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Paleozoology in the Service of Conservation Biology

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Paleozoological data reveal past conditions created by anthropogenic and natural processes. These conditions can serve as benchmarks of ecological properties and processes desired by conservation biologists. Paleozoological data provide empirical evidence analogous to experimental results of anthropogenic and environmental causes. They can be used to determine whether a taxon is native or exotic to an area, distinguish invasive from recolonizing taxa, choose a management action likely to produce a desired result, test benchmarks based on historic data, reveal unanticipated effects of conservation efforts, and identify causes of ecological conditions. It is time to use paleoecological knowledge in the service of modern conservation biology.

Conservation biologists, restoration ecologists, and wildlife managers often select an ecological benchmark,[1,2] ecological baseline,[3] or historical landscape[4,5] that they seek to recreate or maintain in an area. A benchmark is a goal toward which conservation activities are aimed; it is an ecological condition or process that is desired. Benchmarks vary in scale from a particular gene pool or range of phenotypes to the presence or absence of a species in an area of a few hectares to compositions of biological communities occupying tens to hundreds of hectares, as well as to ecosystems consisting of organisms, geology, fire regimes, and so on, as well as ecological and evolutionary processes.[6–8] Typically, a benchmark is established by reference to the early historic period because written records are available and also because anthropogenic, particularly industrial-era influences, are usually undesirable. Conservation biologists realize that any chosen benchmark is a moving target given the vagaries of both particularistic contingencies and evolutionary histories.[9] They worry about long-term climatic change and anthropogenic variables and their influence on plant and animal taxa and ecosystems.[10,11]

R. Lee Lyman became interested in the utility of paleozoological data to conservation biology in the middle 1980s, when he was studying the morphometry of the prehistoric sea otter (*Enhydra lutris*) in the eastern Pacific Ocean. That interest expanded with his examination, in the late 1980s, of the controversy regarding the exotic or native status of mountain goats (*Oreamnos americanus*) in Olympic National Park. Together with Ken Cannon, Lyman recently edited the volume *Zooarchaeology and Conservation Biology.*

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Conservation biologists find multidisciplinary research necessary to contend with ecological, biological, and landscape degradation.[12–14] The Long Term Ecological Research (LTER) Network established by the United States National Science Foundation monitors, over long periods, how and why ecosystems and ecological variables and processes interact and operate.[15] LTER recognizes that research must exceed a season or two, a year or two, or a even decade or two if we are to understand ecosystems. Conservation biologists grapple with the fact that ecosystems and landscapes are not static for natural and anthropogenic reasons.[16] Their desire to manage a minimally anthropogenically influenced ecosystem introduces the difficulty of identifying the boundary between natural and unnatural.[17–19] But nonanthropogenically influenced ecosystems are not always desired. For example, some anthropogenically introduced exotic taxa such as game birds in the western United States are economically beneficial and ecologically benign.

The paleozoological record provides unprecedented data that reflect the long-term operation of many ecological and anthropogenic processes and may provide guidance to distinguishing effects of the two.[20–23] My specific goal here is to show that paleozoological data are a significant source of information on benchmarks. I focus on mammals, but any taxon of plant or animal can provide data concerning a benchmark. My general goal is to encourage paleoecologists to consider how their research might be of value to conservationists and to publish their research in journals such as *Biological Conservation, Conservation Biology, BioScience, Ecological Restoration,* and *Environmental Management* to inform conservation biologists of the value of paleoecological data.

Paleoecologists publish in these venues, but they seldom identify the exact management implications of their observations.[24–30] Perhaps this is because they believe it would be "dangerous" to offer suggestions outside their field of expertise.[31] I believe, however, that we must make explicit suggestions because conservationists do not always perceive the value of

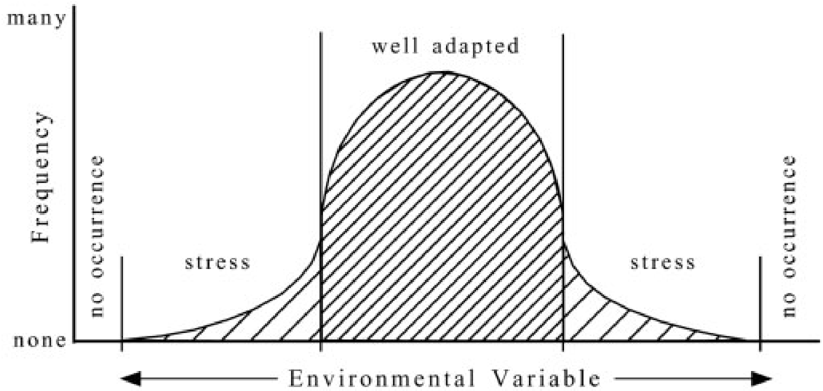

Figure 1. A model of how the environmental tolerances of a species influence its abundance on the landscape. Any environmental variable such as number of frost-free days, annual precipitation, or temperature range can be plotted on the x axis.

paleoecological data. As more papers with such suggestions are published, members of the conservation professions will realize that the long-term data provided by paleoecology is worthy of serious consideration. Then research as well as job opportunities for paleoecologists may increase and a new vault of funding may open.

Conservation biologists often muddle along with imperfect knowledge, not knowing the exact consequences of their activities.[32] To not act because of imperfect knowledge represents the "paralysis of analysis."[33] Not only do paleoecological data represent knowledge, they underscore the moving-target nature of benchmarks, and highlight the fact that ecological stasis is unattainable. They also may suggest which of several benchmarks is the most feasible to attain or maintain. A chosen benchmark will depend on social, political, economic, and ecological variables.[34] To convince anyone of the "applied" value of paleoecological data, examples must be identified. Here I describe several examples in which paleozoological data have been brought to bear on particular conservation, management, and restoration issues. Before doing that, however, I must address two background issues.

BACKGROUND

Many federal agencies such as the United States National Park Service are charged with managing "natural" or "pristine" landscapes and biotas.[35,36] This charge demands that such terms as natural, native, pristine, and the like be explicitly defined. In the United States, the terms usually are defined as "pre-Columbian or immediately post-Columbian."[37,38] It is often implied that "Columbian era" signifies nonanthropogenic, which ignores the 12,000-plus years that American Indians have been in North America and presumes that Native Americans had minimal influence on pre-Columbian ecosystems. Paleoecological data indicate that people throughout the world had all sorts of ecological influences.[39] Terms that imply nonanthropogenically influenced ecosystems and landscapes should be avoided.[34]

The second point is that every taxon has been and continues to be shaped by natural selection to live within a certain range of temperature and precipitation, vegetation, geology and topography, predation, and other environmental variables (Fig. 1). If one of those variables changes, the taxon has three options: to become locally extirpated, migrate to an area where the environmental variable has not changed, or adapt to the new environment.[40] The third alternative can take at least two forms that are not necessarily exclusive. The organism can adapt by decreasing in abundance, altering its morphometry, or a combination of the two.[41] A species may disappear from an area and reappear at a later date; its abundance may increase or decrease only to decrease or increase at a later date; or individuals may shrink or grow larger. In short, an ecological benchmark is a moving target.

EXOTIC TAXA AND NATIVE TAXA

One conservation activity is to translocate animals from one population to another to regulate the size of the donor population to enhance or reestablish another population, or both. Translocation requires that we know the benchmark of local indigenous taxa.[42] Paleozoological data assist with the determination of whether a taxon is native or exotic to a location. Definitions of exotic taxa vary.[43] For purposes of this paper, exotic, alien, nonindigenous taxa are those that did not previously exist in an area.[44] Efforts in many national parks are devoted to eradicating established exotic taxa and ensuring that no new exotic taxa become established.[45–47]

Plans to reintroduce the North American wapiti (*Cervus elaphus*) to the state of Missouri have been discussed for two decades. The historic record indicates that this large ungulate was present in the state in the nineteenth century, but does not indicate all locations where wapiti were found and not found. The paleozoological record indicates that wapiti were only present in the state when climates were cooler than at present and that they occupied the topographically rugged and timbered Ozark Plateau of the south-central portion of the state.[48] The state Fish and Wildlife Department plans to release wapiti in areas with open forest and prairie habitats and little topographic relief. The transplant effort has been delayed, but if the state plan is followed will the wapiti survive where there is no evidence that they are native?

Banff National Park straddles the crest of Canada's Rocky Mountains. Biologists are contemplating releasing bison (*Bison bison*) into this rugged wilderness area. Zooarcheological data indicate that bison were present there during the last 10,000 years and that individuals were adult males; no cow-calf herds are represented.[49] There is no evidence of differential preservation of male remains, so should bison in the park be managed as a sink population into which excess male bison from surrounding areas immigrate or should park bison be managed as a source population with a high reproduction rate and out-migration?[50] The archetypical bison is the Plains bison (*B. b. bison*); the wood bison (*B. b. athabascae*), now extinct, occurred in the northern plains.[51,52] Remains of both have been reported in Banff National Park,[49] so the release of Plains bison there seems acceptable.

Whether a taxon is native or exotic is but one side of the coin, the side concerning determination of which taxa to allow in an area. Some exotic taxa are beneficial or ecologically benign. The other side of the coin concerns determination of which taxa should be denied access to an area. This involves "invasive" taxa, the exotic taxa that cause ecological or economic damage.[44]

DISTINGUISHING INVASIVE TAXA FROM RECOLONIZING TAXA

Invasion biology is presently a major concern.[53,54] An apparent invasion may, however, reflect recolonization of pre-Columbian ranges rather than colonization of new areas.[43] Paleozoological data may distinguish the two. Darwent and Darwent[55] found that paleozoological data indicate that the range and abundance of muskox (*Ovisbos moschatus*) in the high Arctic of eastern Canada and Greenland fluctuated with climatic change over the last 5,000 years. Greenland muskox are not in jeopardy of extirpation, contrary to the belief of local conservation biologists, and one translocated group was released where it is unlikely to survive. Muskox may recolonize some areas if climate changes appropriately and humans do not interfere.

Etnier[56] identified the remains of juvenile male and female Guadalupe fur seal (*Arctocephalus townsendi*) in 500-year-old deposits on the northern coast of Washington State. The farthest north this species had been historically reported was just north of San Francisco Bay. The remains indicate that this taxon would not be invading new territory but instead recolonizing previously occupied range were it to be observed today off the coast of Washington. Prehistoric northern fur seal (*Callorhinus ursinus*) remains from several areas along the Washington, Oregon, and northern California coasts[57–59] indicate that late twentieth-century records of this taxon along the California coast[60] represent recolonization rather than invasion. Stable isotopes in prehistoric remains of this taxon recovered from sites in central California also indicate recolonization.[61]

Grayson and Delpech[26] argue that long-term climatic change represented by the shift from a glacial period to an interglacial period resulted in the loss of reindeer (*Rangifer tarandus*) from southwestern Europe. Their paleozoological data indicate that reindeer will recolonize southwestern Europe if climate shifts to a period of cooler summers and glaciation. Other paleozoological data indicate that numerous taxa will recolonize or invade the presently hyperarid desert of the Eastern Sahara should precipitation increase there.[62] Whether reindeer or Saharan taxa are considered invaders will likely depend on human land use at the time.

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Zooarcheological remains of harbor seals (*Phoca vitulina*) show that this species ascended the Columbia River between Oregon State and Washington State up to Celilo Falls, 324 km upstream of the river's mouth in the Pacific Ocean.[63] Those seals made that journey throughout the Holocene, never getting farther inland due to the impassability of the falls. Construction of Bonneville Dam at river km 250 in 1938 ended the access of pinnipeds to upstream areas. Zooarcheological remains indicate that harbor seals were pursuing salmon (*Oncorhynchus* spp.) that were making their annual spawning run upstream. Were Bonneville Dam to be removed, a remote possibility,[64] it is likely that harbor seals would once again be observed at Celilo Falls. Commercial salmon fishermen are likely to perceive the seals as invasive.

Paleozoological data may reveal prehistoric patterns that contradict historical data or that suggest anthropogenic causes of historically documented patterns. Paleozoological data indicate that ibex (*Capra ibex*) occupied more topographic positions across the Italian landscape than they do today. The mountain habitat at the 2,000 to 3,000 m elevation used by ibex today may be the result of anthropogenic transplanting efforts.[31] Stable isotope analysis of prehistoric bighorn sheep (*Ovis canadensis*) remains in Wyoming State indicates that this taxon's prehistoric seasonal migration has been altered. Bighorn sheep formerly wintered in lowlands now occupied by humans. Today bighorn are (re)utilizing what was formerly their seasonal range, prompting questions about suggested management actions.[65]

CHOOSING MANAGEMENT OPTIONS

Knowledge of the environmental tolerances of endangered taxa, along with knowledge of their prehistoric biogeographic histories, may assist in identifying why those taxa are in jeopardy today and how we might or might not protect them. The pygmy cottontail rabbit (*Brachylagus idahoensis*) is found today in the physiographic Great Basin of western North America (eastern California, Nevada, western Utah, southern Idaho, and southeastern Oregon) and in a small isolated area of eastern Washington State. The modern distribution of the pygmy cottontail implies that a corridor between southeastern Oregon and eastern Washington served as an immigration route for individuals originating in the former population to have established the latter. Late Pleistocene remains of this taxon within this hypothetical corridor indicate that it was the route.[66,67] Were a conservation biologist to want to replenish the Washington population, the genetic source seems clear. However, modern individuals from Washington are genetically distinct from nearby populations.[68] Paleozoological data indicate that the range and the population of pygmy rabbit 8,000 to 4,000 years ago were larger than in those in the twentieth century.[66,67,69] The earlier period was a time when big sagebrush (*Artemisia tridentata*) was widespread and abundant; pygmy rabbits depend on this plant for cover and food. The range and abundance of sagebrush in eastern Washington decreased as the climate cooled and effective moisture increased 4,000 years ago. So, too, did the pygmy rabbit range, and likely its abundance, decrease.[67] But there was still a lot of sagebrush after 4,000 B.P., and it was widespread. Why, then, were there so few pygmy rabbits in the middle of the twentieth century and why were there fewer than 100 individuals remaining in eastern Washington by the year 2000?[70]

Cattle ranching was initiated in late nineteenth century.[71] Open-range grazing destroyed sagebrush. The pygmy rabbit is a burrower and the cattle compacted local soil, making burrowing difficult.[70] Sagebrush loss was exacerbated by tillage agriculture in the early twentieth century. If the remaining population of pygmy rabbits in eastern Washington is to be protected, the last native stands of big sagebrush must not be destroyed.[70] In the case of eastern Washington's pygmy rabbits, migration corridors are implausible. However, decreased destruction of stands of big sagebrush may be plausible. That such destruction depleted the preferred habitat of this small rabbit is suggested by historic data; it is confirmed with the independent data of the paleozoological record.

A related issue concerns rates of extinction of small isolated populations.[72–74] Within the limits of resolution of radiocarbon dating and stratigraphy, causes of varied rates of extinction can be measured.[75] Extinction rates and causes are critical information for conservation biologists, as is information about the opposite process of persistence.[76] In the case of pygmy rabbits, the concern is with managing and protecting a depleted population. In other cases, the concern may be with a population that is too large.

TESTING POPULATION SIZE

In North America, large mammals are today subjects of management plans because they provide prey for hunters or wildlife-viewing opportunities for tourists. The long-term history of how these taxa responded to varying levels of predation, environmental change, and efforts to supplement their gene pools may be revealed by paleozoological data. A taxon's history will reveal benchmarks. Each benchmark will have unique spatio-temporal coordinates and environmental contexts. Thus we must avoid a "one size fits all" solution, which is anathema to biological and ecological diversity.

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Political ecologist Charles Kay[77] argued that wapiti (*Cervus elaphus*) populations in the western United States are too high today as a result of modern hunting regulations and reduced natural predation. This is especially the case in national parks where large populations are having serious impacts on what are supposed to be protected ecosystems.[78–80] Before the historical period, wapiti populations were, Kay[79] believes, much smaller than today, largely as a result of prehistoric human predation. Kay bases his argument on two measures. One is the modern abundance of wapiti in the Yellowstone ecosystem of northwestern Wyoming. The other comprises a paleozoological benchmark made up of the summed pre-Columbian zooarcheological record from seven western states (Wyoming, Montana, Utah, Idaho, Nevada, Oregon, and Washington) and spanning the last 10,000 years. Because the measure representing the modern Yellowstone abundance of wapiti is considerably higher than the abundance of wapiti indicated by the lumped paleozoological data, Kay argues that wapiti should be hunted down to pre-Columbian levels to avoid further degradation of western ecosystems. It is unlikely that his benchmark will be adopted by conservation biologists for two reasons. First, no management application will be uniformly applied to the seven-state area from which his sample derived. Second, wapiti abundances varied across both the area and the last 10,000 years.[81]

Paleozoological taxonomic abundances are, at best, ordinal scale and are best considered relative to the abundances of other taxa.[82–84] Data from eastern Washington State indicate that Kay's benchmark of wapiti population size is unfounded there. If humans depressed local wapiti populations during the first thousand years that people were present, this time period is not represented in the samples of faunal remains that Kay used.[81] Ungulate remains in 86 samples spanning the last 10,000 years indicate that there was no decrease in wapiti abundance relative to other ungulates over this time span (Fig. 2). There is no evidence of intensified processing or alteration in the demography of the kill, both of which are expected to appear if, given an increasingly sophisticated technology and increasing human population, hunters took similar abundances of wapiti from a successively more depressed population over time. There is no evidence here that human hunting influenced the wapiti metapopulation. This does not mean that humans did not influence that metapopulation, only that such an influence is undetectable in the data available. There are no early historic zooarcheological collections from eastern Washington with which to compare modern wapiti abundance; such collections would reveal early impacts, if any, of Euroamerican predation regimes and potentially would corroborate Kay's benchmark.

We can monitor temporal and spatial trends with paleozoological data; trends present a series of benchmarks, each of slightly different magnitude or value in one respect or another. That benchmarks are a time slice of a long-term trend of shifting values underscores the fact that ecosystem management decisions are choices and so are benchmarks. Importantly, paleozoological data may reveal unanticipated effects of conservation efforts.

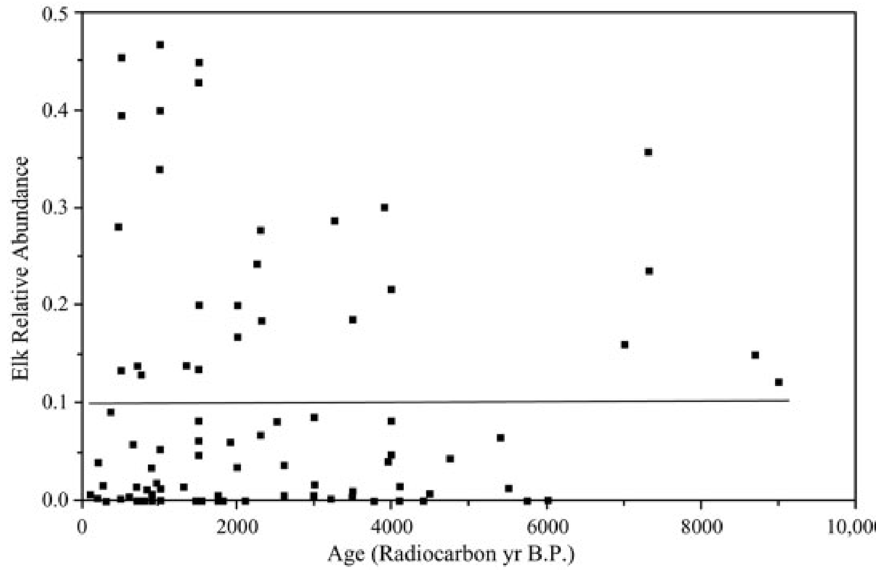

Figure 2. Abundance of elk remains relative to all ungulate remains in 86 assemblages from eastern Washington. The horizontal line is the simple best-fit regression line; its slope (=0.000001, from youngest to oldest) is insignificant.

UNANTICIPATED EFFECTS

Two subspecies of wapiti occurred in Washington State in the nineteenth and twentieth centuries. The eastern quarter of the state is occupied by the Rocky Mountain subspecies (*Cervus elaphus nelsoni*); the western quarter is occupied by the on-average larger Roosevelt wapiti (*C. e. roosevelti*). The identity of the subspecies that occupied the Cascade Mountain range of the central portion of the state is debated.[85] Local wapiti populations were depleted by the beginning of the twentieth century as a result of unregulated hunting. To supplement one remnant population, early in the twentieth century Rocky Mountain wapiti were captured in the Yellowstone ecosystem and transplanted to the southern Cascade Mountains of central Washington and many other locations across the continent.[86]

Late prehistoric (A.D. 1500 to 1792) and early historic (A.D. 1792 to 1835) wapiti remains from near modern Portland, Oregon, are larger than both modern Roosevelt wapiti and Rocky Mountain wapiti (Fig. 3). Deer (*Odocoileus virginianus* and *O. hemionus*) remains from the same collection are the same size as modern deer (Fig. 4). What caused wapiti diminution during the last 180 years but did not affect deer? I hypothesize that the 1920s addition of Rocky Mountain wapiti to the gene pool in the Cascade Mountains, through a process of hybridization with indigenous wapiti and introgression, produced the smaller wapiti present today in southwestern Washington and northwestern Oregon. This is an unexpected outcome. The hypothesis needs to be tested by genetic analysis of prehistoric remains. One test implication is already well established. What might be considered the "Yellowstone genetic signature" has been tracked across various modern populations.[87] That genetic signature should not be detected in late prehistoric and early historic wapiti remains from Washington if the hypothesis is correct.

Any evidence that allows anticipation or retrodictive recognition of the consequences of management activities is of high value. This point arises again in the context of choosing one management option over another based on a suspected cause of a conservation problem.

IDENTIFYING CAUSES

The Columbian white-tailed deer (*Odocoileus virginianus leucurus*) is found today only in southwestern Oregon and on the Columbia River floodplain in the Portland Basin of northwestern Oregon and southwestern Washington. It is one of the original 78 taxa in the United States listed in 1968 as federally endangered. Hunting of this subspecies is now restricted, and many of the Portland Basin population's members are in the Columbian White-Tailed Deer National Wildlife Refuge, established in 1972 to protect the subspecies. The foothills around the floodplain are occupied by the Columbian black-tailed deer (*O. hemionus columbianus*), a subspecies conspecific with the mule deer (*O. h. hemionus*) of the Rocky Mountains and eastern Washington. More or less sympatric with mule deer in the eastern part of the state is the northwest white-tailed deer (*O. v. ochrourus*). Increase in the abundance of both subspecies of white-tailed deer since 1935 is attributed to modern management practices. Received wisdom holds that white-tailed deer were abundant in Washington and Oregon until the second half of the nineteenth century, when habitat modification and human predation depleted the metapopulation. Paleozoological data indicate that this species' prehistoric range was larger than its modern range.[88]

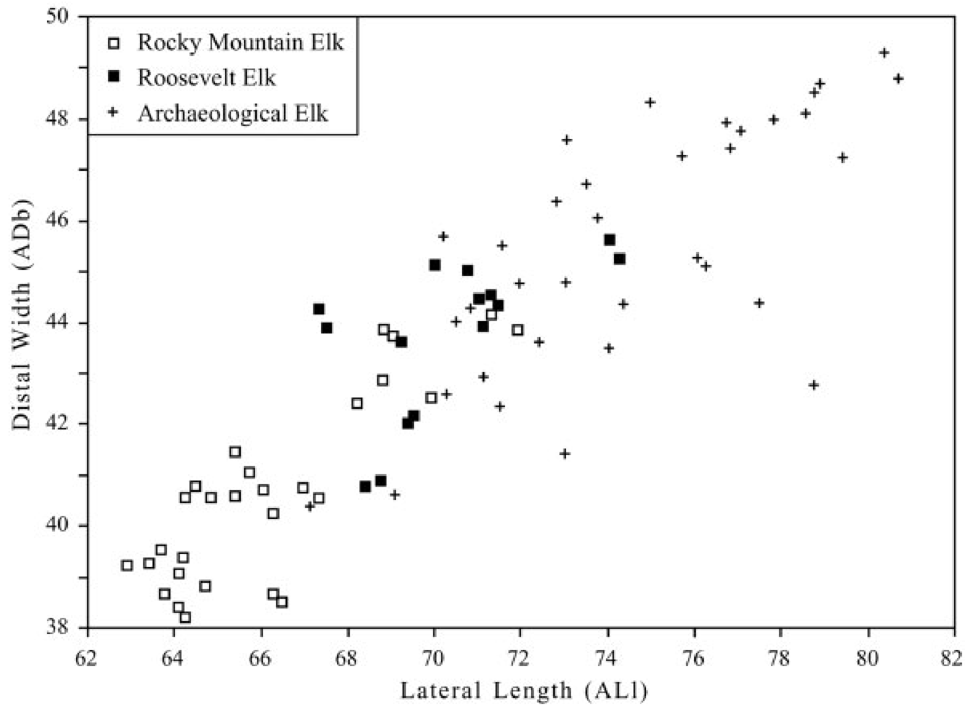

Figure 3. Bivariate scatterplot of distal width (ADb) and lateral length (ALl) of elk astragali from archeological sites in the Portland Basin relative to astragali of two subspecies of modern elk.

Remains of both Columbian white-tailed deer and Columbian black-tailed deer have been identified in the Portland Basin.[89] There was no statistically significant change in the relative abundance of either subspecies of deer from the pre-Euroamerican contact (A.D. 1450 to 1792) period to the post-Euroamerican contact period (A.D. 1792 to 1835). This is surprising, given the loss of half to two-thirds of the local American Indian population during the late eighteenth and earliest nineteenth centuries as a result of introduced European diseases.[90] Foraging theory suggests that release from predation pressure will result in more deer.[91] There is zooarcheological evidence in the area that there were changes in the availability of some animal taxa.[92]

Local precontact and post-contact American Indians set fire to floodplain and foothill vegetation to enhance primary productivity and to create open spaces in which to hunt.[93] Euroamerican fire suppression in the late nineteenth century closed the canopy and depressed primary productivity.[94] This likely resulted in dietary stress that prevented the local deer population from rebounding as a consequence of decreased American Indian predation. The Columbian white-tailed deer population was subsequently depressed by increasing firearm hunting by Euroamericans in conjunction with industrial habitat modification such as logging. If this is correct, and if more Columbian white-tail deer are desired, then conservationists should restrict hunting and initiate traditional use of anthropogenic fire. The latter has been recommended in nearby contexts,[93] but requires public education if it is to be successful.[94] Paleozoological data here reveal a cause for population depletion and what it might take to reverse that depletion.[95]

In Europe, correspondence between cave bear (*Ursus spelaeus*) demography and climate suggests how modern ursids might be managed. During periods of interstadial climates, cave bears were less sexually segregated during hibernation, more bears grew to older ages, and cub mortality was lower relative to that during stadial periods. During the latter, more males died in hibernation loci, fewer bears grew old, and cub mortality was greater.[96] A management implication of these observations is that when climates are harsh, if cub survival (recruitment) is a concern, then the harvest of prime-age male bears should increase because adult males kill youngsters. Here, paleozoological data provide insights into how a chosen condition might be maintained.

CONCLUSION

Anthropologists have long known that humans influence ecosystems.[97] Historical ecologists have demonstrated that modern ecosystems are historical phenomena.[98] Using paleozoological data to assess benchmarks integrates these observations. A benchmark's validity must be subject to testing, its causes must be identified, and it must be determined if it can be created and maintained. Paleozoological data can contribute to all of those points.

Many issues in conservation biology are increasingly important to the long-term health of humanity as we enter the third millennium and as the ever more resource-hungry human

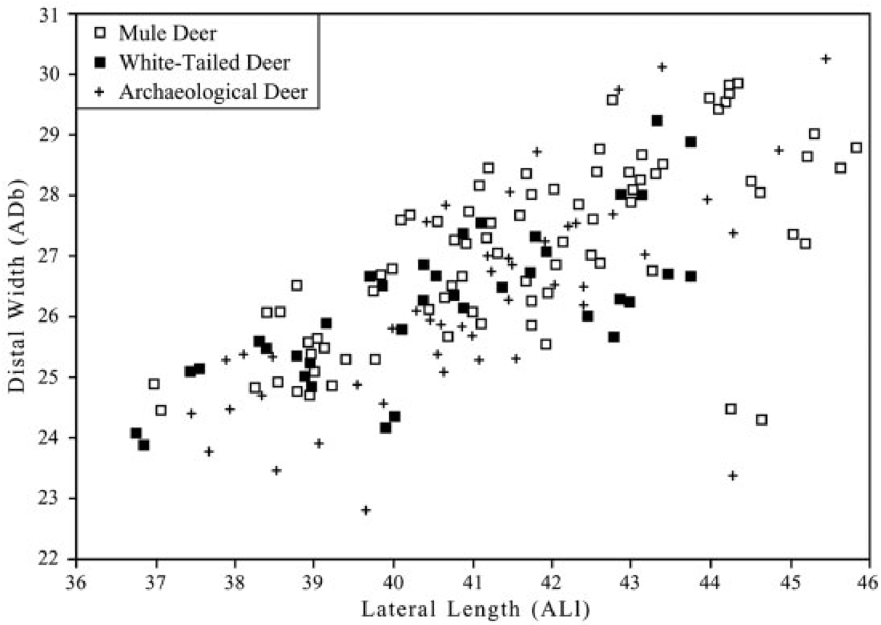

Figure 4. Bivariate scatterplot of distal width (ADb) and lateral length (ALl) of deer astragali from archeological sites in the Portland Basin relative to astragali of two species (three subspecies) of modern deer.

population continues to grow.[99] Numerous conservation issues might be addressed with paleozoological data. For example, based on comparisons between remains of prehistoric wild animals and remains of conspecific zoo-raised animals, O'Regan and Turner[100] show that the latter may be phenotypically ill equipped to survive if released in the wild. Sanders and Miller[101] demonstrate that a historically documented seasonal migration route used by a herd of pronghorn antelope (*Antilocapra americana*) has a time depth of 5,000 to 6,000 years. Late twentieth-century construction may disrupt that behavioral pattern and jeopardize the herd. Badenhorst and Plug[102] highlight the use of paleozoological training to solve forensic problems in wildlife management. Is a hide or skull from a poached animal?

In order to deepen conservation biology's appreciation of what paleozoology can offer, we must advertise our skills.[102] We should publish case studies in journals read by conservation biologists, restoration ecologists, and the like. I have focused here on mammals, but any sort of paleobiological or paleoecological data can be of value to those charged with recreating and maintaining particular kinds of ecosystems. It is time that we speak to those most in need of the data we can provide and that we not only produce, but also use those data in the service of conservation biology.

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REFERENCES

1 Hunter M Jr. 1996. Benchmarks for managing ecosystems: are human activities natural? Cons Biol 10:695–697.

2 Lawton JH. 1997. The science and non-science of conservation biology. Oikos 79:3–5.

3 Young TP. 2000. Restoration ecology and conservation biology. Biol Cons 92:73–83.

4 Jordan WR III. 1999. Nature and culture. Ecol Restoration 17:187–188.

5 Povilitis T. 2002. What is a natural area? Nat Areas J 22:70–74.

6 Crandall KA, Bininda-Emonds ORP, Mace GM, Wayne RK. 2000. Considering evolutionary processes in conservation biology. Trends Ecol Evol 15:290–295.

7 Landres PB. 1992. Temporal scale perspectives in managing biological diversity. Trans N Am Wildl Nat Res Conf 57:292–307.

8 Smith TB, Bruford MW, Wayne RK. 1993. The preservation of process: the missing element of conservation programs. Biodiversity Lett 1:164–167.

9 Russell E. 2003. Evolutionary history: prospectus for a new field. Env Hist 8:204–228.

10 Glick P, Inkley D, Tufts C. 2001. Climate change and wildlife: integrating global climate policy implementation with local conservation action. Trans N Am Wildl Nat Res Conf 66:380–391.

11 Joyce LA, Hansen A. 2001. Climate change: ecosystem restructuring, natural disturbances and land use. Trans N Am Wildl Nat Res Conf 66:327–343.

12 Dayton PK. 2003. The importance of the natural sciences to conservation. Am Nat 162:1–13.

13 Ludwig D, Mangel M, Haddad B. 2001. Ecology, conservation, and public policy. Ann Rev Ecol Syst 32:481–517.

14 Noss R. 1999. Is there a special conservation biology? Ecography 22:113–122.

15 Hobbie JE. 2003. Scientific accomplishments of the Long Term Ecological Research Program: an introduction. BioSci 53:17–20.

16 Suding KN, Gross KL, Houseman GR. 2004. Alternative states and positive feedbacks in restoration ecology. Trends Ecol Evol 19:46–53.

17 Angermeier PL. 2000. The natural imperative for biological conservation. Cons Biol 14:373–381.

18 Higgs ES. 1997. What is good ecological restoration? Cons Biol 11:338–348.

19 Huff DE. 1997. Defining ecosystem health in national parks. Trans N Am Wildl Nat Res Conf 62:448–453.

20 Deevey ES. 1969. Coaxing history to conduct experiments. BioSci 19:40–43.

21 Jackson JBC. 2001. What was natural in the coastal oceans? Proc Natl Acad Sci (USA) 98:5411–5418.

22 Lyman RL. 1996. Applied zooarchaeology: the relevance of faunal analysis to wildlife management. World Archaeol 28:110–125.

23 Stahl PW. 1996. Holocene biodiversity: an archaeological perspective from the Americas. Ann Rev Anthropol 25:105–126.

24 Barsh R. 2003. Shell middens yield rich cultural deposits for fine-scale modeling of preindustrial ecosystems. Ecol Restoration 21:319–320.

25 Bowen T. 2004. Archaeology, biology and conservation on islands in the Gulf of California Env Cons 31:199–206.

26 Grayson DK, Delpech F. 2005. Pleistocene reindeer and global warming. Cons Biol 19:557–562.

27 Hadly EA. 2003. The interface of paleontology and mammalogy: past, present, and future. J Mamm 83:347–353.

28 Peacock E, Haag WR, Warren ML Jr. 2005. Prehistoric decline in freshwater mussels coincident with the advent of maize agriculture. Cons Biol 19:547–551.

29 Swetnam TW, Allen CD, Betancourt JL. 1999. Applied historical ecology: using the past to manage for the future. Ecol Applications 9:1189–1206.

30 van der Leeuw S, Redman CL. 2002. Placing archaeology at the center of socio-natural studies. Am Antiquity 67:597–605.

31 Phoca-Cosmetatou N. 2004. A zooarchaeological reassessment of the habitat and ecology of the ibex. In: Lauwerier RCGM, Plug I, editors. The future from the past: archaeozoology in wildlife conservation and heritage management. Oxford: Oxbow Books. p 64–78.

32 Bailey JA. 1982. Implications of "muddling through" for wildlife management. Wildl Soc Bull 10:363–369.

33 Hutchins M. 1995. Olympic mountain goat controversy continues. Cons Biol 9:1324–1326.

34 Lyman RL, Cannon KP. 2004. Applied zooarchaeology, because it matters. In: Lyman RL, Cannon KP, editors. Zooarchaeology and conservation biology. Salt Lake City: University of Utah Press. p 1–24.

35 Bonnicksen TM, Stone EC. 1985. Restoring naturalness to national parks. Env Management 9:479–486.

36 Bowden MJ. 1992. The invention of American tradition. J Hist Geogr 18:3–26.

37 Graber DM. 2003. Ecological restoration in wilderness: natural versus wild in National Park Service wilderness. George Wright Forum 20:34–41.

38 Houston DB, Schreiner EG. 1995. Alien species in national parks: drawing lines in space and time. Cons Biol 9:204–209.

39 Redman CL. 1999. Human impact on ancient environments. Tucson: University of Arizona Press.

40 Gauthreaux SA Jr. 1980. The influences of long-term and short-term climatic changes on the dispersal and migration of organisms. In: Gauthreaux SA, editor. Animal migration, orientation, and navigation. New York: Academic Press. p 103–174.

41 Lyman RL, O'Brien MJ. 2005. Within-taxon morphological diversity as a paleoenvironmental indicator: Late-Quaternary *Neotoma* in the Bonneville Basin, northwestern Utah. Quaternary Res 63:274–282.

42 Seddon PJ, Soorae PS. 1999. Guidelines for subspecific substitutions in wildlife restoration projects. Cons Biol 13:177–184.

43 Shrader-Frechette K. 2001. Non-indigenous species and ecological explanation. Biol Philos 16:507–519.

44 Lodge DM, Shrader-Frechette K. 2003. Nonindigenous species: ecological explanation, environmental ethics, and public policy. Cons Biol 17:31–37.

45 Goigel M, Bratton S. 1983. Exotics in the parks. National Parks 57:24–29.

46 Hester FE. 1991. The U. S. National Park Service experience with exotic species. Nat Areas J 11:127–128.

47 Lyman RL. 1998. White goats, white lies: the abuse of science in Olympic National Park. Salt Lake City: University of Utah Press.

48 Harpole JL. 2004. Zooarchaeological implications for Missouri's elk (*Cervus elaphus*) reintroduction effort. In: Lyman RL, Cannon KP, editors. Zooarchaeology and conservation biology. Salt Lake City: University of Utah Press. p 103–115.

49 Langemann EG. 2004. Zooarchaeological research in support of a reintroduction of bison to Banff National Park, Canada. In: Lauwerier RCGM, Plug I, editors. The future from the past: archaeozoology in wildlife conservation and heritage management. Oxford: Oxbow Books. p 79–89.

50 Pulliam HR. 1988. Sources, sinks, and population regulation. Am Nat 132:652–661.

51 Polziehn RO, Beech R, Sheraton J, Strobeck C. 1996. Genetic relationships among North American bison populations. Can J Zool 74:734–749.

52 van Zyll de Jong CG, Gates C, Reynolds H, Olson W. 1995. Phenotypic variation in remnant populations of North American bison. J Mamm 76:391–405.

53 Mooney HA, Cleland EE. 2001. The evolutionary impact of invasive species. Proc Natl Acad Sci (USA) 98:5446–5451.

54 Vermeij GJ. 1996. An agenda for invasion biology. Biol Cons 78:3–9.

55 Darwent CM, Darwent J. 2004. Where the muskox roamed: biogeography of tundra muskox (*Ovisbos moschatus*) in the eastern Arctic. In: Lyman RL, Cannon KP, editors. Zooarchaeology and conservation biology. Salt Lake City: University of Utah Press. p 61–87.

56 Etnier MA. 2002. Occurrences of Guadalupe fur seals (*Arctocephalus townsendi*) on the Washington coast over the past 500 years. Marine Mamm Sci 18:551–557.

57 Crockford SJ, Frederick SG, Wigen RJ. 2002. The Cape Flattery fur seal: an extinct species of *Callorhinus* in the eastern north Pacific? Can J Archaeol 26:152–174.

58 Lyman RL. 1988. Zoogeography of Oregon coast marine mammals: the last 3000 years. Marine Mamm Sci 4:247–264.

59 Hildebrandt WR. 1984. Archaeological presence of the northern fur seal (*Callorhinus ursinus*) along the coast of northern California. Murrelet 65:28–29.

60 Peterson RS, Le Boeuf BJ, Delong RL. 1968. Fur seals from the Bering Sea breeding in California. Nature 219:899–901.

61 Burton RK, Snodgrass JJ, Gifford-Gonzalez D, Guilderson T, Brown T, Koch PL. 2001. Holocene changes in the ecology of northern fur seals: insights from stable isotopes and archaeofauna. Oecologia 128:107–115.

62 Peter J, Pöllath N. 2004. Holocene faunas of the Eastern Sahara: zoogeographical and palaeoecological aspects. In: Lauwerier RCGM, Plug I, editors. The future from the past: archaeozoology in wildlife conservation and heritage management. Oxford: Oxbow Books. p 34–50.

63 Lyman RL, Harpole JL, Darwent C, Church R. 2002. Prehistoric occurrence of pinnipeds in the lower Columbia River. Northwest Nat 83:1–6.

64 Levine PS, Schiewe MH. 2001. Preserving salmon biodiversity. Am Sci 89:220–227.

65 Hughes SS. 2004. Postcontact changes in the behavior and distribution of Rocky Mountain bighorn sheep (*Ovis canadensis*) in northwestern Wyoming. In: Lyman RL, Cannon KP, editors. Zooarchaeology and conservation biology. Salt Lake City: University of Utah Press. p 116–135.

66 Lyman RL. 1991. Late Quaternary biogeography of the pygmy rabbit (*Brachylagus idahoensis*) in eastern Washington. J Mamm 72:110–117.

67 Lyman RL. 2004. Biogeographic and paleoenvironmental implications of late Quaternary pygmy rabbits (*Brachylagus idahoensis*) in eastern Washington. Western N Am Nat 64:1–6.

68 Warheit KI. 2001. Genetic diversity and population differentiation of pygmy rabbits (*Brachylagus idahoensis*). Olympia: Washington Department of Fish and Wildlife.

69 Grayson DK. 1987. The biogeographic history of small mammals in the Great Basin: observations on the last 20,000 years. J Mamm 68:359–375.

70 Thines NJS, Shipley LA, Sayler RD. 2004. Effects of cattle grazing on ecology and habitat of Columbia Basin pygmy rabbits (*Brachylagus idahoensis*). Biol Cons 119:525–534.

71 Galbraith WA, Anderson EW. 1971. Grazing history of the Northwest. J Range Management 24:6–12.

72 Foley P. 1994. Predicting extinction times from environmental stochasticity and carrying capacity. Cons Biol 8:124–137.

73 Pimm SL, Jones HL, Diamond J. 1988. On the risk of extinction. Am Nat 132:757–785.

74 Steadman DW. 1995. Prehistoric extinctions of Pacific Island birds: biodiversity meets zooarchaeology. Science 267:1123–1131.

75 Steadman DW, Pregill GK, Burley DV. 2002. Rapid prehistoric extinction of iguanas and birds in Polynesia. Proc Natl Acad Sci (USA) 99:3673–3677.

76 Mangel M, Tier C. 1994. Four facts every conservation biologist should know about persistence. Ecol 75:607–614.

77 Kay CE. 1994. Aboriginal overkill: the role of Native Americans in structuring western ecosystems. Hum Nat 5:359–398.

78 Hess K Jr. 1993. Rocky times in Rocky Mountain National Park. Niwot: University Press of Colorado.

79 Kay CE. 1997. Ungulate herbivory, willows, and political ecology in Yellowstone. J Range Management 50:139–145.

80 Porter WF, Underwood HB. 1999. Of elephants and blind men: deer management in the U.S. National Parks. Ecol Applications 9:3–9.

81 Lyman RL. 2004. Aboriginal overkill in the intermountain west of North America: zooarchaeological tests and implications. Hum Nat 15:169–208.

82 Gilinsky NL, Bennington JB. 1994. Estimating numbers of whole individuals from collections of body parts: a taphonomic limitation of the paleontological record. Paleobiology 20:245–258.

83 Grayson DK. 1984. Quantitative zooarchaeology. Orlando, FL: Academic Press.

84 Lyman RL, Power E, Lyman RJ. 2003. Quantification and sampling of faunal remains in owl pellets. J Taphonomy 1:3–14.

85 Bryant LD, Maser C. 1982. Classification and distribution. In: Thomas JW, Toweill DE, editors. Elk of North America: ecology and management. Harrisburg, PA: Stackpole Books. p 1–59.

86 Robbins RL, Redfearn DE, Stone CP. 1982. Refuges and elk management. In: Thomas JW, Toweill DE, editors. Elk of North America: ecology and management. Harrisburg, PA: Stackpole Books. p 479–507.

87 Polziehn RO, Hamr J, Mallory FF, Strobeck C. 1998. Phylogenetic status of North American wapiti (*Cervus elaphus*) subspecies. Can J Zool 76:998–1010.

88 Livingston SD. 1987. Prehistoric biogeography of white-tailed deer in Washington and Oregon. J Wildl Management 51:649–654.

89 Lyman RL. n.d. Late prehistoric and early historic abundance of Columbian white-tailed deer, Portland Basin, Washington and Oregon, U.S.A. J Wildl Management 69. In press.

90 Boyd R. 1999. The coming of the spirit of pestilence. Vancouver, BC: University of British Columbia Press.

91 Grayson DK. 2001. The archaeological record of human impacts on animal populations. J World Prehist 15:1–68.

92 Butler VL. 2000. Resource depression on the Northwest Coast of North America. Antiquity 74:649–661.

93 Leopold EB, Boyd R. 1999. An ecological history of old prairie areas in southwestern Washington. In: Boyd R, editor. Indians, fire and the land in the Pacific Northwest. Corvallis: Oregon State University Press. p 139–163.

94 Dods RR. 2002. The death of Smokey Bear: the ecodisaster myth and forest management practices in prehistoric North America. World Archaeol 33:475–487.

95 Wray J, Anderson MK. 2003. Restoring Indian-set fires to prairie ecosystems on the Olympic Peninsula. Ecol Restoration 21:296–301.

96 Germonpré M. 2004. Influence of climate on sexual segregation and cub mortality in peniglacial cave bear. In: Lauwerier RCGM, Plug I, editors. The future from the past: archaeozoology in wildlife conservation and heritage management. Oxford: Oxbow Books. p 51–63.

97 Heizer RF. 1955. Primitive man as an ecologic factor. Kroeber Anthropol Soc Papers 13:1–31.

98 Balée W, editor. 1998. Advances in historical ecology. New York: Columbia University Press.

99 Lyman RL, Cannon KP, editors. 2004. Zooarchaeology and conservation biology. Salt Lake City: University of Utah Press.

100 O'Regan HJ, Turner A. 2004. The interface between conservation biology, palaeontology and archaeozoology: morphometrics and population viability analysis. In: Lauwerier RCGM, Plug I, editors. The future from the past: archaeozoology in wildlife conservation and heritage management. Oxford: Oxbow Books. p 90–96.

101 Sanders PH, Miller ME. 2004. Archaeological evidence of pronghorn (*Antilocapra Americana*) migration in the Upper Green River Basin of Wyoming: implications for wildlife management. In: Lyman RL, Cannon KP, editors. Zooarchaeology and conservation biology. Salt Lake City: University of Utah Press. p 164–177.

102 Badenhorst S, Plug I. 2004. Archaeozoology, law enforcement and nature conservation in the Republic of South Africa: perspectives from the Transvaal Museum, Pretoria. In: Lauwerier RCGM, Plug I, editors. The future from the past: archaeozoology in wildlife conservation and heritage management. Oxford: Oxbow Books. p 117–121.

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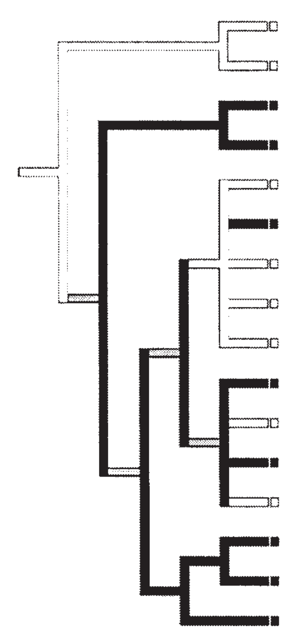

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