800 B.P. on Tikopia (Kirch and Yen, 1982). Invertebrates were not immune to this process, as the declining sizes and changing age structures of mollusk populations through time in response to human harvesting pressure have shown in so many parts of the world (e.g., Keogh *et al.*, 1993; Lightfoot *et al.*, 1993; Spenneman, 1987, 1989; Swadling, 1986). Wherever population sizes are large enough, and technology effective enough, prehistoric responses become evident, just as they are known to do ethnographically (Smith and Wishnie, 2000).

DISCOVERED IMPACTS: ANIMAL TRANSLOCATIONS AND EXTINCTIONS

The general results derived from applications of foraging theory to archaeological contexts, and in particular to instances of resource depression, were intuited by perceptive scholars long before these theory-driven applications had been done. The value of these applications resides in part in the fact that they provide quantitative predictions concerning biotic responses to human predation at the same time as they allow human responses to their own impacts to be measured. In addition, these applications have provided novel insights into human–landscape interactions, including detailed assessments of the impacts of transport costs on human mobility and on foraging decisions.

In addition to these theory-derived confirmations of human impacts on regional biotas, however, there are several categories of effects that were not tightly predicted from theory but were instead discovered empirically. These empirical discoveries are just as important for our understanding of the impacts that small-scale human societies have on biotas as are the theory-derived analyses. Here, I will focus on the long-distance transport of nondomesticated animals, both vertebrate and invertebrate, to areas in which they did not previously occur, and on the most famous impact of all, extinction.

Animal Translocation

Conservation biologists tend to define "translocation" as the "intentional release of animals in the wild in an attempt to establish, reestablish, or augment a population" (Griffith *et al.*, 1989, p. 477; see also Dodd and Siegel, 1991; Haight *et al.*, 2000; Reinert, 1991). Archaeologists and paleontologists, however, have used the same term to refer to the human introduction of organisms to novel landscapes, regardless of the nature and intent of the introduction (e.g., Flannery and White, 1991). Given that biologists working with contemporary organisms also use the term in this latter way (e.g., O'Dwyer *et al.*, 2000) and that my concerns are less with nature and intent than with result, I follow the latter usage here. Because it is obvious that people possessing domesticated animals—pigs, chickens, and dogs in Oceania, for instance, or sheep, goats, and cattle in the Mediterranean—moved their livestock across the landscape, my concern is again only with nondomesticated species.

The variety of animals archaeologically demonstrated to have been translocated by human colonists and their descendants is astonishing. A sample of these translocations is provided in Table II for invertebrates, and in Table III for vertebrates. I have in some cases cheated by including a few taxa whose prehistoric translocation has been inferred from modern distributions but for which archaeological confirmation is not yet available—for instance, the click beetle *Simodactylus delfini* on Easter Island, earthworms on the Faroe Islands, and the harvest mouse *Reithrodontomys megalotis* on the southern Channel Islands, California (throughout this section, references provided in the tables are not repeated in the text). These are clearly indicated in the tables. I have left nearly all unconfirmed prehistoric translocations off the list, including various species of ants in Polynesia (Morrison, 1996a,b) as well as a variety of lizards in Oceania for which compelling mitochondrial DNA evidence of recent but prehistoric transport has been developed (Austin, 1999; Austin and Zug 1999). All other species on these tables are known archaeologically, including the insects introduced by Norse colonizers to Iceland and Greenland and the land snails introduced to various Polynesian islands. Given the frequency with which such translocations are known to have occurred, an enormous number must remain to be discovered.

These translocations began during the Pleistocene. The earliest known instance involves the introduction of the gray cuscus *Phalanger orientalis* to New Ireland about 19,000 years ago, appearing at the same time as obsidian transported from New Britain (Allen *et al.*, 1989; Flannery and White, 1991). A small marsupial weighing about 2 kg (Winter, 1983), the gray cuscus, was also introduced to Buka in the Solomon Islands by 9000 B.P., to Nissan, also in the Solomons, by 4300 B.P., and to Timor by 4500 B.P.

While translocations began during the Pleistocene, however, those that occurred during the Holocene have had the most impact. On the islands of the Mediterranean, for instance, endemic terrestrial mammal faunas were routinely replaced by mammals introduced by people (Cheylan, 1984). On Corsica, to take a very well-studied example, the seven or so species of mammals that were present at the end of the Pleistocene gave way to a suite of mammals, large and small, that began to arrive soon after 9000 B.P. with the earliest documented human occupations here. This process has been so thorough throughout the Mediterranean that only two, relictual Pleistocene species remain, both of which are shrews (Blondel and Vigne, 1993; see also Payne, 1995 and Alcover *et al.*, 1999).

Little purpose would be served by discussing all the translocations listed in Tables II and III. I must, however, mention the extinct flightless rail *Nesotrichis debooyi.* This bird was introduced prehistorically (the timing is not clear) to St. Thomas, St. John, St. Croix, and, perhaps, Virgin Gorda, in the Virgin Islands. Related to other flightless Caribbean rails, the original homeland of this bird appears to have been Puerto Rico, where it is known paleontologically, and from which it was taken to the Virgin Islands, where it is

Table II. A Sample of Invertebrate Translocations

Place	Taxon	Date	References
I. North Atlantic			
Faroe Islands	Lumbricidae (earthworms)*	Norse	Enckell and Rundgren, 1988; see also Hannon and Bradshaw, 2000
Greenland	*Damalina ovis* (sheep louse)	Norse	McGovern *et al.*, 1983, Sadler, 1991; Sadler and Skidmore, 1995
	Pediculus humanus (human louse)	Norse	
	Nabis flavomarginatus (bug)	Norse	
	Eusphalerum sorbi (rove beetle)	Norse	
	Omalium excavatum (rove beetle)	Norse	
	Othius angustus (rove beetle)	Norse	
	Philonthus politus (rove beetle)	Norse	
	Xylodromus concinnus (rove beetle)	Norse	
	Caenoscelis ferruginea (fungus beetle)	Norse	
	Corticaria rubripes (scavenger beetle)	Norse	
	Lathridius minutus (scavenger beetle)	Norse	
	Melophagus ovinus (sheep ked)	Norse	
	Heleomyza borealis (fly)	Norse	
	Pulex irritans (human flea) and other insects	Norse	
Iceland	*Damalina ovis* (sheep louse)	Norse	Buckland *et al.*, 1991a,b; Sadler, 1991; Sadler and Skidmore, 1995
	Pediculus humanus (human louse)	Norse	
	Creophillus maxillosus (rove beetle)	Norse	
	Omalium excavatum (rove beetle)	Norse	
	Philonthus politus (rove beetle)	Norse	
	Phyllodrepa floralis (rove beetle)	Norse	
	Xylodromus concinnus (rove beetle)	Norse	
	Catops fuliginosus (fungus beetle)	Norse	
	Aphodius fimetarius (dung beetle)	Norse	

(Continued)

Table II. (Continued)

Place	Taxon	Date	References
	Aphodius lapponum (dung beetle)	Norse	
	Oryzaephilus surinamensis (grain beetle)	Norse	
	Corticaria elongata (scavenger beetle)	Norse	
	Sitophilus granarius (grain weevil)	Norse	
	Melophagus ovinus (sheep ked) and other insects	Norse	
Iceland: Papey	*Damalina ovis* (sheep louse)	Norse	Buckland *et al.*, 1995
	Pediculus humanus (human louse)	Norse	
	Xylodromus concinnus (rove beetle)	Norse	
	Lathridius minutus (scavenger beetle)	Norse	
	Melophagus ovinus (sheep ked)	Norse	
II. Oceania			
Cook Islands: Mangaia	*Melania* sp. (land snail)	by 1000 B.P.	Kirch *et al.*, 1995; Steadman and Kirch, 1990
Easter Island	*Simodactylus delfini* (click beetle)*		Desender and Baert, 1997; Dumont *et al.*, 1998
	Pancidonus bryani (weevil)*		
	Meyenia sp. (sponge)	650 – 500 B.P.	
Fiji: Yanuca Island	*Lamellaxis gracilis* (land snail)	by 3000 B.P.	Hunt, 1981
	Gastrocopta pediculus (land snail)	by 3000 B.P.	
Hawai'i: O'ahu	*Lamellaxis gracilis* (land snail)	Late prehistoric	Christensen and Kirch, 1986

Marquesas: Tahuata	*Lamellidea oblonga* (land snail)	ca. 700 B.P.	Rolett, 1992, 1998
	Pacificella cf. *variabilis* (land snail)	ca. 700 B.P.	
	Gastrocopta pediculus (land snail)	ca. 700 B.P.	
	Lamellaxis gracilis (land snail)	ca. 700 B.P.	
Marquesas: Uahuka	*Lamellidea oblonga* (land snail)	Prehistoric	Kirch, 1973
	Gastrocoptera pediculus (land snail)	Prehistoric	
Samoa: Ofu (Manu'a group)	*Assiminea* cf. *nitida* (land snail)	by 2450 B.P.	Hunt and Kirch, 1997; Kirch, 1993
	Lamillidea pusilla (land snail)	by 2450 B.P.	
	Gastrocopta pediculus (land snail)	by 2450 B.P.	
	Liardetia samoensis (land snail)	by 2450 B.P.	
	Lamellaxis gracilis (land snail)	by 2450 B.P.	
Solomon Islands: Tikopia	*Lamellidea pusilla* (land snail)	by 2850 B.P.	Christensen and Kirch, 1981; Kirch and Yen, 1982
	Gastrocopta pediculus (land snail)	by 2850 B.P.	
	Lamellaxis gracilis (land snail)	by 2850 B.P.	
	Liardetia samoensis (land snail)	by 550 B.P.	
	Wilhelminaia mathildae (land snail)	by 550 B.P.	
	Coneuplecta microconus (land snail)	by 550 B.P.	
Tahiti	*Lamellaxis gracilis* (land snail)	by 600 B.P.	Orliac, 1997
	Lamillidea pusilla (land snail)	by 600 B.P.	
	Lamellidea oblonga (land snail)	by 600 B.P.	
Tonga: Niuatoputapu	*Lamellaxis gracilis* (land snail)	by 1100 B.P.	Kirch, 1988
	Gastrocopta pediculus (land snail)	by 1100 B.P.	
	Lamillidea pusilla (land snail)	by 1100 B.P.	

Note. The translocation of species marked with an asterisk have been inferred from current distributions; areas are listed alphabetically.

Table III. A Sample of Vertebrate Translocations

Place	Taxon	Date	References
I. Caribbean			
Antigua	*Dasyprocta leporina* (Brazilian agouti)	500–900 B.P.	Wing *et al.*, 1968; agoutis were widely introduced into the Lesser Antilles from the South American mainland (Wing, 1993)
Dominican Republic	*Capromys pilorides* (Desmarest's hutia)	Prehistoric	Olson, 1982; Cuban native
Little Swan Island	*Geocapromys brownii* (Brown's hutia)	Prehistoric	Woods, 1989; inferred from distribution
Puerto Rico	*Isolobodon portoricensis* (Puerto Rican hutia)	Prehistoric	deFrance *et al.*, 1996; Olson, 1982; Olson and Pregill, 1982; Wing, 1993; Woods, 1990; extinct; Hispaniola native
San Salvador	*Geocapromys ingrahami* (Bahamian hutia)	Prehistoric	Morgan, 1989; Olson, 1982; Olson *et al.*, 1990; Wing, 1993
Virgin Islands	*Isolobodon portoricensis* (Puerto Rican hutia)	Prehistoric	deFrance *et al.*, 1996; Olson 1982; Olson and Pregill, 1982; Wing, 1993; Woods, 1990; extinct; Hispaniola native
Virgin Islands: St. Thomas, St. John, St. Croix, and Virgin Gorda (?)	*Nesotrichis debooyi* (extinct rail)	Prehistoric	Olson, 1974, 1977, 1982; Olson and Pregill, 1982; extinct; Puerto Rican native
II. Greenland	*Mus musculus* (house mouse)	Norse	McGovern *et al.*, 1983
III. Indonesia			
Moluccas: Gebe	*Dorcopsis muelleri* (brown dorcopsis)	7400 B.P.?	Flannery *et al.*, 1998
Timor	*Phalanger orientalis* (gray cuscus) *Macaca* sp. (macaque) cf. *Paradoxurus hermaphroditus* (Asian palm civet) *Rattus exulans* (Polynesian rat)	4500 B.P. ca. 4500 B.P. 4500 B.P. "late"	Glover, 1986

IV. Mediterranean			
Corsica	*Erinaceus europeaus* (western European hedgehog)	ca. 6000 B.P.	Blondel and Vigne, 1993; Vigne, 1987a,b, 1988, 1990, 1992; Vigne and Marinval-Vigne, 1990; Vigne and Valladas, 1996
	Apodemus sylvaticus (long-tailed field mouse)	ca. 6000 B.P.	
	Myoxus (=Glis) glis (fat dormouse)	ca. 6000 B.P.	
	Crocidura suaveolens (lesser shrew)	<2500 B.P.	
	Suncus etruscus (white-toothed pygmy shrew)	<2500 B.P.	
	Mus musculus (house mouse)	<2500 B.P.	
	Eliomys quercinus (garden dormouse)	<2500 B.P.	
	Rattus rattus (house rat)	ca. 2200 B.P.	
	Cervus elaphus (red deer)	ca. 1600 B.P.	
Crete	*Cervus elaphus* (red deer)	Late Neolithic	Payne, 1995; Reese, 1996
	Capra hircus (=aegagrus) (wild goat)	Late Neolithic	
	Crocidura suaveolens (lesser shrew)	Minoan	
	Suncus etruscus (white-toothed pygmy shrew)	Minoan	
	Dama dama (fallow deer)	Minoan	
	Apodemus mystacinus (broad-toothed field mouse)	Minoan	
	Mus cf. *musculus* (house mouse)	Minoan	
	Apodemus cf. *sylvaticus* (long-tailed field mouse)	Iron Age	
Cyprus	*Vulpes vulpes* (red fox)	Aceramic Neolithic	Davis, 1984, 1987, 1989, 1994; Schwartz, 1973; Steensma and Reese, 1999
	Felis silvestris (cat)	Aceramic Neolithic	
	Genetta cf. *plesictoides ?* (genet)	Aceramic Neolithic	
	Dama mesopotamica (Mesopotamian fallow deer)	Aceramic Neolithic	
V. North America			
Channel Islands: San Clemente, Santa Catalina, San Nicolas	*Urocyon littoralis* (island gray fox)	3880 – 2200 B.P.	Collins, 1991; Collins and George, 1990
Channel Islands: Santa Catalina, Santa Cruz	*Reithrodontomys megalotis* (western harvest mouse)	Prehistoric	Collins and George, 1990; prehistoric transport inferred from presence, morphology and genetics

(Continued)

Table III. (Continued)

Place	Taxon	Date	References
VI. Oceania			
Cook Islands: Mangaia	*Rattus exulans* (Polynesian rat)	by 1000 B.P.	Kirch *et al.*, 1995; Steadman and Kirch, 1990
Easter Island	*Rattus exulans* (Polynesian rat)		Dransfield *et al.*, 1984
Henderson Island	*Rattus exulans* (Polynesian rat)	A.D. 1283	Weisler, 1994
Marianas: Aguiguan	*Rattus exulans* (Polynesian rat)	ca. 1000 B.P.	Steadman, 1998; see also Pregill, 1998
Marianas: Rota	*Rattus exulans* (Polynesian rat)	ca. 1000 B.P.	Steadman, 1998; see also Pregill, 1998
Marianas: Tinian	*Rattus exulans* (Polynesian rat)	ca. 1000 B.P.	Steadman, 1998; see also Pregill, 1998
New Ireland	*Phalanger orientalis* (gray cuscus)	19,000 B.P.	Allen *et al.*, 1989; Flannery and White, 1991
	Thylogale brunii (dusky pademelon)	7000 B.P.	
	Rattus exulans (Polynesian rat)	3000 B.P.	
	Rattus praetor (spiny rat)	3000 B.P.	
New Zealand	*Rattus exulans* (Polynesian rat)	2000 B.P.	Holdaway, 1996, 1998, 1999a Holdaway and Beavan, 1999
Papua New Guinea: Manus Island	cf. *Echymipera kalubu* (Kalubu echymipera)	ca. 12000 B.P.	Frederickson *et al.*, 1993
Solomon Islands: Buka	*Phalanger orientalis* (gray cuscus)	by 9000 B.P.	Flannery *et al.*, 1988; Flannery andWickler, 1990; Wickler, 1990
	Rattus praetor (spiny rat)	1850 B.P.	
	Thylogale brunii (dusky pademelon)	ca. 1500 B.P.	
Solomon Islands: Nissan	*Phalanger orientalis* (gray cuscus)	>4300 B.P.	Flannery *et al.*, 1988
	Rattus exulans (Polynesian rat)	3100–2500 B.P.	
	Rattus praetor (spiny rat)	860 B.P.	
Solomon Islands: Tikopia	*Rattus exulans* (Polynesian rat)	by 2850 B.P.	Kirch and Yen, 1982
VII. Outer Hebrides	*Cervus elaphus ?* (red deer)	>2000 B.P.?	Serjeantson, 1990
VIII. South America			
Falkland Islands	*Dusicyon australis* (Falkland Island wolf)	Prehistoric	Buckland and Edwards, 1998; prehistoric translocation inferred from presence

Note: For extant mammals, scientific nomenclature follows Wilson and Reeder, 1993, and common names generally follow Wilson and Cole, 2000; a question mark after the scientific name indicates that an anthropogenic origin is uncertain; areas are listed alphabetically.

known archaeologically. Although the timing of its extinction is not known, it may have survived into historic times on both Puerto Rico and Virgin Gorda. In fact, the bird is not known archaeologically from Virgin Gorda; its possible prehistoric introduction here has been inferred from historic accounts of a flightless rail on the island (Olson, 1977; Olson and Pregill, 1982). Although other bird translocations are known—the scarlet macaw (*Ara macao*) in the late prehistoric southwest (Akins, 1985; Hargrave, 1970; Minnis *et al.*, 1993), for instance—this is the only securely documented instance of prehistoric interisland transport of live nondomesticated birds of which I am aware.

The very fact of these translocations raises a number of substantial issues, none of which can currently be resolved. For instance, the Polynesian rat was introduced by human colonists throughout much of the Pacific from a homeland in southeast Asia, either purposefully or accidentally or both (Holdaway, 1999a; Matisoo-Smith *et al.*, 1998; Roberts, 1991; Spenneman, 1997). The effect that this introduction had on native plants and animals is unclear, but it must have been substantial. Polynesian rats have been implicated in playing a role in the extinction of, among other things, snails, lizards, frogs, wrens, and other organisms on New Zealand (Brook, 1999; Holdaway, 1999b; Holdaway and Worthy, 1994; Towns and Daugherty, 1994); giant iguanas on Lifuka (Kingdom of Tonga; Pregill and Dye, 1989), bats on 'Eua (Kingdom of Tonga; Koopman and Steadman, 1995); birds throughout Polynesia, including Henderson Island (Wragg and Weisler, 1994), Huahine (Society Islands; Steadman, 1989a), Mangaia (Cook Islands; Steadman and Kirch, 1990), and Tikopia and Anuta (Solomon Islands; Steadman *et al.*, 1990b); and, the palm *Paschalococos disperta* on Easter Island (Dransfield *et al.*, 1984; Flenley, 1993; Uhl and Dransfield, 1999). By gnawing holes in coconuts, they are even known to increase breeding habitat for mosquitoes; 34 species of mosquitoes are known to breed in the liquid that is exposed in this way. Among them is *Aedes polynesiensis*, a vector for Bancroftian filiariasis, a disease known to have been present in Polynesia prehistorically (Martin and Combes, 1996; Rivière *et al.*, 1998).

Even when direct evidence for Polynesian rat predation on an extinct species is available, as with gnaw marks on the seeds of the extinct Easter Island palm (Flenley *et al.*, 1991; Flenley, 1993), it is not possible to know the exact role that these rodents played in the extinction of that species. That they decreased the richness of island biotas, however, cannot be doubted. For instance, while several species of the frog genus *Leiopelma* and the lizard genus *Cyclodina* became extinct on the New Zealand mainland after Polynesian rats were introduced, related forms still exist on nearby rat-free islands. In addition, lizard abundances have increased on nearby islands from which Polynesian rats have been removed, while the abundances of the tuatara

(*Sphenodon punctatus*) are lower on islands with Polynesian rats than they are on islands without them (Atkinson, 1996; Atkinson and Moller, 1990; Towns, 1994, 1996; Towns and Daugherty, 1994). Very similar observations have been made about a variety of other organisms, from insects to birds (see the review in Atkinson and Moller, 1990; Booth *et al.*, 1996; Clout and Mertin, 1998).

Known Polynesian rat impacts, however, are not limited to animals. By comparing vegetation on New Zealand-area islands with and without Polynesian rats, and, for those islands with rats, inside and outside of areas from which rats had been excluded, Campbell and Atkinson (1999) have shown that seed predation by these rodents has a substantial impact on the abundances of a subset of coastal trees. As a result, the presence of these animals can have an important effect on forest regeneration after disturbance by fire or any other mechanism. And, of course, by preying on tree seeds, insects, and other organisms, Polynesian rats are also competing with other organisms for food, just as they would have competed with moas in this realm.

Because of all this, even though it is not possible to document that the introduction of these rodents led to the extinction of any particular organism, there is no reason to doubt that the impact on the biotas of all islands to which they have been introduced has been substantial.

We know a great deal about the impact of introduced Polynesian rats on the flora and fauna of the New Zealand area. We know less about the potential prehistoric impact of other introduced organisms – hutias on the Virgin Islands, for instance, or foxes on the Channel Islands (see Table III). There is, however, little reason to believe that they would not have had some, and perhaps a major, impact on native plants and animals, either directly through predation, or indirectly, through such things as competition for resources or as a result of the introduction of diseases for which they served as vectors.

Chickens, for instance, were carried throughout much, though not all, of Oceania by human colonists. These birds are known to carry a wide variety of disease organisms, at least some of which can spread to native birds. On the Galápagos Islands, for instance, endemic mockingbirds and Darwin's finches are known to have been impacted by introduced avian pox, and infectious bronchitis (*Trichomonas gallinae*) has been detected in native Galápagos doves (Vargas and Snell, 1997). Steadman *et al.* (1990a) have shown a lack of protozoan parasites in a sample of birds from the Cook Islands, strongly suggesting that prehistoric bird extinctions here were not caused by such parasites, but other kinds of diseases remain possibilities and other places may not have been so fortunate.

Similarly, the brushtail possum (*Trichosurus vulpecula*), introduced historically into New Zealand, belongs to the same family as the gray cuscus, introduced prehistorically on a number of Pacific Islands (Table III). The brushtail possum is currently seen as one of the most problematic of New Zealand's translocated mammals, primarily because of its impact on native vegetation and also for a broad variety of other reasons (Cowan, 1990; King, 1990) Our knowledge of the secondary impacts of animals introduced by prehistoric people is very incomplete.

The introduction of animals by humans to islands can be relatively easy to detect. It must be shown that the animal involved was not present on the island prior to human colonization, that its arrival coincides with or occurred after human arrival, and that it is highly unlikely to have gotten there on its own. Such demonstrations have been made for the flightless rail *Nesotrichis debooyi* in the Caribbean, the gray cuscus in the Pacific, and the Polynesian rat throughout much of the same region. Polynesian rats, for instance, are not happy swimmers. They can stay afloat for less than 3 h in tropical waters, and less than 20 min in the waters of New Zealand (Atkinson and Moller, 1990; Storer, 1962)—hardly long enough to swim from island to island. And, although there is some slim chance that they reached an island by rafting or through some other extremely low-probability event, it is hardly likely to be coincidental that their arrival is almost always associated with human colonization. It is for this reason that the presence of Polynesian rats on New Zealand at ca. 2000 B.P. would almost certainly imply human contact at this time, even if the standard archaeological record does not begin for another 1,000 years or so (Higham *et al.*, 1999; Holdaway, 1996, 1998, 1999a; Holdaway and Beavan, 1999; but see also Anderson, 2000; Brook, 2000).

The translocation of nondomesticated animals in continental settings is also well-known archaeologically. Obvious examples are provided by the spread of the house rat (*Rattus rattus*) from its south Asian homeland (Armitage, 1994; Audoin-Rouzeau and Vigne, 1994), and, as discussed earlier, the movement of scarlet macaws into the late prehistoric American Southwest. The translocation of the European rabbit (*Oryctolagus cuniculus*) in multiple directions from its southwestern European homeland beginning in the later Holocene (Flux, 1994; Gibb, 1990; Rogers *et al.*, 1994) probably does not count, as the source populations are likely to have been domesticated, animals "whose ancestral home is a cage, not Spain" (Flux, 1994, p. 11).

The frequency with which such translocations may have occurred is unknown but they were likely common, especially given the frequency with which wild vertebrates are known to have been transported across the landscape ethnographically (e.g., Fowler, 1992; Nabhan, 2000; Wragg and

Weisler, 1994). As Wing (1993) has observed, the challenge is in detecting such translocations and in not confusing them with some other kind of biogeographic event. For biogeographers struggling to understand modern distributional data, the challenge lies in distinguishing disjunct distributions caused by either the loss of intervening populations (as with the pygmy cottontail *Brachylagus idahoensis* in arid western North America; see Grayson, 1977, 1987b, 1993; Lyman, 1991) or by "natural" dispersal (as with the cattle egret *Bubulcus ibis*; see Blake, 1977) from disjunctions caused by human transport—as, for instance, must have occurred with the distinctive ectoparasites of Caribbean hutias (Price and Timm, 1997).

Extinctions: Islands

In 1982, Olson and James documented that the Hawaiian Islands had seen massive bird extinctions during the relatively recent past (Olson and James, 1982a,b). Soon, they had shown that 44 of 68 species of landbirds known from fossil-bearing sites in Hawaii had become extinct, either globally or locally, during relatively recent times (Olson and James, 1984; for a more recent assessment, see James, 1995).

This demonstration documented that analyses of equilibrium island biogeographic theory that did not take history into account were, in Olson and James' words, "spurious" (1982a, p. 634), a conclusion that was soon broadened by Pregill (1986), Vigne (1987b, 1988, 1990), Balouet (1987) and others. In addition, many of the specimens from extinct species that they had described had been found in archaeological contexts. "The Polynesian residents," they concluded, "may have been responsible for the disappearance of more than half of the endemic avifauna of the Hawaiian Islands" (Olson and James, 1982a, p. 634). Three factors, they suggested, had caused these extinctions: direct predation by people; predation by Polynesian rats, dogs, and pigs that had been introduced by people; and massive vegetation changed caused by anthropogenic fires.

This general point had, of course, already been made from New Zealand; by 1982, it was well-known that prehistoric avian extinctions had removed not just moas but also a diverse assemblage of small birds (e.g., Fleming, 1962b). As a result, and as Olson and James (1984) noted, the real significance of their work, beyond its biogeographic implications, was the suggestion that prehistoric anthropogenic bird extinctions in Oceania had extended well beyond New Zealand.

Olson and James' work did have evident weaknesses. They had not provided detailed descriptions of the fossils on which their conclusions were based, a weakness that was soon remedied (Olson and James, 1991a,b). In addition, their work did not provide an adequate chronology, either absolute (they had available only a few radiocarbon dates) or relative (they provided no detailed stratigraphic information on the sites that had provided their specimens). As a result, what they had essentially done was to provide a set of important assertions about the Polynesian past, assertions that were now very much in need of confirmation.

That confirmation soon followed. On Mangaia (Cook Islands), Kirch and his colleagues have shown that 13 of 17 species of landbirds known from archaeological deposits no longer occur on the island (Kirch, 1997a,c; Kirch *et al.*, 1995; Steadman, 1985; Steadman and Kirch, 1990). On Henderson Island, Wragg and Weisler (1994; see also Weisler, 1994), following on earlier work by Steadman and Olson (1985) and Schubel and Steadman (1989), have shown that 5 of 9 species of landbirds known from archaeological contexts are at least locally extinct. On Tahuata (Marquesas Islands), the numbers are 7 and 10, respectively (Rollett, 1998; see also Rolett, 1992; Steadman and Rollett, 1996); on Huahine (Society Islands), 10 and 15 (Steadman, 1997a). Results of this sort are now known from many islands in Oceania (see Table IV and the review by Steadman, 1995).

Table IV certainly exaggerates the magnitude of prehistoric anthropogenic landbird extinction that actually occurred in Oceania. I have not included the number of species of landbirds known on these islands today that are unknown archaeologically, although this is often done (e.g., Balouet and Olson, 1989; Steadman and Olson, 1985). In addition, and as Watters (1989) has appropriately noted for the Lesser Antilles, some of the species involved may have succumbed after European contact had occurred. Some of the birds recorded archaeologically may have been introduced by people, a phenomenon well documented ethnographically in this region (Rinke, 1989; Wragg and Weisler, 1994). It is also possible that some of these birds arrived on their own while the archaeological record was accumulating but failed to become established for reasons unrelated to the human presence. Such colonization events are well documented for oceanic islands (e.g., Diamond, 1975, pp. 377–378; see also Steadman, 1986, p. 87 for recent bird arrivals on Isla Floreana, Galápagos, and Fleming, 1962a, for recent arrivals on New Zealand).

Nonetheless, bird extinctions clearly increased substantially in Oceania after human colonization. One obvious way to test for the interrelationship between human colonization and bird extinction in this setting is by examining fossil avifaunas from islands that saw no significant pre-European human occupation, and Steadman (1986; see also Steadman *et al.*, 1991) has done just this on Floreana Island, in the Galápagos. His cave excavations on this

Table IV. A Sample of Landbird Extinctions on Oceanic Islands

Island	Number of archaeological landbird species	Number extinct or extirpated	References
I. With prehistoric human occupation			
Cook Islands: Mangaia	17	13	Kirch *et al.*, 1995; Steadman, 1985, 1995, 1997a; Steadman and Kirch, 1990
Easter Island	6	6	Steadman, 1995
Hawaiian Islands: Hawaii	16	5	Olson and James, 1982a,b, 1984, 1991a,b
Hawaiian Islands: Kauai	23	13	Olson and James, 1982a,b, 1984, 1991a,b
Hawaiian Islands: Maui	37	29	Olson and James, 1982a,b, 1984, 1991a,b
Hawaiian Islands: Molokai	23	19	Olson and James, 1982a,b, 1984, 1991a,b
Hawaiian Islands: Oahu	35	23	Olson and James, 1982a,b, 1984, 1991a,b
Henderson	10	6	Wragg and Weisler, 1994; see also Steadman and Olson, 1985; Schubel and Steadman, 1989; Weisler, 1994
Mariana Islands: Aguiguan	9	2	Steadman, 1999
Mariana Islands: Rota	20	14	Steadman, 1999
Mariana Islands: Tinian	15	8	Steadman, 1999
Marquesas: Hiva Oa	7	7	Rolett, 1998; Steadman and Rollett, 1996
Marquesas: Nuku Hiva	9	6	Rolett, 1998; Steadman and Rollett, 1996
Marquesas: Tahuata	10	7	Rolett, 1992, 1998; Steadman and Rollett, 1996
Marquesas: Ua Huka	15	13	Rolett, 1998; Steadman, 1997a; Steadman and Rollett, 1996
New Caledonia	27	11	Balouet, 1987; Balouet and Olson, 1989; does not include passerines
New Zealand	93	32	Worthy, 1999; see also Holdaway, 1989
Society Islands: Huahine	15	10	Steadman, 1989a, 1997a
Solomon Islands: Anuta	3	0	Steadman *et al.*, 1990b
Solomon Islands: Tikopia	10	2	Steadman *et al.*, 1990b
Tonga: ’Eua	26	14	Steadman, 1993, 1995
Tonga: Lifuka	7	5	Steadman, 1989c
II. Without prehistoric human occupation			
Galápagos: Isla Floreana	14	1?	Steadman, 1986

island provided him with the remains of 18 species of birds of late Holocene age. Of these 18 species, 4 are now extinct. Of those 4, 3 are known to have been present historically, and the fourth was probably present as well. That is, Steadman's work here has shown that in the absence of people prior to the arrival of Europeans, the Floreana late Holocene avifauna was also marked by an absence of extinction.

These demonstrations are important for a number of reasons. First, and just as Olson and James (1982a) argued, they show that tests of certain kinds of biogeographic theory are not likely to produce trustworthy results if deeper history is not taken into account, a point also made by the translocation literature (Blondel and Vigne, 1993; Flannery and White, 1991; Vigne, 1988, 1990, 1992). Second, they document how significant the impact of human colonization can be on island faunas. Third, and as both Steadman and Olson have cogently argued on a number of occasions (e.g., Steadman, 1989b, 1999; Steadman and Olson, 1985), the anthropogenic nature of these extinctions has critically important conservation implications. They strongly suggest, for instance, that the reintroduction of species of birds on islands where they can be shown to have once occurred might well be successful if appropriate steps are taken to minimize human impacts after the reintroduction has been made.

What might these anthropogenic impacts be? Here I can do little more than repeat the widespread agreement, already noted in my discussion of moa extinctions, that these losses were caused by some combination of human hunting, habitat destruction caused by fire and other means, and the effects of introduced rats, pigs, dogs, and, perhaps, chickens, the last by carrying communicable avian diseases (e.g., James *et al.*, 1987). As Steadman (1999, p. 319) has noted, the extinctions were quite clearly due to "prehistoric human activities, including habitat alteration, direct predation, and predation from introduced vertebrates," to, as Holdaway (1989, p. 18) has observed for New Zealand, "the manifold effects of human colonization."

Of course, it is not just islands that have seen the arrival of human hunters, the introduction of human commensals and domesticates, and anthropogenic burning. Prehistoric, and often deeply prehistoric, burning has been observed throughout the world (Table V). Dogs are virtually ubiquitous. Some 10,000 years of prehistoric human hunting in North America is not associated with widespread extinction (discussed later), and dogs were presumably present throughout this period of time (Morey, 1996). In the Great Basin of the western United States, human population densities fell dramatically during the very dry Middle Holocene, but when this region was recolonized some 5,000 years ago, extinctions did not follow (Grayson, 2000a). Why islands?

Table V. A Sample of Anthropogenic Burning Hypothesized From Archaeological Data, Emphasizing Burning Attributed to Early Human Occupations of a Given Area

Place	Onset	References
I. Australia		
New South Wales	ca. 128,000 B.P.	Singh and Geissler, 1985; Walker and Singh, 1993; but see Head, 1989; Horton, 1982
Queensland	ca. 38,000 B.P.	Kershaw, 1986
Tasmania	7200 B.P.	MacPhail, 1984
II. Europe		
Scotland: Western and Northern Isles	12,400 B.P. ? 8000–6000 B.P.	Edwards, 1996; Edwards and Mithen, 1995; but see also Macklin *et al.*, 2000; Tipping, 1996
Ireland	3500 B.P.	O'Connell *et al.*, 1988
British Uplands	7000 B.P.	Caseldine and Hatton, 1993
III. Madagascar	1900 B.P.	Burney 1987a,b, 1993, 1997a
IV. North Atlantic		
Iceland	A.D. 900	Buckland *et al.*, 1995; Smith, 1995
Greenland	ca. A.D. 1000	Fredskild, 1988
V. Oceania		
Cook Islands: Mangaia	2500 B.P.	Kirch, 1997a; Kirch *et al.*, 1992; Kirch and Ellison, 1994
Easter Island	1630 B.P.	Flenley, 1996; see also Flenley, 1993, 1998; Flenley and King, 1994; Bahn and Flenley, 1992; for opposing views, see Hunter-Anderson, 1998 and Orliac and Orliac, 1998
Hawai'i: O'ahu	1100 B.P.	Athens, 1997
Mo'orea	1400–900 B.P.	Lepofsky *et al.*, 1996
New Guinea: Irian Jaya	28,000–25,000 B.P.	Haberle *et al.*, 1991

New Guinea: Papua New Guinea	32,000–28,000 B.P.	Hope, 1982; Hope and Golson, 1995
New Zealand: North Island	700–450 B.P.	Horrocks and Ogden, 1998, 2000; Newnham *et al.*, 1998a,b; Wilmshurst, 1997; Wilmshurst *et al.*, 1999; see also McGlone, 1983
New Zealand: South Island	1000–800 B.P.	Anderson and McGlone, 1992; Burrows and Russell, 1990; McGlone *et al.*, 1994, 1996; McGlone and Wilmshurst, 1999; see also McGlone, 1983
Yap	3300 B.P.?	Dodson and Intoh, 1999
VI. South America		
Chile: Isla de Chiloé	>49,700 B.P.	Heusser, 1994; but see also Markgraf, 1993a,b; Markgraf *et al.*, 1996
Chile: Isla Grande de Tierra del Fuego	13,280 B.P.	Heusser, 1994; but see also Markgraf, 1993a,b; Markgraf *et al.*, 1996
Chile: Tagua Tagua	ca. 11,000 B.P. 45,000 B.P.	Heusser, 1983, 1990, 1994; but see also Markgraf, 1993a,b; Markgraf *et al.*, 1996
Chile: Torres del Paine	11,000 B.P.	Heusser, 1987, 1994; but see also Markgraf, 1993a,b; and Markgraf *et al.*, 1996
Falkland Islands	ca. 4500 B.P.	Buckland and Edwards, 1998
Panama	11,000 B.P.	Cooke *et al.*, 1996; Pearsall 1995; Pearsall *et al.*, 1990; Piperno *et al.*, 1991a,b; see also Haberle and Ledru, 2001

Note. Areas are listed alphabetically.

The answer is obvious. As Steadman (1989b, p., 178) has carefully observed, island birds are vulnerable because they have relatively small population sizes, are confined to well-delineated areas of land that may undergo rapid environmental change, and have likely lost, and in some cases have clearly lost, the mechanisms needed to cope successfully with introduced predators, pathogens, and competitors. Because of all this, Steadman (1997a) has noted, insular faunas and floras are even more readily depleted on low, small islands than they are on high, large ones. To the factors mentioned by Steadman, we can add the fact that the isolated nature of islands means that there is no ready source of conspecific individuals to replenish dwindling populations, one of the fundamental precepts of island biogeographic theory (Brown, 1995; MacArthur, 1972; MacArthur and Wilson, 1967; Rosenzweig, 1995). These phenomena are, of course, well-recognized (e.g., Dewar, 1997a; Enright and Gosden, 1992; Kirch and Ellison, 1994; Rolett, 1998; Paulay, 1994). While we may not be able to pinpoint the exact cause of extinction of any animal on any island (James *et al.*, 1987), we most certainly can conclude with Steadman *et al.* (1991, p. 126) that "animals on oceanic islands tend to be more vulnerable to extinction or extirpation than their continental counterparts" and, with Paulay (1994, p. 134), that island faunas are "among the most vulnerable in the world." It is this fact that makes their postcolonization extinction records so pronounced. Thus, it is not at all surprising that while I have emphasized Oceania in my discussion, other islands show very similar patterns, including the West Indies (Morgan and Woods, 1986; Steadman *et al.*, 1984; Woods, 1989, 1990; Woods and Eisenberg, 1989), Madagascar (Burney, 1997b, 1999; Dewar, 1997a,b), Corsica (Blondel and Vigne, 1993; Vigne, 1987a,b, 1988, 1990, 1992; Vigne and Marinval-Vigne, 1990; Vigne and Valladas, 1996), and other Mediterranean islands (Alcover *et al.*, 1999). Even if the argument that human predation caused the extinction of the pygmy hippopotamus (*Phanourios minutus*) on Cyprus (Hadjisterkotis *et al.*, 2000; Simmons, 1999) is not compelling (Binford, 2000; Bunimovitz and Barkai, 1996; Grayson, 2000b; Vigne, 1996), this is precisely the kind of place where anthropogenic extinctions of this sort are to be expected, just as Simmons (1999) has argued.

Extinction: Continents

While Oceania may provide compelling evidence for massive prehistoric vertebrate extinctions due to human colonization, it is not the most widely discussed of such colonization-driven losses. That honor is shared by North America and Australia.

North America

In North America, some 35 genera of primarily large mammals became extinct toward the end of the Pleistocene, with the extinctions over by about 10,500 years ago. The array of mammals involved was astounding, including four genera of huge ground sloths, two perissodactyls (horses and tapirs), two tayassuids (peccaries), two cervids (deer-like animals), three antilocaprids (animals related to modern pronghorns), a whole suite of carnivores (the dhole, two bears, three cats, and a skunk), a rabbit, and, of course, the mammoth and mastodon (see the review in Grayson, 1991b).

There is an enormous literature on the causes of these extinctions, one that continues to grow (e.g., MacPhee and Marx, 1997; Martin and Steadman, 1999), and one that extends back to the beginning of the nineteenth century. Indeed, the discipline of vertebrate paleontology emerged with the explanation of these, and related European, extinctions as one of its core problems (Grayson, 1983, 1984b).

Today, there are two prime explanations of the North American losses: climate change (e.g., Graham and Lundelius, 1984) and human predation (e.g., Martin, 1967, 1984; Martin and Steadman, 1999). MacPhee and Marx (1997) have recently suggested that the extinctions may have been driven by a hyperlethal disease, but this intriguing hypothesis is still in its formative stages and will not be discussed in detail here.

The most famous of these explanations is provided by Martin's "overkill hypothesis," which pins the North American extinctions squarely on the initial human colonizers of this region. This is an argument that has been widely accepted by superb ecologists whose research focuses on contemporary organisms, often in other parts of the world (e.g., Alvard, 1994, 1998b; Balée, 1993; Brown and MacDonald, 1995, 1997; Diamond, 1984, 1986, 1989; Rosenzweig, 1995). It is also an argument that most scientists fully versed in the relevant archaeology and paleontology firmly reject (e.g., Graham and Lundelius, 1984; Guthrie, 1984; Kelly and Todd, 1988; Meltzer, 1995). It is no accident that Martin's recent list of scientists who support the North American overkill model includes no archaeologist or paleontologist who specializes in this realm (Martin and Burney, 1999). To understand why this is the case requires a brief discussion of the issues involved.

No one involved in the debate questions that the extinctions were functionally over by 10,500 years ago. Thus, it is intriguing, though not necessarily relevant, that the earliest well-dated North American cultural complex, Clovis, dates to between about 11,300 and 10,800 years ago (the earliest well-dated New World archaeology, however, is much older; see Dillehay, 1997; Meltzer *et al.*, 1997).

Clovis is marked not just by a distinctive, fluted projectile point, but also by the fact that Clovis artifacts have been found associated with mammoth in over a dozen sites scattered across the Plains and the southwestern United States. While some of these mammoths may have been scavenged, there is no convincing reason to doubt that Clovis peoples had the behavioral and technological wherewithal to hunt mammoth successfully (Haynes, 1991).

As developed in detail by Martin (1967, 1984; Martin and Steadman, 1999), the overkill hypothesis combines the apparent magnitude and chronology of the North American extinctions with the presence of Clovis, observes that the human colonization of islands has routinely been followed by extinctions, and concludes that the human colonization of North America caused extinctions here as well. This is an argument that may make intuitive sense. We all know that human hunters can at least cause local extinctions in continental settings (e.g., Bodmer *et al.*, 1997), and Winterhalder and Lu (1997), using a simulation derived from foraging theoretic principles, have shown that some versions of the overkill hypothesis are at least conceptually plausible. In fact, the intuitively pleasing nature of the hypothesis would seem to go far toward explaining its acceptance by so many who are not expert in this time and place.

Others, as I have noted, reject the hypothesis firmly. There are many reasons for this, but two loom largest, and have done so for quite some time (Grayson, 1984a, 1989, 1991b; Hester, 1967).

It is important to stress that these reasons do not include apparent conflicts between Martin's firm acceptance of Clovis as representing the earliest human colonization of the New World and developing evidence that it does not. Referring to the famous Monte Verde site (Dillehay, 1989, 1997), located some 16,000 km south of the Bering Land Bridge, Martin and Steadman (1999, p. 34) observed that the overkill model "loses credibility. . .if humans in Chile lived in houses covered with skins of gomphotheres over 1000 years before proboscideans became extinct in North America." Although they called for independent verification of the claim that this site is 12,500 years old, this verification had been provided by an international team of scholars well before Martin and Steadman (1999) had appeared in print (see Meltzer, 1997; Meltzer *et al.*, 1997).

It is surprising that this verification was not discussed by Martin and Steadman (1999), given that they discussed research published as recently as 1999 (e.g., Miller *et al.*, 1999; O'Connell and Allen, 1998), and that the Monte Verde verification was so well-publicized that Martin could hardly have been unaware of it. The reason may relate to the disdain that Martin has shown for the search for pre-Clovis sites in the New World, an effort he has criticized as "something less than serious science, akin to the ever popular search for 'Big Foot' or the 'Loch Ness Monster'" (Martin 1999, p. 278), suggesting that this entire realm is out-of-bounds for him.

While Martin and Steadman's lack of recognition of the Monte Verde verification is surprising, what is even more surprising is their statement that this would matter at all. Martin has been carefully covering this eventuality for decades. In 1967, he noted that "the possibility that *Homo sapiens* spread into the Americas long before the late-glacial by no means eliminates the hypothesis of overkill" (Martin, 1967, p. 101), and, in 1984, that "whether or not prehistoric people were in the Americas earlier, 11,000 B.P. is the time of unmistakable appearance of Paleo-Indian hunters using distinctive projectile points" (Martin, 1984, p. 363). As a result, it is hard to see that a dozen Monte Verdes, with a tool kit poor in projectile points and a diet apparently rich in plant foods (Dillehay, 1997), could possibly make a difference (see the discussion in Grayson, 1984a). Only the discovery of Clovis-like hunting implements thousands of years before the extinctions had ended has not been covered, and this is a discovery no one expects. As a result, the chronology of the human colonization of the Americas poses far less of a problem for the overkill hypothesis than do other matters.

First, the hypothesis requires that early Americans hunted a diverse variety of now-extinct mammals in substantial numbers. This would in turn seem to require that we have some evidence of that hunting (as we do in New Zealand for moas), but such evidence exists only for mammoth and, far less securely, for mastodon. There is no evidence that people hunted, or even scavenged, any of the other ungulates—or sloths, dayspodids, glyptodonts, or rodents. Just as important, this lack of evidence does not seem to result from some sampling fluke. Horses and camels are extremely well represented in the late Pleistocene paleontological record of North America, but there are no kill sites for them.

Martin, of course, is well aware of this, and has long argued that the extinctions occurred so quickly that associations with people are not to be expected (Martin, 1984; Martin and Steadman, 1999; Mosimann and Martin, 1975). Even if the rapidity of the hypothesized overkill process could somehow account for this scarcity, however, it could not account for the fact that such sites are convincingly available only for mammoth (Grayson, 1984c). To help explain why "the archaeology of extinction is obscure" (Martin and Steadman, 1999, p. 359) and why archaeological associations with extinct mammals are not to be expected, Martin and Steadman (1999, p. 26) note that it is only on New Zealand and "some islands in the Polynesian heartland" that such associations have been documented.

However, the remains of now-extinct birds and other organisms have been found in archaeological contexts on island after island in Oceania and elsewhere. The anthropogenic nature of these extinctions, and the possible role that direct human predation may have played in causing them, has been accepted because of this evidence, not in spite of the lack of it. It is thus not unreasonable that Steadman (1989c, p. 539) gave the name *Megapodius alimentum* to a new species of large, extinct megapode from archaeological deposits in Lifuka, with the name *alimentum* referring "to the presumed eating of this species by the early Tongans who deposited their bones at Tongoleleka." On the other side of the world, Steadman *et al.* (1984, p. 4450) strengthened their argument for human-driven extinctions in Antigua by observing "bones that are charred or broken in a manner indicative of human consumption." Statements of this sort are common in the island literature (e.g., Kirch *et al.*, 1995, p. 56; Olson and James, 1982a, p. 634; Rolett, 1998, p. 104). Any appeal to the better preservation afforded by the relative recency of these sites fails in the face of the rich faunas found in late Pleistocene archaeological sites ranging from France (e.g., Audouze and Enloe, 1997; Costamagno, 1999) to Tasmania (e.g., Cosgrove, 1999).

Perhaps, as Owen-Smith (1987; see also Owen-Smith, 1999) has argued, it was the cascading ecological impact of the human-caused demise of the largest of the herbivores that led to the extinction of all the others. If this were the case, mammoth and mastodon must have become extinct, or at least significantly diminished in number, before the others (the third megaherbivore noted by Owen-Smith, the ground sloth *Eremotherium*, was confined to the far southeast). Not only is there no evidence of this, but the available radiocarbon chronology, including a rich new set of unpublished dates (R. W. Graham, personal communication), suggests that mammoth and mastodon were among the last to go.

Worse, it cannot even be shown that a majority of the extinctions occurred during Clovis times, providing a second fundamental empirical problem for the overkill hypothesis. Of the 35 or so genera, only 15 can be shown to have survived after 12,000 years ago and thus into Clovis times. In western Europe, blessed with numerous well-stratified and carefully excavated paleontological and archaeological sites that span the latest Pleistocene, late Ice Age extinctions were staggered in time and space, closely reflecting the climate and glacial history of this region (Delpech, 1999; Stuart, 1999). Because no comparable suite of sites is available for North America, there is no comparable chronology here. For 30 years, it has been assumed that since some genera can be shown to have become extinct around 11,000 years ago, all genera became extinct at that time throughout North America. This is an enormous assumption and one that has framed the nature of the debate since 1967 (Grayson, 1991b), even though there is no compelling evidence that North American late Pleistocene extinctions were not just as, or more, staggered in time and space as were the European ones.

Because some of my earlier work in this area stressed the significant unknowns in the North American extinctions chronology (Grayson, 1987a, 1989, 1991a,b), Martin and Steadman (1999, p. 34) have asserted that I am a proponent of "a gradual extinction," but this is not at all the case. My point has been not that the extinctions were necessarily gradual, but that we do not know when a majority of them occurred and that we should not assume, as Martin does, that they all occurred at about 11,000 years ago. To take but one example, Martin and Steadman (1999, p. 34) suggest that the extinct *Aztlanolagus* was "large enough" to have been terminated by human predation during Clovis times. However, there is no compelling evidence that this "pygmy-sized leporid" (Russell and Harris, 1986, p. 636) survived the glacial maximum. While U-Bar Cave in New Mexico contains specimens stratigraphically dated to as late as ca. 13,000 B.P., this site was excavated in arbitrary levels, contains deposits that are full-glacial in age, and was demonstrably mixed (Harris, 1989). Russell and Harris (1986) suggested that the animal may not have survived the full-glacial, and there is not much to suggest otherwise. A possible 10,000-year gap between *Aztlanolagus* and Clovis would appear to be problematic, and that is my point.

These are not the only difficulties confronting the North American version of the overkill hypothesis. The relentless focus on large mammals may trick the unwary into thinking that other organisms were unaffected by whatever it was that caused the extinction of so many large vertebrates. However, the North American latest Pleistocene was also a time of dramatic alterations in the ranges of many small mammals (FAUNMAP Working Group, 1994, 1996; Stafford *et al.*, 1999) and saw the extinction of at least one plant species, the spruce *Picea critchfieldii* (Jackson and Overpeck, 2000; Jackson and Weng, 1999). These changes are attributed without controversy to terminal Pleistocene climate fluctuations and attendant massive reorganization of biotic communities. They are also at least broadly coeval with the vertebrate extinctions at issue here. These conjunctions point directly at climate change as the driving mechanism, but the North American overkill hypothesis requires that the extinctions be removed from this more general biotic context and thus makes them appear inexplicable in ways other than those suggested by Martin.

If the overkill hypothesis is confronted by what would seem to be overwhelming empirical difficulties and has as a result been rejected by most scientists with the relevant expertise, why has it not been rejected by all scientists? That it has not been so rejected is, perhaps, the most interesting remaining aspect of the overkill position.

The overkill hypothesis has survived for several reasons. First, it has been clear for quite some time that restatements of the hypothesis are not being made for the experts who have rejected it, but instead to convince those who are consumers, not producers, of information dealing with this period of time. This is made clear by the fact that adherents of the overkill notion generally ignore the problems that confront it. It is for this reason that the nature of the argument has not changed since it was first made in a coherent way in 1967 (Martin, 1967). The same pieces that drove the argument at that time continue to drive it now. The extinctions occurred 11,000 years ago; Clovis peoples were the first to enter North America, about 11,000 years ago; Clovis people were hunters who preyed on a diverse set of now-extinct large mammals; we know from the records provided by islands that human colonists cause extinctions; therefore, Clovis caused extinctions. Rather than responding in detail to strong critiques, these pieces have simply been repeated over and over, with details updated, across the years (e.g., Martin, 1967, 1984, 1990; Martin and Steadman, 1999).

Of course, as I have said, we do not know that all the extinctions occurred at 11,000 years ago; there is much earlier New World archaeology than Clovis; there is no secure evidence that Clovis people hunted any now-extinct mammal other than mammoth. We do, however, know from island records that human colonists caused extinction in isolated, tightly-bounded settings, and every version of the overkill argument across the years has stressed this fact. It is fascinating to realize how many scientists who have accepted the overkill argument have expertise, and often profound expertise, in island biogeography: Diamond (1984, 1986, 1989) and Brown (Brown and MacDonald, 1995, 1997) are just two of them. It is clear that the magnitude of anthropogenic extinctions on islands has made these scientists very willing to accept that the same processes must have been at work in North America 11,000 years ago.

Islands are fundamentally different from continents but even those who work in island contexts and explicitly recognize that the two settings are not comparable compare them anyway. Steadman provides a superb example. On the one hand, he observes how very prone island biotas are to extinction (Steadman, 1989b, 1997a), that animals on islands are more prone to extinction than are those on continents no matter what the cause (Steadman *et al.*, 1991), and that island extinctions resulted from "habitat alteration, direct predation, and predation from introduced vertebrates" (1999, p. 319). On the other, he depends heavily on those same island extinctions to argue for overkill in continental North America, where, with the exception of mammoth kill sites, none of these things has been documented (Martin and Steadman, 1999). Steadman is not alone in this. For instance, while Paulay (1994, p. 134) notes that island biotas are "among the most vulnerable in the world," he at the same time concludes that "similarities between insular bird extinctions and the late Quaternary demise of continental vertebrate megafaunas lends [*sic*] strong support to the interpretation that the latter were also human-caused" (1994, p. 141). That is, the overkill argument has gained a significant amount of its support by comparing the incomparable.

If the overkill hypothesis continues to survive primarily by repetition of its core assertions, by side-stepping empirical evidence that strongly suggests that it is incorrect, by depending heavily on comparing spatial contexts that its own adherents have explicitly noted are not comparable, and has won little support from experts in the North American empirical records involved, then it might be reasonable to wonder if the description "hypothesis" is appropriate. After all, hypotheses are formulated to be tested; that is one of the attributes that makes them part of the scientific process.

In fact, it might be better to refer to this argument as the "overkill credo," a five-part statement of faith rather than an appeal to scientific reason. It is also a statement with striking chronological connections to the environmental movement, having been introduced in its current form in 1967, a time when human impacts on the biosphere were coming to be of heightened concern. Temporally wedged between *Silent Spring* (Carson, 1962) and *The Population Bomb* (Ehrlich, 1968), Martin's "Prehistoric Overkill" (Martin, 1967) caught the environmental wave that helped launch the Environmental Defense Fund in 1967 (Taylor, 1989), the U.S. National Environmental Policy Act in 1969, and Earth Day in 1970 (Baden, 1980). While the initial presentation of the overkill hypothesis was good and productive science, its history since that time suggests that it has become something more akin to a faith-based policy statement than to a scientific statement about the past. The overkill credo thus survives in spite of the lack of support it receives from the archaeological and paleontological record of North America. The support it does receive stems primarily from comparing islands to continents and from the belief systems of the descendants of the Europeans who colonized this region long after the arrival of the people implicated by the credo.

Australia

The Australian situation shares significant attributes with the American one. Extinctions were massive, with some 28 genera of primarily large reptiles, birds, and mammals lost (Flannery and Roberts, 1999). In addition, Martin (1967, 1984) has long argued that these disappearances were due to predation by expanding human colonists, a view that has gained some adherents (e.g., Flannery, 1994), but kill sites are even rarer here than they are in North America (e.g., Allen, 1997; Choquenot and Bowman, 1998; Miller *et al.*, 1999; O'Connell, 2000). In fact, there are none.

There are, however, significant dissimilarities as well. The extinctions chronology for Australia is extremely weak. With the possible exception of the large, flightless bird *Genyornis newtoni*, which has terminal dates of 40,000–50,000 B.P. in east-central Australia (Miller *et al.*, 1999), it is not known when the losses occurred (Flannery and Roberts, 1999). It is also not known when people first reached Australia. Although estimates focus on 40,000 to 50,000 B.P., the timing of the human colonization of Australia is as hotly debated as it is for the New World (Bowler and Magee, 2000; O'Connell and Allen, 1998; Turney *et al.*, 2001).

If it is not known when the animals became extinct or when people entered Australia, then any attempt to explain the extinctions is bound to be even more speculative than it is in North America. All participants in the debate over the cause of the Australian extinctions recognize this, including Martin (e.g., Martin and Steadman, 1999). In addition, and perhaps in part as a result, multivariate hypotheses are being seriously considered. Miller *et al.* (1999, p. 208), for instance, suggest that the extinction of *G. newtoni* may have been due to a combination of human-induced vegetational change (through burning), climate change, and human predation.

Such hypotheses remain out of favor in North America. While it remains true that there are important strategic reasons for this (Grayson, 1984a), it is also true that there is no evidence for significant, colonization-linked anthropogenic impacts on North American vegetation of the sort that are so evident in such places as New Zealand, Hawaii (Athens, 1997), Mangaia (Kirch, 1997a,b), Yap (Dodson and Intoh, 1999), Easter Island (Flenley, 1996), Mo'orea (Lepofsky *et al.*, 1996), and Australia (Kershaw, 1986). In southern South America, Heusser (1983, 1987, 1990, 1994) has attributed an increase in charcoal particle abundance in latest Pleistocene pollen cores to anthropogenic burning, and evidence is accumulating for increased terminal Pleistocene fire frequencies not only in this area (Moreno, 2000), but in northern South America and Central America as well (Haberle and Ledru, 2001; Hansen and Rodbell, 1995; Piperno *et al.*, 1991a). Markgraf (1993a,b; Markgraf *et al.*, 1996) finds the more southerly increases far more likely to be climatically induced, a conclusion similar to that reached by Hansen and Rodbell (1995) for the eastern Peruvian Andes. As Haberle and Ledru (2001, p. 101) note, however, the chronological coincidence between human arrival and climatic variability can make separating these two possible causes problematic. There is, however, no suggestion of widespread anthropogenic vegetational change in North America during Clovis times.

Closing Notes on Overkill

The human colonization of the world's islands led to widespread vertebrate extinction. This did not occur simply as a result of human hunting. No one has ever securely documented the prehistoric extinction of any vertebrate as a result of human predation alone, though this may certainly have happened. Instead, these island extinctions occurred as a result of drastic changes to the landscape on which those vertebrates depended, changes that included hunting but that also included vegetational change due to burning or other forms of clearing, and the introduction of a wide range of predators and competitors. No such massive, anthropogenic changes are associated with the colonization of the New World. While the overkill notion as applied to North America may be intuitively pleasing and conceptually convenient, there is no reason to believe that the early peoples of North America did what the argument says they did. All this makes sense only if the overkill position is seen as a statement of faith. As such, it makes a good deal of sense indeed.

Resource Competition

"A bird so familiar as the Bluebird needs no introduction," wrote Frank Chapman in 1895 of the Eastern Bluebird (*Sialia sialis*), "he seems so at home in our orchards and gardens or about our dwellings" (1895, p. 403). Sixty years later, however, these birds were not common at all (Adkisson, 1988; Elton, 1958; Gowaty and Plisner, 1998), in large part because of competition over nesting cavities with two introduced European species, the house sparrow (*Passer domesticus*) and the European starling (*Sturnis vulgaris*). This phenomenon differs little from the decline in the abundance of cave-dwelling fruit bats that followed the human occupation of Gua Siti Nafisah Cave on Halmahera (North Moluccas, Indonesia) some 5,100 years ago (Flannery *et al.*, 1995).

In 1958, Bjorn Kurtén observed that the fossil remains of cave bears (*Ursus spelaeus*) declined significantly in number as morphologically modern humans entered the European archaeological record. Neanderthals, he suggested, did not have any dramatic impact on cave bear populations, "but the invasion of Aurignac Man and the subsequent increase of human populations" (1958, p. 48) led to the exclusion of cave bears from their winter denning sites. Ultimately, cave bear populations dwindled and became fragmented. Extinction was the end result. Kurtén had abandoned this interesting argument by 1968, in the face of Kowalski's observation that cave bears also became extinct in areas that showed no Paleolithic occupation at all (Kowalski, 1967; Kurtén, 1968).

Even though it might be true that these bears dwindled in the absence of a human presence, it is also true that there is a negative correlation between the intensity of human occupation within Eurasian Pleistocene caves and the degree to which those caves contain the remains of cave bears (e.g., Stiner *et al.*, 1998; Straus, 1982). Although Kowalski was likely correct in suggesting that there was no reason to think that cave bears denned only in caves, there is also no reason to think that the increasing loss of caves as hibernaculae would have had no impact on the health of their populations. Eastern bluebirds have recovered in part because of nesting box programs, but there is little reason to think that Paleolithic peoples would have been equally solicitous of huge carnivores. Perhaps Kurtén's original argument merits resurrection (Grayson and Delpech, in press).

The kind of sequence Kurtén had in mind when he made this argument, albeit a sequence much more detailed than was available to him in the 1950s, is shown in Fig. 7. This figure shows the ratio of cave bears to ungulate specimens through time at Grotte XVI, in the Dordogne region of southwestern France (Delpech, unpublished data; Grayson *et al.*, 2001; Grayson and Delpech, in press; Rigaud *et al.*, 1995). Although work continues at this site, and on the faunas it contains, the cave bear history presented here will not change significantly. The Grotte XVI Mousterian assemblage (C) was certainly, and the Châtelperronian assemblage was very probably, produced by Neanderthals. The later assemblages, which date to between about 29,000 and 12,000 years ago, were all presumably produced by anatomically modern peoples. What might be called the Kurtén Response is obvious here. Cave bear/ungulate ratios plummet with the advent of "Aurignac Man."

This may well be the result of competition for a limiting resource. There is no reason to think that a Neandertal presence would not have displaced cave bears from caves, but there is good reason to think that post-Neanderthal human populations in this part of the world were much larger than Neanderthal ones (e.g. Mellars, 1996), and some combination of increased human group size and longer residence times can readily account for the Kurtén Response.

The majority view is that the Aurignacian is the archaeological manifestation of the arrival of morphologically modern peoples in southwestern Europe, peoples who quickly caused the extinction of, and then replaced, Neanderthals, perhaps also through resource competition (Klein, 1999; Ovchinnikov *et al.*, 2000). Even if this is not a colonization event, however, the Kurtén Response may well reflect the dramatic impact that people had on a particular species by restricting access to a mutually limiting resource.

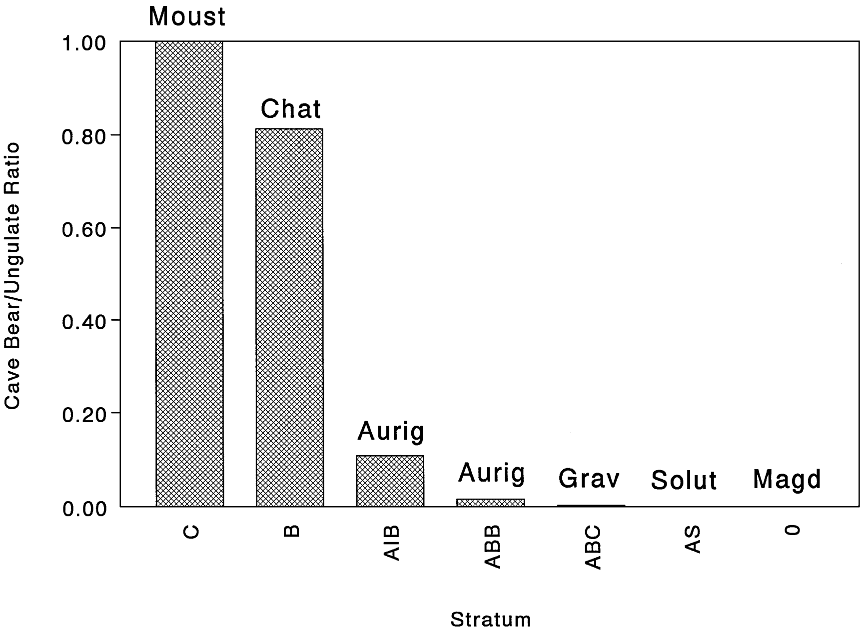

Fig. 7. The ratio of cave bear to ungulate specimens at Grotte XVI (Moust = Mousterian; Chat = Châtelperronian; Aurig = Aurignacian; Grav = Gravettian; Solut = Solutrean; Magd = Magdalenian; Delpech and Grayson, unpublished data).

CONSERVATION BIOLOGY AND THE ARCHAEOLOGICAL RECORD

Kirch, whose critically important work has done so much to demonstrate what might be called the hominization of Polynesian landscapes (e.g., Kirch, 1997c), has observed that anthropogenic impacts in island settings come so quickly that they may indicate a human presence in the absence of more standard archaeological data (Kirch, 1997b; Kirch and Ellison, 1994), an argument made by others as well (e.g. Athens, 1997; Burney, 1997b, 1999; Edwards, 1996). Certainly, the developing evidence for the translocation of the Polynesian rat to New Zealand some 1,000 years before any standard archaeological evidence for a human presence is a case in point. Nonetheless, as Tipping (1996) and Macklin *et al.* (2000) have discussed, such proxy data can be problematic. One need look no further than the suggestion by Heusser (1994) that charcoal in lacustrine sediments from Isla Grande de Chiloé, southern South America, may reflect a human presence here prior to some 47,000 years ago. In most cases, as Burney (1997b, 1999) has discussed in some detail, multiple proxy indicators will likely be necessary, a point Kirch has made as well, but the very fact that human occupation of islands may have been detected in the absence of what archaeologists tend to think of as archaeological data shows how sensitive these environments are to human colonization.

"Indigenous people," Alcorn (1993, p. 425) has suggested, "demonstrate a concern for maintaining the ecological processes and the species that mediate those processes . . . the commitment of indigenous peoples to conservation is complex and very old." Redford and Stearman (1993b; see also the important analyses by Alvard, 1994, 1995, 1998a,b) correctly took issue with this assertion. As Smith and Wishnie (2000) have recently discussed, there is very little ethnographic evidence from contemporary small-scale human societies for behaviors designed to prevent or mitigate resource depletion and habitat degradation. The archaeological research reviewed here matches Smith and Wishnie's conclusions. It also underlines the importance of Hill *et al.*'s (Hill *et al.*, 1997, pp. 1351–1352) observation that "the current set of Neotropical species has never existed as a 'natural community' without human activities," a point Kay (1994) has made in a North American context.

The archaeological record shows that human impacts, including those of small-scale hunter–gatherers, on the landscape are substantial, complex, and very old. It now appears extremely unlikely that there are any habitable places on earth whose terrestrial biotas were not structured by prehistoric human activities, a point that some archaeologists attempted to make for some regions more than 30 years ago (e.g., Jones, 1969; see also Head, 1989). It follows from this that the creation of reserves from which people are entirely excluded cannot be grounded in the argument that the result will be the recreation of biotic communities that once existed in the absence of human influence (see also Redford and Stearman, 1993a). Setting aside an entire Polynesian island as a biotic reserve cannot bring back the extinct birds that once existed on that island. Setting aside a significant part of the American landscape devoid of human influence cannot recreate a prehuman biota, since people were in the Americas before the end of the Pleistocene (Dillehay, 1997): Pleistocene biotas cannot be recreated no matter how hard we try, and, to one degree or another, all subsequent American biotic landscapes bear the formative imprint of human activities. Suggesting that such things be done is to suggest that people somehow exist outside of the natural world, when it is the activities of those same people that have been critical in creating the biodiversity that conservation biologists are trying to preserve. The clear implication is that it is the active management of biotic landscapes, not the exclusion of human influence, that is needed to accomplish these goals.

Indeed, in some cases prehistoric human activities have increased vertebrate diversity, if by diversity we mean species richness. As the important work by Vigne (Blondel and Vigne, 1993; Vigne, 1987a,b, 1988, 1990, 1992; Vigne and Marinval-Vigne, 1990; Vigne and Valladas, 1996) has shown, the number of taxa of mammals on Corsica is far greater now than it would have been had people not begun translocating mammals to the island soon after they themselves arrived (Fig. 8). Of course, genetic diversity is quite a different thing. As Vigne has also shown, at least four, and perhaps as many as seven (see Vigne, 1996), species of mammals were lost on Corsica after human arrival, but all of the introduced species now found here also exist on the mainland. Similarly, although human activities dramatically decreased the number of terrestrial bird species on islands in Oceania, human modification of the landscape in this region also created habitats for a subset of bird species whose presence is likely dependent on those modifications (Steadman, 1997b). On Crete, the wild goat *Capra aegagrus* (synonymized with *C. hircus* by Wilson and Reeder, 1993) is listed as Vulnerable by the International Union for Conservation of Nature and Natural Resources (IUCN; Hilton-Taylor, 2000) and has been given formal protection (Porter, 1996). This animal, however, would not even be here

Fig. 8. Changing richness of the Corsican terrestrial mammal fauna during the Holocene (after Blondel and Vigne, 1993; Vigne 1990, 1992). This figure tallies taxa at the subspecies level, and includes domesticated forms (which are not included in Table III).

were it not for people, who introduced it during the Late Neolithic (see Table III).

The lessons that archaeology has for conservation biology are profound, as Kirch (1997c), Lyman (1996), and others have noted. Those lessons may be that people living in small-scale social groups are not natural conservationists or that human impacts on the environment are complex and ancient, but such generalizations are of little practical value. Instead, the conservation value of the archaeological endeavor lies in what it has taught us about the biotic past, along with the implications of that past for management policy. While paleontological data have the same value, the bulk of what we know about Holocene vertebrate histories has been generated through excavation conducted for archaeological purposes.

Steadman's very important work provides a case in point. His research has not simply demonstrated the magnitude of anthropogenic bird extinctions in Polynesia, but also the likelihood of success of reintroductions of particular taxa to particular places, of which the suggested reintroduction of the pigeon *Ducula galeata* to Henderson Island is but one example (Steadman and Olson, 1985; see also the important discussion in Steadman, 1997b). Lyman (1996) has made similar points concerning the reintroduction of sea otters (*Enhydra lutris*) along the west coast of the United States. Archaeological research has also documented the history of pygmy rabbits (*Brachylagus idahoensis*) in arid western North America during the past 12,000 years or so (Butler, 1972; Grayson, 1977, 1987b, 1993, 2000b; Lyman, 1991). This species is listed as Near Threatened by the IUCN (Hilton-Taylor, 2000) and as endangered in Washington State (Washington State Department of Fish and Wildlife, 1995). While there is no evidence for serious prehistoric human impacts on pygmy rabbit populations, the late Pleistocene and Holocene history of this mammal documents that at least the Washington State populations are unlikely to survive under conditions of global warming without very significant human intervention. Similarly, archaeologically derived data on past mammal histories have direct relevance to the construction of biotic reserves, as has been noted by a number of authors (e.g., Graham, 1992; Grayson and Madsen, 2000; Lyman, 1996).

Kirch (1997c) noted that archaeologists have not been particularly effective in communicating our knowledge of past human impacts on biotic landscapes to those working in contemporary contexts, but this is a situation that appears to be changing (Foster, 2000; Holland, 2000). In sharp distinction with ecologists (e.g., Kohm *et al.*, 2000), it remains a rare archaeologist who has become forcefully involved with ground-level decisions regarding conservation biology—Lyman (1998) is one of them—but this may change as well. This would be all to the good. Conservationists may well be “clamoring for an answer” to the question as to whether “indigenous peoples” conserve biodiversity (Alcorn, 1996, p. 233), but archaeologists answered that question long ago. The issue now is what one does with this answer.

ACKNOWLEDGMENTS

I thank Michael D. Cannon, Angela E. Close, Jonathan C. Driver, Barbara E. Grayson, Shepard Krech III, Eric A. Smith, and James F. O’Connell for extremely helpful comments on the paper, and Kristine M. Bovy, Christina M. Giovas and Russell W. Graham for help along the way. The cave bear analysis reported here was done in concert with Françoise Delpech; funding for this analysis was provided by the National Science Foundation (SBR98-04692) and the Sous Direction de l’Archéologie et Direction des Musées de France (Ministère de la Culture).

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