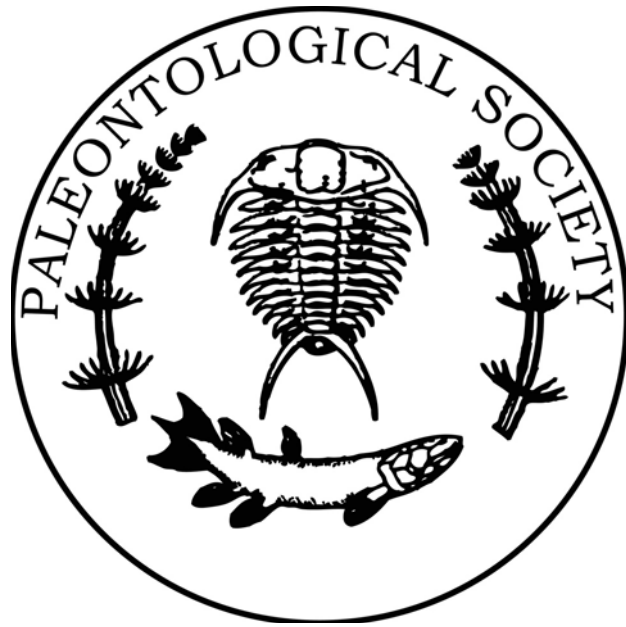


CONSERVATION PALEOBIOLOGY

Using the Past to Manage for the Future



Gregory P. Dietl and Karl W. Flessa
Editors

The Paleontological Society Papers

Volume 15

October 2009

A Publication of the Paleontological Society

Series Editor

Sankar Chatterjee
Museum of Texas Tech University
MS/Box 43191
3301 4th Street
Lubbock, TX 79409-3191

Copyright © 2009 by the Paleontological Society

ISSN 1089-3326

All rights reserved. This entire publication may not be reproduced, stored in a retrieval system, or transmitted, in any form or by any means, electronic, mechanical, photocopying, recording, or otherwise, without permission in written form from the Secretary of the Society. Diagrams, figures, tables, illustrations, and graphs may be reproduced by photocopying and distributing free of charge for educational purposes, if proper credit is given to the author(s) and the Society.

Printed by Yale University Printing and Publishing Services.

VERTEBRATE FOSSILS AND THE FUTURE OF CONSERVATION BIOLOGY

ELIZABETH A. HADLY¹ AND ANTHONY D. BARNOSKY²

¹Department of Biology, Stanford University, Stanford, CA 94305 USA

²Department of Integrative Biology and Museums of Paleontology and Vertebrate Zoology, University of California, Berkeley, CA 94720 USA

ABSTRACT.—The science and practice of conservation biology face new challenges in the next few decades that will require application of the vertebrate fossil record. The new challenges are how to preserve not only individual species, but also natural ecosystem function through a time that is seeing unprecedented rates of climate change, human-population growth, and habitat fragmentation. Under these circumstances, linkages between vertebrate paleontology and conservation biology are needed to: (1) define the range of normal variation that ecosystems typically experience in their lifespan; (2) provide metrics for monitoring ecosystems that are useful for conservation biologists and benchmarks for recognizing successful ecosystem management; and (3) develop effective conservation strategies for species and ecosystems. Here we summarize some ways vertebrate paleontological work on genetics, populations, species diversity, and extinction is contributing to these needs. For example, the application of ancient DNA techniques in the context of life history strategies provides a means of determining when modern populations are in trouble. Species composition, abundance, and richness in modern ecosystems all can be compared to the paleontological record to assess when an ecosystem is exhibiting unusual changes. Past extinctions offer insights as to how to avoid future ones. New conservation efforts such as assisted migration will require information on which kinds of species substitutions maintained ecological function in the past. We anticipate that as ecosystems require more and more human manipulation to sustain biodiversity, the paleontological record will become even more important as a baseline against which to assess ecological health.

“The first step in park management is historical research, to ascertain as accurately as possible what plants and animals and biotic associations existed originally in each locality.”—Leopold et al. (1963)

INTRODUCTION

IN TODAY’S world, it is difficult to find a major group of organisms that does not have species in danger of extinction (Wake and Vredenburg, 2008; Davidson et al., 2009; IUCN, 2009). The poster children for endangered species, however, are usually vertebrates—amphibians, reptiles, birds, and especially the so-called charismatic mammals, like primates, tigers, elephants, and whales. Thus, it is particularly important to define the “range of normal” fluctuations that vertebrates typically experience through evolutionary and ecological history, so that we can recognize not only when various animals and communities are truly imperiled but also when the conservation goal of maintaining “naturally-functioning” ecosystems has been achieved.

Vertebrate paleontology already has contributed to those goals in numerous ways (Hadly, 2003; Lyman and

Cannon, 2004; Lyman, 2006). For example, the proportions of species among orders of North American mammals show little deviation over time-scales of millions of years (Alroy, 2000). At the hundred-thousand-year scale, vertebrate paleontology has demonstrated that while mammalian communities may change in species composition, the numbers of species in trophic and size categories remain relatively constant within a given kind of ecosystem (mountain, desert, etc.), and links between ecological niches are maintained although the species filling those niches may change (Owen et al., 2000; Hadly and Maurer, 2001; Barnosky et al., 2004a; Barnosky and Shabel, 2005; McGill et al., 2005; Hadly et al., in press). At the more resolved thousand-year time scale, it becomes apparent which kinds of species in a particular community typically respond to non-human caused perturbations, notably climate change, and which kinds of species can be expected to persist or disappear through the normal course of environmental variation (Guilday, 1971, 1984; Graham and Grimm, 1990; Wood and Barnosky, 1994; Graham et al., 1996; Hadly, 1996; Graham, 1997; Grayson, 1998, 2005, 2006; Barnosky, 2004a; Blois and Hadly, 2009).

Useful as these kinds of information have been in the theoretical realm, they have been little utilized by land managers simply because it has been difficult to develop direct comparisons between present and past. Where these comparisons have been made, they have been extremely powerful for the management community; for example, studies of Holocene fauna that were instrumental in assessing elk populations and restoring wolves to Yellowstone National Park (Hadly, 1996; NRC, 2002), and in establishing a context in which to manage mountain goats in Olympic National Park (Lyman, 1998).

Accordingly, here we provide information on methods that rely on the vertebrate paleontological record and that directly link past and present in order to manage for the future. At the local scale we discuss how to infer the health and prognosis of mammalian populations using analyses of fossil and modern DNA. At regional and continental scales, we provide methods for assessing “normal” levels of biodiversity in mammalian communities, in order to establish conservation benchmarks that can be relatively easily monitored. And at the global scale, we refer to the fossil record to suggest how species might be expected to respond to the current threats of habitat fragmentation and global climate change, and suggest mitigation strategies.

NEW CHALLENGES IN CONSERVATION BIOLOGY

Conservation biology has at its core the mission to save Earth’s biodiversity; from a practical standpoint, the goals have been to save individual species, to save products and services of ecosystems that people need, and to save places where people can still experience a feeling of wilderness (Meine et al., 2006). From a philosophical perspective, all three of those goals have heretofore been achievable by simply setting aside a large enough tract of land and attempting to manage it in a way that keeps it in its “normal” state. “Normal” has been implicitly defined by the landmark Leopold Report (Leopold et al., 1963), which set forth the working definition: “to preserve, or where necessary to recreate, the ecologic scene as viewed by the first European visitors.” Although originally formulated for management of U.S. National Park lands, this philosophy has become the guiding light for much of land management and for the conservation ethic in general.

The first lesson of the vertebrate fossil record is

that this criterion for “normal” is based on a fixed point in time, generally around a century or two ago that in North America is thought to precede significant European human impact. This view of “normal” does not take into account the range of variation ecosystems experience through their existence. Thus, an initial challenge for conservation biology is to explicitly shift the paradigm for conservation from one that emphasizes holding ecosystems at a static point defined by an arbitrary temporal benchmark, to one that focuses on maintaining key ecosystem functions within the range of variation exhibited through past environmental perturbations.

In this context we suggest a workable definition for “normal” might be: “maintaining ecosystems within the limits of variation they experience in times or regions where humans were not abundant on the landscape.” Although humans colonized the continents at different times, in fact our dominance of the global ecosystem is relatively recent, coinciding with the advent of agriculture about 8,000-10,000 years ago and subsequent urbanization. Thus, the global dominance of humans is of much shorter duration than is the backdrop on which most living species evolved to interact, which is on the timescale of the glacial-interglacial climatic excursions beginning some 2.6 million years ago. The time of human dominance also is considerably shorter than the life spans of most species on Earth, which in general last about one to several million years (Alroy, 1996; Avise et al., 1998; Johns and Avise, 1998; Alroy, 2000). While we might quibble about the exact wording, the key concept we endorse is that a given ecosystem is characterized by a core set of ecological niches—for example, the “ground squirrel niche,” or the “grass niche”—and although the particular species filling those niches through time may change, in the absence of significant human perturbation the niches, and the connections between them, remain through at least hundreds of thousands of years. This has been demonstrated not only for vertebrates (Barnosky, 2004a; Barnosky et al., 2004a; McGill et al., 2005; Hadly et al., in press), but for plants and invertebrates as well (Pandolfi, 2002; Hughes et al., 2003; DiMichele et al., 2004; Flessa and Jackson, 2005; Jackson and Erwin, 2006; Pandolfi, 2006).

The second big challenge facing conservation biology is that abnormally rapid global warming (IPCC, 2007) has changed the rules of the conservation game, such that even the straight-forward practice of

preserving species by simply setting aside a protected tract of land no longer is viable (Barnosky, 2009). The basic problem is that as climate changes rapidly within protected areas, the species we have become used to in those places lose the climate they need to survive there (e.g., McMenamin et al., 2008). Whereas during past times of rapid climate change, like glacial-interglacial transitions, species have tracked their required climate as it shifts across the landscape. This type of response is not an option for species whose last refuge is in nature reserves, which is the case for many endangered vertebrate species. At best, legislatively protected nature reserves comprise only 12% of Earth's land surface (NGS, 2006), and reserves typically are widely separated from one another by human-altered landscapes such as farms, ranches, cities, and dams. This makes each reserve essentially a small, isolated island.

The problems species face on that kind of landscape are threefold. First, there is little, if any, suitable habitat immediately outside the boundaries of most nature reserves, so species cannot track their climate zone from one to the next, even if they could disperse fast enough. Second, the rate of warming is so much faster than even the most rapid climate changes that species have seen in their past—some 10% to 300% faster than changes experienced at the Medieval Warm Period or glacial-interglacial transitions (e.g., Barnosky et al., 2003; Barnosky, 2009; Blois and Hadly, 2009)—that it is unknown whether many species are capable of dispersing at fast enough rates, even if suitable habitat corridors existed. Third, Earth is actually entering a new climate state in respect to what extant species and ecosystems have evolved in. No matter which IPCC scenario (IPCC, 2007) plays out, by approximately 2050 the global mean temperature will be hotter than it has been since *Homo sapiens* first evolved some 160,000 years ago, and under the more carbon-intensive A2 scenario, by 2100 Earth could be hotter than it has been in 3 million years, longer than many vertebrate species, and virtually all mammal species, have been in existence (Alroy, 1996; Avise and Walker, 1998; Avise et al., 1998; Alroy, 2000).

Those realities mean that saving individual species—that is, preserving biodiversity—will become increasingly difficult without intensive human manipulation of species ranges. Saving species as their climate disappears in a given reserve may well require moving them to other reserves where suitable climate exists; such “assisted migrations” already are underway

for insects and in active discussion phases for plants and other organisms (McLachlan and Hellmann, 2007; Zimmer, 2009). However, such human manipulation of species distributions could be the antithesis of maintaining naturally functioning ecosystems, if the assisted migrations result in ecological interactions that are outside the range of normal as we define it above (e.g., outside the variations a given ecosystem experiences through thousands of years in the absence of significant human intervention).

To sum up: today and in the coming decades, the successful practice of conservation biology requires (1) the recognition that ecosystems experience natural variation through time; (2) a means of distinguishing when the boundaries of that natural variation have been exceeded, and (3) understanding that the goal of saving species may soon be decoupled from the goal of maintaining ecosystems whose species interactions are not primarily orchestrated by humans. Therefore, the first essential contribution of vertebrate paleontology is to establish, in metrics that are easy to understand and possible to apply to modern systems, the range of variation that can be considered normal in the absence of significant human impact. The second essential contribution is to use what we know about past ecosystem dynamics to help structure biodiversity preserves that will become increasingly manipulated by humans, as we strive to keep endangered species alive.

DEFINING THE NATURAL RANGE OF ECOSYSTEM VARIATION THROUGH TIME

Ecosystems experience many kinds of variation through time. Over human lifetimes, for example, populations within species are known to wax or wane; new species may enter into an area because of natural dispersal or deliberate or unintentional introduction by people, or species may be lost from an area (extirpation) or globally (extinction). The relevant question for most land managers is a straightforward one: When are these kinds of observed changes a signal that something is going wrong with the ecosystem under their jurisdiction, and when do the observed changes simply reflect natural variation in a highly complex system? Here we give examples of how the vertebrate-fossil record can be used to separate signal (a change that indicates an ecological problem) from noise (natural variation in the ecosystem) using three different kinds

of metrics that are relevant and commonly considered in ecosystem management and conservation biology: population genetics, species composition and diversity, and extinction risk.

Population genetics

Species are comprised of populations, and together, those populations determine the geographic distribution of the species. The environment acts on the individuals in populations through time to influence where they can persist and where they thrive. All species have evolved suites of physiological, morphological, and behavioral attributes that they use to handle changes to their abiotic and biotic environments (Blois and Hadly, 2009). Variation in these attributes usually means that species can handle a greater range of challenges, and usually is underlain by genetic variation. Hence, assessing genetic variation within and between populations is a key aspect of assessing the viability of species within ecosystems (Gilpin and Soulé, 1986; Soulé, 1987). Genetic variability also provides evidence suggestive of the abbreviated history of events that populations experience through time (Ramakrishnan and Hadly, in press). Particularly large and recent events can leave profound marks on the genetic diversity of a species. For example, a severe reduction in population size of a species can eliminate almost all its genetic diversity through the process of random drift such as occurred, for example, in the cheetah (Menotti-Raymond and O'Brien, 1993), the elephant seal (Hoelzel et al., 1993) and the Wollemi pine (Peakall et al., 2003). Thus, not only does a severe population bottleneck event leave its historic mark on the genetic diversity of a species, it also increases the susceptibility of the species to stochastic environmental catastrophes because the species has fewer tools in its genetic toolkit. However, over long periods of time (hundreds of millennia to millions of years), if the species recovers and persists, even evidence of severe bottlenecks can be erased or mitigated since mutation and recombination will eventually contribute genetic novelty to the species. Our own species provides such an example, since *Homo sapiens* experienced very recent population expansion about 50,000 years ago (Atkinson et al., 2008). Without a temporal record of genetic diversity, discerning how frequently recovery from these bottleneck events occurs is impossible, yet it is critical since many species and their populations are now imperiled (Ceballos et al., 2005).

Where the right preservation conditions exist for long periods of time, fossil and subfossil specimens of vertebrates can harbor sufficient organic material to preserve DNA and thus temporal variations in genetic diversity, gene flow, and population size can be accessed. These prehistoric and historic samples of DNA, called 'ancient DNA' can reveal not only the identity of species in the absence of characteristic morphological traits, but also much about the genetic diversity of species and their populations through time. The fossil samples provide an empirical benchmark to which similar genetic assessments of extant populations can be compared and modeled, in order to identify any current population-genetic attributes that are out of the ordinary. This ancient genetic diversity can also reveal a "moving picture" of the population through time, indicating how and if species responded to environmental events in their history.

The practical applications of data from aDNA are diverse. For example, changes in genetic diversity of populations can be used to unravel specific responses to past climatic events, which is a powerful way to use the past to predict the future of certain species in the face of the current global warming crisis. While only a few species have been examined in this manner, it is becoming apparent that a species' genetic response to climate change is tightly tied to its life history strategy, and that fossil data are essential to interpreting what genetic variation in modern populations reveals about their future viability. In Yellowstone Park, for instance (Hadly et al., 2004), species characterized by low dispersal rates, such as pocket gophers, maintain similar haplotypes and low genetic diversity through climatic fluctuations that include a $\sim 1^{\circ}\text{C}$ local warming during the Medieval Warm Period and subsequent cooling during the Little Ice Age, and current populations are genetically very similar to ancient ones in spite of climate fluctuations. In contrast, species characterized by high dispersal per generation, such as voles, exhibit dramatic differences in particular genotypes between current and past populations, and highlight how misleading it may be to assume high genetic diversity in itself indicates sustainable populations. As population-size of certain species of *Microtus* decreased locally in northern Yellowstone Park during the Medieval Warm Period, their apparent diversity markedly increased. Modeling these data showed that the only way to explain this anomaly was that the local populations were replaced by extralocal ones, signaling that the area had

become a genetic sink rather than a source of genetic diversity. From the standpoint of conservation biology and ecosystem management, these fossil data provide critical insights that are simply impossible to gain by looking only at extant populations, namely: (1) low genetic diversity in pocket gophers (and by inference, in other kinds of low-dispersal species) is not necessarily a cause for concern in the face of global warming; and (2) high genetic diversity in voles (and by inference, other high-dispersal species) does not ensure that they are not under stress from habitat loss; in fact, it can indicate just the opposite. For high-dispersal species, landscape connectivity is clearly essential for population movement and recolonization.

In the bigger picture, studies on a variety of species hint at how changing environments, particularly climatic changes of the last 20 millennia, have governed past population movements (gene flow) in mammals, and thus what we might expect to see in extant species as environmental changes unfold in the future. Among the species for which ancient genetic information is now available are: brown bears (Barnes et al., 2002; Calvignac et al., 2008; Valdiosera et al., 2008), cave bears (Hofreiter et al., 2002; Orlando et al., 2002; Hofreiter et al., 2007), foxes (Dalen et al., 2007), gophers (Hadly et al., 1998), gray whales (Alter et al., 2007), horses (Orlando et al., 2006), humans (Lalueza-Fox et al., 2005; Weaver and Roseman, 2005; Belle et al., 2006; Lalueza-Fox et al., 2006), northern fur seals (Newsome et al., 2007), rats (Barnes et al., 2006), squirrels (van Tuinen et al., 2008), and voles (Hadly et al., 2004).

Ancient and historic data from museum specimens can also help to unravel histories of human manipulation of populations including hybridization between species and the impacts of overharvesting (e.g., Leonard, 2008). Studies detailing ancient genetic data for invertebrates and plants are much more limited, but can reveal the biotic compositions of ancient communities (e.g., Willerslev et al., 2007) and plant domestication (e.g., Gugerli et al., 2005).

Ancient DNA studies also have tracked genetic diversity associated with climatic change before and during population size change, in organisms such as bison (Shapiro et al., 2004), voles and gophers (Hadly et al., 2004), tuco-tucos (Chan et al., 2005, 2006), wolves and dogs (Leonard et al., 2002), horses (Weinstock et al., 2005; Orlando et al., 2008), and mammoths (Barnes et al., 2007). In some cases, nuclear genetic analysis has been used to ascertain phenotypic traits characteristic

of particular environments such as light versus dark coat color (Rompler et al., 2006).

In North American bison, a lineage that shows dwarfing during the latest Pleistocene to Holocene (Hill et al., 2008), ancient genetic data assembled from both North America and Asia from the past 150,000 years were interpreted to show evidence of population growth until approximately 37,000 years ago, when the population suffered loss in genetic diversity consistent with population size decline (Shapiro et al., 2004). Shapiro et al. (2004) concluded that the decline was likely due to climatic change since the timing of the decline was coincident with initiation of the last glacial maximum in Beringia and preceded evidence of human migration into the Americas. A subsequent, more sensitive analysis using the same data detected another more subtle event: population size in bison was at its minimum ~10,000 years ago (Drummond et al., 2005), a time coincident with extinction of megafauna in North America (Barnosky et al., 2004b; Koch and Barnosky, 2006), the peak in the last glacial maximum, and arrival of humans to North America. The analysis by Drummond et al. (2005) revealed that humans may also have played a role in the reduction in bison populations in Beringia, albeit subsequent to the initial effects of climatic change. Bison after 10,000 years ago showed population size recovery in North America until intensive historic hunting by European settlers. Thus, unraveling the timing of population size contraction and expansion using ancient genetic data and population genetic modeling enables us to better understand which factors may be responsible for events in species population histories. In the case of bison, these analyses also revealed that the species narrowly missed the fate of extinction that other megafauna suffered, and that the genetic diversity of this species today is but a vestige of its relatively recent past.

Besides its direct practical application in comparing present with past genetic variation, the study of ancient DNA has matured to the point where it is beginning to contribute substantially to population genetic theory, which underpins assessments of population viability in conservation applications. Empirical temporal data has been critical, because genetic change within lineages is a result of population-level processes that take place over generations, with cumulative effects building up over hundreds to thousands of years (Ramakrishnan and Hadly, in press). The key processes are recombination, mutation, selection, random genetic drift and

gene flow, with all but mutation strongly influenced by population size (Ramakrishnan and Hadly, in press). A persistent problem in population genetics has been sorting out which of these population-level processes dominates in explaining the genetic signature of a given population, especially when trying to assess whether environmental change has influenced (or is influencing) a genetic signature, because each process (except possibly recombination) is known to be influenced by the abiotic and biotic environments. For example, mutagenesis has been shown to vary by environment in some organisms, and further, environmental correlates such as rates of ultraviolet radiation may play an important role (Pawlowski et al., 1997). Environmental changes cause individuals to move in search of favorable habitats; as a result, individuals may disperse from one population to the next (gene flow); populations can increase or decrease in numbers of individuals (population size), and/or they may shuffle the percentage of adaptive or maladaptive traits (selection).

To untangle the role of environmental change from stochastic process, it is now possible to examine the expectations of genetic diversity using theoretical models of mutation, selection pressure, population size and gene flow that were developed to analyze ancient DNA sequence data (Ramakrishnan and Hadly, in press). When genetic change is directly observed through time, it becomes possible to disentangle which population processes were most likely responsible for the observed genetic diversity (Anderson et al., 2005; Drummond et al., 2005; Ramakrishnan et al., 2005; Chan et al., 2006). Such models, when supported by empirical temporal data, can discriminate whether populations were connected or isolated during periods of climatic change (Hadly et al., 2004; Hofreiter et al., 2004), the probable size of ancient populations (Chan et al., 2006) and whether changes in population size are concordant with what is known about the population biology of the species (Hadly et al., 2004). Indeed, the addition of ancient temporal data has been shown to increase the probability of revealing the correct evolutionary history of populations and species over modern data alone (Ramakrishnan et al., 2005), and to markedly enhance our ability to determine whether and how populations and species might adapt to climatic or other environmental changes.

Ancient DNA from species that became extinct at the Pleistocene-Holocene transition, such as mammoth or giant ground sloth (Poinar et al., 1998, 2003; Barnes

et al., 2007; Hofreiter, 2008a), or in the very recent past such as dodos, moas, and other birds (Sorenson et al., 1999; Huynen et al., 2003, 2008; Bunce et al., 2005; Allentoft et al., 2009), has yielded insights about how climatic or human perturbations affected the last populations of the species, and in turn inform us about signs of impending extinction in today's animals. Such ancient samples are not yet sufficient to quantify how much reduction in genetic variation signals impending extinction, although studies of threatened animals show that the majority suffer loss in genetic diversity before they are driven to extinction (Spielman et al., 2004). Ancient genetic studies have the potential to help us understand whether the majority of species experiencing extinction did so prior to losing genetic diversity because of events affecting populations, or whether the loss of genetic diversity itself makes species more extinction-prone.

Obtaining information from aDNA is not without its challenges. It requires a dedicated lab physically separated from facilities where modern DNA is extracted and sequenced, and extraordinary procedures to guard against contamination. Reconstructing the ancient genetic sequences of individuals of course also requires adequate fossil localities that preserve fossil vertebrates (usually bones or teeth). In order to preserve DNA, specimens must be rapidly buried and protected from wide swings in temperature. Favorable conditions are most frequently found at high latitudes where bones may be preserved in permafrost, or within sheltered environments such as caves, or where the environment is exceptionally arid (Hofreiter et al., 2001). Tropical areas generally are not optimal for long-term organic preservation, and thus ancient DNA from the tropics is rare. Additionally, sequencing and amplifying ancient genetic data is difficult because the pieces of DNA that manage to be preserved for even brief periods of time after the death of an animal are usually short (~100-300 basepairs) and over time, the number of copies of this sequence will decline dramatically, meaning that accessing ancient DNA sequences has a hypothesized limit of less than 100,000 years (Handt et al., 1994; Lindahl, 2000; Willerslev and Cooper, 2005). Rarely DNA may be preserved longer than 100,000 years in very cold environments (Willerslev et al., 2007), and there are reports of much older protein sequences (Asara et al., 2007). Finally, most aDNA studies are constrained to use mitochondrial DNA because of its abundance in the mammalian genome: it is at least 3600 times more

common than nuclear DNA in humans (Miller et al., 2003).

Despite these limitations, molecular paleontologists already have the ability to determine the cadence of genetic variation within populations over time in important cases, as exemplified by the numerous studies cited above. Further, as sequencing technology becomes more streamlined, it should eventually be possible to reconstruct genomic-level variation, which holds great promise for understanding both variation in neutral regions of the genome as well as those genetic areas under selection (Hofreiter, 2008b).

Species composition and diversity

Three important metrics that are useful and relatively easy to monitor in ecosystems are species composition (what species are there), species abundance (how common or rare individuals of a species are), and species richness (how many species there are). Species composition is important because species are thought to conserve their ecological niches through time (Ackerly, 2003; Martinez-Meyer et al., 2004; Wiens and Graham, 2005; Hadly et al., in press). Thus, the presence of a given species indicates the presence of a given ecological niche, and in turn, the persistence of species indicates persistence of the ecological niches that define a given ecosystem. Species abundance is related to the life history attributes of a species (body size, generation time, habitat preference, trophic group, etc.) and also to the abundance of habitats within the ecosystem that can support individuals of a given species (Blois and Hadly, 2009). Pronounced changes in abundance, particularly in the relative abundance of species as compared to each other, indicates at least changes in landscape characteristics (for example, expansion of arid microhabitats at the expense of mesic ones) and can indicate major shifts in how species interact (for example, decrease in predators that in turn lead to increased herbivore populations with attendant effects on vegetation). Species richness is critical to monitor because it is correlated with important ecosystem attributes such as productivity, disturbance regime, and habitat heterogeneity (Rosenzweig, 1995; Barnosky et al., 2001; Hadly and Maurer, 2001; Cardinale et al., 2002); dramatic changes in richness thus indicate fundamental changes in the ecological niches within an ecosystem and in the connections between niches.

In the fossil record it is usually possible to identify mammal species by dental, cranial, or other osteologi-

cal features, and many amphibian, reptile, and bird species also can be identified from bones. In cases where morphological features are not diagnostic, the ancient DNA techniques discussed above can often be applied to assess species identity. For example, in a study of the influence of tectonics and climate on the long-tailed vole (*Microtus longicaudus*) in the Greater Yellowstone Ecosystem, ancient DNA was used to discern the frequency of *M. montanus* vs. *M. longicaudus*, which lack diagnostic traits on isolated teeth necessary to distinguish between the two species (Spaeth et al., 2009). From the perspective of conservation biology, identifying which species were present in the past becomes critical, because the management questions of interest typically require knowing: (1) what species “should” be present in a given ecosystem in the absence of significant human manipulation; (2) is the loss or gain of a given species unusual; and (3) are the normal number of species one would expect the ecosystem to support actually there? As with analyses of ancient DNA to assess population-level changes, the vertebrate fossil record offers a rich source of answers for these species- and community-level questions, which yield both practical and theoretical information for land managers.

The most relevant fossil information to apply to the first two questions comes from paleontological deposits that accurately sample the living communities of the past, and from time frames during which extant species, or at least species that are closely related to extant ones, had already evolved. Typically these are fossil deposits that extend back a few thousands to a few hundreds of thousands of years (although essential information also comes from older deposits; see below). Some of the best community samples come from deposits in caves and rockshelters, where woodrats (*Neotoma* spp.) den and drag bone-laden pellets of carnivores, raptors, and small pieces of decomposing large-mammal skeletons into their nests. The same caves or rockshelters are often used by large carnivores for their dens, and their bones and the bones of their prey add to the sample of skeletal materials that eventually become fossilized. Typically, abundant organic material in these deposits, including the bones themselves, provide opportunity for multiple radiocarbon dates that can be used to refine chronologies, and to assess the extent of time-averaging (that is, how many years a given community-sample actually took to accumulate). Detailed analyses of modern communities sampled by similar vectors demonstrates very high fidelity between the sample and the living animals

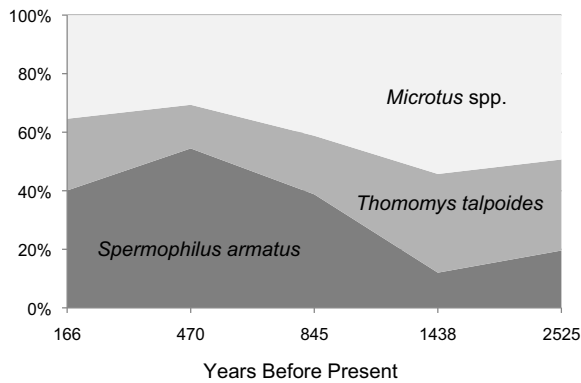


FIGURE 1.—Relative abundance fluctuations of the three most common small mammals through the late Holocene at Lamar Cave, Yellowstone National Park, Wyoming (N=2835 *Microtus* spp. specimens; N=2210 *Spermophilus armatus* specimens; N=1552 *Thomomys talpoides* specimens). Ages are median calendar years before present of several stratigraphic levels based on a detailed radiocarbon chronology. Note that during relatively arid times such as during the Medieval Warm Period (~800-1200 ybp), *Spermophilus* rises in abundance at the expense of *Microtus* and *Thomomys*, and declines during cooler, wetter intervals. Nevertheless, these three taxa remain as the most common taxa in the community, which includes a total of 40 mammalian species from the cave. Data are from Hadly (1996).

on the landscape, especially for presence-absence and relative abundance of small mammals, birds, and amphibians that live within about 5 km of the fossil site (Hadly, 1999; Porder et al., 2003; Terry, 2008). Fortunately, cave and rockshelters that hold such deposits are widely distributed throughout the Appalachians, Rocky Mountains, Great Basin, Pacific Northwest, and Sierra Nevada—exactly the areas that hold abundant publicly administered lands so important in conserving species and ecosystems. Where caves and rockshelters are not present, the opportunity for high-fidelity samples of fossils sometimes exists in fluvial and riparian environments, as shown by recent studies that compare bone accumulations with the living community in Africa (Behrensmeier et al., 2003; Western and Behrensmeier, 2009).

When adequate fossil information is available it is relatively straightforward to determine whether modern species composition has been significantly perturbed from what existed prior to anthropogenic dominance. The approach of using Holocene fossil deposits to inform land management decisions has already been used in Yellowstone National Park, where fossils

from Lamar Cave demonstrated that all of the mammal species now protected in the park, including wolves, grizzly bears, and elk, species whose management has been controversial (NRC, 2002), were common in that ecosystem for at least the past 3000 years. The only mammal species that is missing is a vole (*Microtus ochrogaster*) that always was at very low abundance (Hadly, 1996, 1999). Although the birds and amphibians from the deposit have not been studied in as much detail, species composition in those groups likewise seems to have remained relatively stable over the past few thousand years. Examples of other areas where the Holocene fossil record is rich and useful in demonstrating that the mammals on the landscape today largely reflect the species composition of the past few thousand years include northern California (Blois, 2009), the Great Basin (Grayson, 1998; Grayson and Madsen, 2000; Grayson, 2006; Terry, 2007), the Great Plains (Semken and Graham, 1996), and the Appalachians (Guilday, 1971, 1984).

A great value of cave and rockshelter sites that have successive layers of high-fidelity fossil deposits—or any such stratigraphic sequence—is their utility in tracking fluctuations in abundance of various taxa through time. Usually, it is only the small-mammal component of the community for which numbers of specimens are adequate to analyze abundance changes; nevertheless, those are precisely the kinds of organisms that can also be easily monitored in modern ecosystems in order to compare present with past, and they have greater sensitivity to microhabitat changes than do larger mammals (Hadly, 1996). The fossil deposits demonstrate that pronounced fluctuations in abundance are characteristic in a given ecosystem over the 100-year, 1000-year, 10,000-year, and 100,000-year time scales. Relative abundance fluctuations clearly are the normal, early response to climatic changes of the past. For example, in Lamar Cave in Yellowstone Park, voles of the genus *Microtus* are the most abundant small mammals during cool, moist periods, and ground squirrels (genus *Spermophilus*) are most abundant during arid times (Hadly, 1996; Hadly et al., 2004) (Fig 1.). Each abundance state lasts at least a few hundred years. But the same kinds of relative abundance shifts also manifest at longer time scales: for example, at Porcupine Cave, Colorado, voles and lemmings are most abundant during cool, moist glacial times, but ground squirrels increase in abundance during more arid interglacials (Barnosky, 2004b). In this case, the

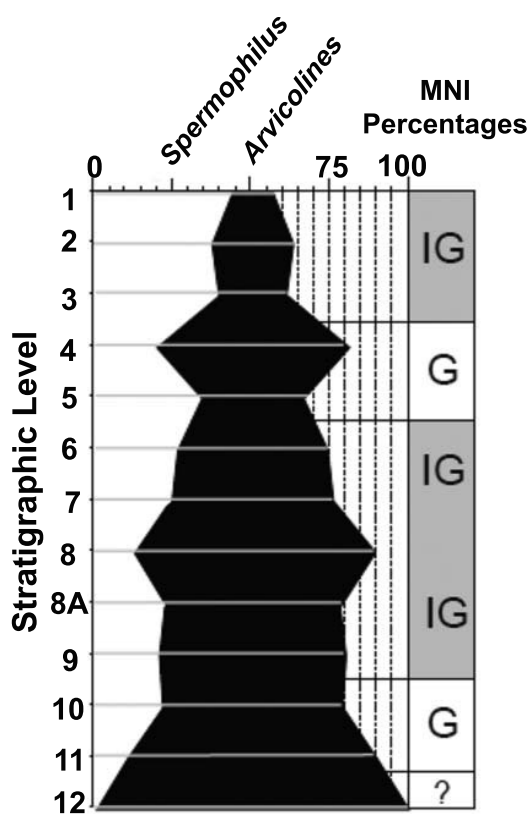


FIGURE 2.—Relative abundance of ground squirrels (*Spermophilus* spp.) in respect to voles and lemmings (arvicolines) through >100,000 years at Porcupine Cave, South Park, Colorado. Level 1 is roughly dated to 800,000 years old (but could be somewhat younger) and Level 12 to at least 900,000 years (but could be somewhat older). Climatic interpretations for each group of stratigraphic levels are interpreted from the sediments, not from the fauna, and are indicated by the abbreviations on the right of the diagram; IG=interglacial; G=glacial. The sediments indicate that the topmost interglacial (Levels 1-3) was dramatically more arid than any previous time represented by the record. Note that both ground squirrels and arvicolines are common throughout the >100,000 years represented by the record, but that during the very arid time represented by Levels 1-3, ground squirrels begin to outnumber arvicolines after tens of thousands of years of arvicolines being generally more abundant. Data are from Barnosky (2004b).

abundances appear relatively stable for thousands of years, before switching in pace with climatic changes (Fig. 2). From the land-management perspective, then, observed shifts in relative abundance of taxa provide an early warning signal that environmental changes are

affecting an ecosystem, but in themselves do not indicate an ecosystem has been perturbed from its “normal” state. Access to such paleontological data enables researchers to predict which species are likely to be affected by global change, whether they will increase or decrease in abundance, and to what extent their populations have adjusted in the past.

However, in terms of relative abundance of taxa, the paleontologic record also demonstrates that in terrestrial ecosystems where we have adequate records (Appalachians, Rocky Mountains, Great Basin, Great Plains, California), three or four genera tend to dominate in abundance throughout hundreds to thousands of years in a given place, even though rank-order abundance among the three or four most common genera fluctuates in accordance with environmental changes. For example, the top three genera in abundance throughout the entire 3000-year record for Lamar Cave are *Spermophilus* (ground squirrel), *Microtus* (vole) and *Thomomys* (pocket gopher) (Hadly, 1996) (Fig. 1); and for most of the >100,000 year record at Porcupine Cave, the dominant genera are *Mictomys* (vole), *Spermophilus* (ground squirrel), and *Neotoma* (wood rat) (Barnosky, 2004b). In fact, abundances of all small mammal genera are significantly correlated between these two sites, which are separated by 785 km and some 900,000 years (Fig. 3). These genera (listed in Fig. 3) clearly serve as important components—essentially defining a core set of taxa—in the North American montane taxon pool. Abundance changes that would indicate perturbation from a normal ecosystem state, then, are, if any of the most abundant genera dwindled to lower ranks in the abundance hierarchy, or more critically, became extinct. Actual loss of genera from an area would provide a very clear signal that an ecosystem has been perturbed into a new state, since the fossil record demonstrates constancy in genera and abundance patterns through nearly 1 million years in the studied mammalian communities (Fig. 3) (Hadly and Maurer, 2001; McGill et al., 2005).

The Holocene and Pleistocene fossil records indicate that minor changes in species composition also are normal through the course of time ecosystems typically exist. Generic similarity of communities in space and time is apparent across even isolated montane regions (Hadly and Maurer, 2001). Perhaps most indicative of this are records such as Porcupine Cave, which demonstrated species turnover within genera, but very little change in the number of species found in each

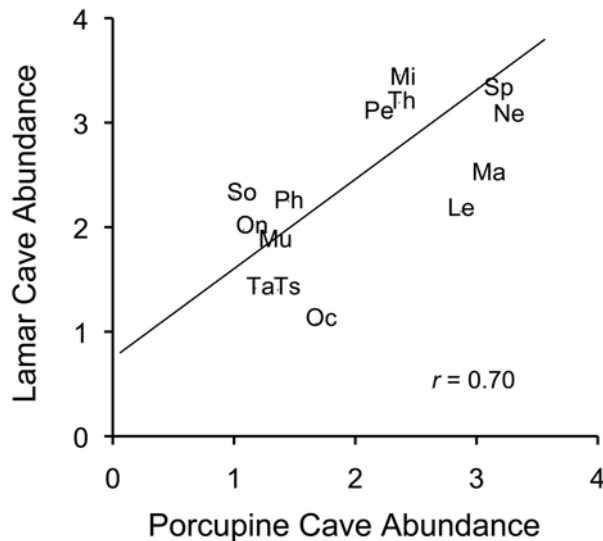


FIGURE 3.—Assessment of community composition and abundance of individuals at the taxonomic level of genus for a relatively recent paleontological site (Lamar Cave, Wyoming, <3200 years) and a relatively old site (Porcupine Cave, Colorado, >600,000-900,000 years), both in a Rocky Mountain ecosystem though widely separate both spatially and temporally. The axes are log₁₀-scale in units of number of identified bones. Each symbol on the graph represents the number of specimens of a particular genus found at each site, summed across all levels. The Pearson r value is significant at $P = 0.001$. The line is a ranged major axis regression. Pairwise comparisons of other sites indicate a similar result, namely, that the characteristic assemblage of small mammals in mountain and intermontane ecosystems of the United States includes not only genera typically represented by abundant numbers of individuals, such as *Spermophilus*, *Microtus*, and *Thomomys*, but also “rare” genera represented by few individuals such as the western jumping mouse *Zapus*, and thus the ‘species pool’ of western North America has persisted with the same constituents for at least ~900,000 years (McGill et al., 2005). Abbreviations: Cl—*Clethrionomys*; Le—Leporidae; Ma—*Marmota*; Mi—*Microtus*; Mu—*Mustela*; Ne—*Neotoma*; Oc—*Ochotona*; On—*Ondatra*; Pe—*Peromyscus*; Ph—*Phenacomys*; So—*Sorex*; Sp—*Spermophilus*; Ta—*Tamias*; Ts—*Tamiasciurus*; Th—*Thomomys*; Za—*Zapus*.

trophic and body-size group through >100,000 years and at least two glacial-interglacial climatic transitions (Fig. 4) (Barnosky, 2004a, b; Barnosky et al., 2004a). This, and the abundance data summarized above, suggests that a key indicator that an ecosystem is functioning within its natural range of variation is simply

maintaining adequate numbers of species within each genus, with species identity being less important. Put simply, in terms of ecosystem function, one species of pocket gopher (genus *Thomomys*) may be as good as the next, but pocket gophers are long-term dominant members of North American mammalian communities and fill a critical niche.

Such species substitutions in a given place are most evident coincident with rapid climate changes, such as the warming that accompanies the shift from glacial to interglacial climate states (Guilday, 1971, 1984; Barnosky, 2004a; Blois, 2009; Blois and Hadly, 2009). In that light, counter-intuitively, maintaining species diversity becomes particularly important, especially in the face of today’s known environmental pressure of rapid climate change. This is because the only way it is possible to substitute one species for another to maintain ecosystem function as climate changes is if there is a large reservoir of species to draw on (Hadly et al., in press), and if those species can disperse between sites. Numerous paleontologic and neontologic studies have demonstrated that species divide their geographic range by climate space (Martinez-Meyer et al., 2004; Davis, 2005; Wiens and Graham, 2005; Elith et al., 2006; Hijmans and Graham, 2006; Nogues-Bravo et al., 2008; Blois, 2009; Hadly et al., in press). To continue with the pocket gopher example, while any species of *Thomomys* might be suitable for filling the pocket gopher niche in an ecosystem, only certain species seem able to thrive in specific places characterized by certain climatic parameters. Some species inhabit relatively cooler, moister parts of the entire range of the genus, whereas other congeners are restricted to relatively more arid parts of the range (Blois, 2009). For instance, in northern California, where the geographic ranges of three species of *Thomomys* are in close proximity, it is evident that the species that adapted to cool, moist microhabitats was replaced by the species adapted to drier habitats at the Pleistocene-Holocene transition (Blois, 2009). It seems likely that such “climatic plasticity” for a genus is possible only by maintaining multiple congeneric species (Hadly et al., in press).

Another important lesson of the fossil record is that the number of species in a given ecosystem—species richness—tends to vary little over at least thousands to hundreds of thousands of years, despite species turnover. For example, characteristic species richness during interglacial climates for non-volant terrestrial mammals in Rocky Mountain ecosystems seems to

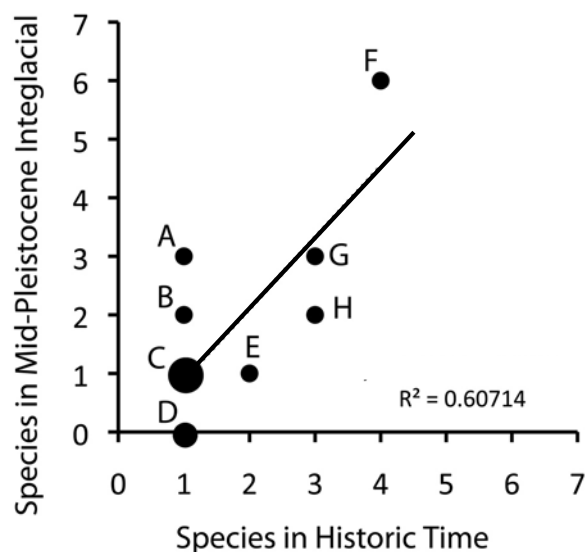


FIGURE 4.—Comparison of numbers of species within each higher taxonomic group in the modern community around Porcupine Cave, Colorado, and the >600,000-year-old fossil community from a mid-Pleistocene interglacial (Level 1). Size of circle represents number of groups for each comparison. Abbreviations for each taxon: A—*Neotoma*; B—*Cynomys*; C—*Ochotona*, *Marmota*, *Tamiasciurus*, *Peromyscus*, *Thomomys*, *Ondatra*, *Erethizon*; D—*Sciurus*, *Zapus*, *Castor*; E—*Tamias*; F—Arvioclines (voles and lemmings); G—Leporids (rabbits); H—*Spermophilus*. While species numbers are similar for most taxonomic groups, the species in the fossil deposits are for the most part different species than those representing the corresponding genera today (Barnosky et al., 2004a).

be around 40 species as demonstrated over thousands of years in Yellowstone Park (Hadly, 1996) and 45-50 species as tracked over hundreds of thousands of years in South Park, Colorado (Barnosky et al., 2004a; Barnosky and Shabel, 2005). Thus, reduction of mammalian species much below those numbers would clearly be an ecological danger sign in a Rocky Mountain land-management unit. Similar comparison of Pleistocene and Holocene diversity with modern diversity can provide the same kind of valuable information in other regions, although we are only just now reassessing modern species richness subsequent to climatic change and the massive landscape alteration that has characterized the last few decades in North America.

Non-anthropogenic climate change seems to affect species richness primarily in the lower size and lower trophic categories. For example, the character-

istic glacial fauna in Colorado has 29 species in those categories, and the characteristic interglacial fauna has 24; little change is evident across climatic boundaries in other size and trophic groups (Barnosky et al., 2004a). In northern California, the small mammal component exhibits declines in both richness (from 13 species to 9 species) and evenness (with deer mice becoming much more common) as climate warms at the beginning of the Holocene (Blois, 2009). Decline in species richness as Holocene warming commenced has been reported for voles and shrews, voles in sites from Pennsylvania, extending south through the Appalachians into Tennessee, into Texas (Graham, 1976). Mechanistically, the loss in richness at the beginning of the Holocene seems to involve geographic range shifts of climatically sensitive species into refugia (Graham and Grimm, 1990; FAUNMAP Working Group, 1996). These observations suggest that in modern land-management units, a decline in small mammal richness and/or evenness might be an early warning sign that global warming is beginning to alter community structure, and thus, ecological relationships.

On a broader scale, with the advent of computerized databases that make it possible to map fossil mammal occurrences from just a few hundred years back through millions of years ago (Carrasco et al., 2007; MIOMAP, 2009; NEOTOMA, 2009; NOW, 2009; PBDB, 2009), it now is possible to assess the range of normal for species richness for entire biogeographic provinces and for large portions of continents. Comparisons of these regional baselines determined from the fossil record with corresponding current species richness values can reveal which landscapes are least impacted by human activities, and serve as benchmarks by which to assess the success of conservation efforts in the future.

Extinction

One of the most cogent lessons from the fossil record is that the coincidence of unusual events can elevate extinction rates to dangerous levels (Arens and West, 2008; Brook, 2008; Brook et al., 2008; Brook and Barnosky, in prep.). While each of the 'Big Five' mass extinctions (Jablonski and Chaloner, 1994) illustrates that in its own way, perhaps the most relevant example from the standpoint of conservation biology is the end-Pleistocene megafauna extinction, which deleted approximately half of the mammal species alive that were in the >44 kg body size categories. While

considerable debate has raged as to the primary cause of those extinctions (Martin and Wright, 1967; Martin and Klein, 1984; MacPhee, 1999), it is now clear that most taxa succumbed only after human populations on a given continent or island reached critical mass (MacPhee and Marx, 1997; MacPhee and Fleming, 1999; Alroy, 2001; Brook and Bowman, 2002; Barnosky et al., 2004b; Wroe et al., 2004; Steadman et al., 2005; Koch and Barnosky, 2006; Brook et al., 2007; Barnosky, 2008; Brook and Barnosky, in prep.). It is also clear that end-Pleistocene global warming contributed to extinction in some places where animals couldn't migrate in response to climate change either because of natural barriers or because of intervening human populations or land alteration (Barnosky, 1986; Barnosky et al., 2004b; Koch and Barnosky, 2006). Finally, extinctions were most severe in areas where first human entry into the ecosystem coincided with end-Pleistocene warming (Barnosky et al., 2004b; Koch and Barnosky, 2006; Nogues-Bravo et al., 2008; Barnosky, 2009; Brook and Barnosky, in prep.). The general picture that emerges is that the synergistic effects of abnormally fast human population growth and abnormally fast global climate change were particularly pernicious in the past, and direct human impacts often affect animals in the highest size and trophic categories (e.g., the big animals), in contrast to climate change, where effects are most obvious in the lower size and trophic categories.

There are clear parallels with what is happening today and projections for the next few decades, as the human population rises from an already all-time high of near 7 billion to an inevitable 9 billion or so, and as global temperatures rise at unprecedented rates to take us into a global climate hotter than humans have ever seen, all by the year 2050 (IPCC, 2007). On that landscape, direct human effects will be impacting large animals dramatically and climate change will be impacting small animals and plants; ecosystems will be squeezed from both the top down and the bottom up. Non-human species are certain to have their geographic ranges fragmented even more than they already are, and will see severe diminishment of opportunities to track their needed climate envelope as Earth's climate zones shift around the landscape. Inevitably, many species can be expected to perish under this scenario without stepped-up conservation efforts that recognize both what the past has to teach us about what is "normal," and also that new strategies must be implemented to cope with the new challenges (Barnosky, 2009).

SUGGESTIONS FOR THE FUTURE

Key lessons from the vertebrate fossil record are that population genetic structure, rank-order generic abundance, and species richness tend to remain remarkably stable in ecosystems through thousands of years, with relatively minor adjustments at lower size and trophic levels triggered by climate changes. Most of the adjustments—for example, switches in which of the top-ranked genera are most abundant, the replacement of species by congeners, or loss or gain of a few small herbivore species—ultimately result from shrinking or expanding populations that build up to major alterations in geographic ranges for species as they track their habitats across a dynamically changing landscape (Blois and Hadly, 2009). We also now know that at least the mammalian component of communities is structured differently than it was for millions of years prior to anthropogenic dominance, in that the largest mammals—essentially the entire right tail of the characteristic body size distribution for mammal communities—have been lost from most ecosystems. The only remaining exceptions are in some nature preserves in Africa, which still have nearly the full complement of large-bodied species (Lyons et al., 2004).

The good news for conservation biology is that some 46% of Earth's terrestrial landscape can be classified as reasonably ecologically intact, if "ecologically intact" is defined as patches of land that are at least 10,000 km², inhabited by <5 people/km², and containing at least 70% native vegetation (Mittermeier et al., 2003). Species in some of those ecologically intact places (the 12% of Earth's surface that comprises nature reserves, as noted above) are legislatively protected. A major challenge for conservation biology in the 21st century, however, is how to keep ecosystems in such places functioning as they have for millennia, given the pressures they are facing. Long recognized threats include habitat fragmentation, invasive species, and resource consumption by ever-growing human populations, and added to these is the newest threat of abnormally rapid and severe global warming (Barnosky, 2009).

All of these pressures combine to prevent the very mechanism that has allowed ecosystems to equilibrate to environmental perturbations in the past: the expansion and contraction of populations across the landscape to rapidly adjust species ranges such that the particular ecological niches that define a given kind of ecosystem can be filled in a given locale. Species have

increasingly fewer avenues open to them to relocate to novel protected geographic locations within their preferred environment. Especially problematic in this context is the rapidity of global warming and the fact that the Earth is entering a new climate state in respect to the species that now exist on it. It is unknown whether many species even have the inherent capacity to keep pace with the climate changes now in progress, even if needed dispersal routes were available.

In view of that, it will not be enough to simply try to preserve species where they now exist; for many species, it will also become necessary to predict where they will be able to exist as changing climate deletes their current habitats in the places where they now are restricted. In that context, vertebrate paleontology has been (Graham, 1984, 1997; Graham and Mead, 1987; Graham and Grimm, 1990; Wood and Barnosky, 1994; Blois, 2009; Blois and Hadly, 2009; Hadly et al., in press) and will continue to be important in developing and ground-truthing ecological niche models.

Critical to conservation will be providing mechanisms by which species can actually get to the places they need to be. On landscapes increasingly fragmented by human use, those mechanisms very likely will include “assisted migration,” a conservation approach already employed for butterfly species (Zimmer, 2009), and under active discussion by the conservation community (McLachlan and Hellmann, 2007). In essence, assisted migration is an approach where people decide which species need to be moved and where they need to go, and put them in a truck or car to transport them.

The obvious problem with assisted migration is deciding which species can be inserted into a new place without disrupting the ecological structure and function that already exist there. In that context, the lessons from the vertebrate fossil record become extremely important. They show, for example, that in the face of environmental perturbations, ecosystems tend to maintain species richness by substituting congeners, particularly at lower trophic levels. Thus, as monitoring identifies certain small mammal species that may be foundering as climate change degrades their habitat, it may well be ecologically sound to introduce congeners that have demonstrated climatic suitability, but that could not disperse there naturally. On the other hand, it probably would not be ecologically sound to introduce species from size or trophic groups, or taxonomic groups, which had not been present in the ecosystem for thousands of years, if the goal was to maintain eco-

system structure and function within the range of variation exhibited over millennia.

The vertebrate fossil record also has an important statement to make about conservation of species in Africa. Africa is the only place left on Earth that still has ecosystems that are operating much as they have for hundreds of thousands of years, in that they still have almost the full complement of animals in the largest size categories. Those ecosystems somehow escaped the ecological restructuring that humans precipitated everywhere else by contributing to extinctions of megafauna (Lyons et al., 2004; Barnosky, 2009). In that light, preservation of megafauna in Africa is doubly important, in that its loss would not only mean loss of the species themselves, but also loss of the only remaining ecosystem that gives us a hint of how Earth functioned with a fully-stocked complement of mammalian species.

Solving the problem of how to preserve those large-bodied species in Africa is particularly complex, given human needs, cultural traditions, and climate trends on the continent. One innovative suggestion originating from a group of vertebrate paleontologists and conservation biologists is a new strategy called “Pleistocene Re-wilding,” which seeks to restore non-African ecosystems to their Pleistocene condition of including many species in the largest body-size categories (Donlan, 2005; Martin, 2005; Donlan et al., 2006; Caro, 2007). In brief, “Pleistocene Re-wilding” would use African species as ecological analogs to repopulate ecosystems in North America with large-bodied animals. Opponents have pointed out many serious political and ecological problems that would result (Chapron, 2005; Dinerstein and Irvin, 2005; Schlaepfer, 2005; Shay, 2005; Smith, 2005; Rubenstein et al., 2006). Not least among those is introducing new genera of animals into ecosystems that had never seen them, or even seen their ecological analogs in more than 10,000 years. There are also the theoretical difficulties of trying to reconstruct what is essentially a cool-climate ecosystem in an interglacial time that is becoming abnormally hot, and arbitrarily choosing the pre-Holocene ecosystem as the definition for “normal.” Nevertheless, if “Pleistocene Re-wilding” were restricted to large game-parks set aside outside of Africa with the explicit recognition that the goal was simply to preserve endangered species in an ecological setting that would allow individuals to maintain viable population reservoirs, it could accomplish a valuable conservation goal. It would be impor-

tant to acknowledge, however, that such places were in effect large zoos, not ecosystems that were functioning within the bounds of variation that had existed in those areas through the last several millennia.

CONCLUSIONS

Vertebrate paleontology has matured to the extent that it has much to offer conservation biology. Foremost is that the vertebrate fossil record provides a practical and theoretically sound way to define 'natural' for the purposes of establishing conservation targets: essentially, as maintaining the ecological structure and function of a given area within the range of variation that existed before humans dominated the landscape. Since we live in an interglacial, a practical guideline would be to maintain ecosystems within the range of variation they exhibit during interglacial times. Since we live in a rapidly warming world, another guideline would be to facilitate the adaptive response that species showed to previous times of rapid warming, exemplified by the transition from glacial to interglacial times. In practice, this will mean facilitating the dispersal of the right kinds of species into suitable refugia.

Vertebrate paleontology also offers practical guidelines for monitoring ecosystems to assess how closely they approximate the natural condition as defined above. At the population level, genetic structuring and diversity can now be sampled locally and across space, and then modern conditions compared with the temporal changes to assess whether they fall within or outside the range of variation exhibited in the past. Analyses of ancient DNA have demonstrated that interpretations of modern genetic diversity must be made in the context of life-history strategy of the species in order to be meaningfully applied towards conservation goals. At the species level, vertebrate paleontology has shown that many areas still have the complement of species that can be considered normal for an interglacial climate, and where they don't, which kinds of species are missing. It also becomes clear through the vertebrate fossil record that the rank-order abundance of genera remains fairly stable through time, and that most changes in rank-order involve primarily just two or three of the top-ranked genera whose abundance changes in step with local environmental changes. Species richness, both overall and within size and trophic category, is likewise reasonably stable through long time periods, although species composition may change. Changes in species

composition usually take place simply by replacing one species within a genus with another species of the same genus, with the replacing species being more adapted to local microhabitats. Finally, the vertebrate fossil record has shown that species richness through most of the present interglacial is depauperate with respect to glacial times, previous interglacials, and pre-Pleistocene times. In large part this is because the synergy between human population expansion and end-Pleistocene climate changes resulted in widespread megafaunal extinctions, but for small mammals, may also reflect an overall pattern of decreased diversity during warmer times, at least in the conterminous USA.

These benchmarks derived from the vertebrate fossil record provide practical ways to recognize danger signs in modern ecosystems, that is, signs that the ecosystem is changing more than it has in thousands of years. Among these danger signals are: declines in genetic diversity (taking into account life history strategy of the species of interest and the diversity baseline established through ancient DNA analyses of similar taxa); declines in the population size of species in top-ranked genera, especially when a formerly top-ranked species falls into rarer categories; loss of species without replacement by a congener; decline of species richness below normal values demonstrated by the fossil record for that ecosystem; and, especially for Africa, loss of any large mammals. Because the synergy between a fast-changing climate and increasing human populations that caused megafauna extinction in the past is ramping up again today, it is particularly critical to anticipate the elevated extinction pressures before it is too late to do anything about them.

Finally, it is clear that in the next few decades, conservation efforts will have to employ some new strategies to conserve biodiversity in an increasingly human-dominated world. In this too, information from the vertebrate fossil record will be essential to predict, among other things, the ecological effects of attempting to save species and ecosystem function and structure by assisting the migration of species. For example, past ecological adjustments in the absence of humans suggest species richness and ecosystem function might effectively be maintained by replacing a species that may be dwindling in a given ecosystem with a congener that likely would have been able to get there in the absence of human-induced habitat fragmentation. However, there is no paleontological justification for introducing a supposed ecological analog that is taxo-

nominally distant.

As we move into a world where extinction pressures intensify and correspondingly step up efforts to save individual species, there is a hidden danger. Increasingly, what it will take to save individual species will be the opposite of what it will take to save ecosystems that maintain some semblance of the interactions of species that operate and adjust in the absence of human domination. For example, strategies such as assisted migration and Pleistocene Re-wilding, important as they may be in keeping species alive, ultimately result in ecosystems that are manipulated by humans, which means the loss of places where ecosystem processes play out without a heavy human hand. Thus, to attain a full range of nature preservation, it will also be necessary to set aside preserves where species manipulation is off-limits, essentially Earth's control plots where we simply observe how ecosystems cope in this new world. In this vein, we suggest that vertebrate fossil record will be particularly crucial, as it will be a key yardstick by which we can ascertain how much terrestrial species, communities, and ecosystems of the future are changing, and what that means for planetary health.

ACKNOWLEDGMENTS

We thank Jessica Blois, Robert Feranec, Greg Dietl, and an anonymous reviewer for commenting on the manuscript. Thanks to Greg Dietl and Karl Flessa for inviting us to the Paleontological Society Short Course on Conservation Paleobiology. Funding that contributed to these ideas and research was provided by grants from the National Science Foundation programs in Sedimentary Geology and Paleobiology and the Ecology Cluster of Division of Environmental Biology.

REFERENCES

- ACKERLY, D. D. 2003. Community assembly, niche conservatism, and adaptive evolution in changing environments. *International Journal of Plant Sciences*, 164(3):S165-S184.
- ALLENTOFT, M. E., S. C. SCHUSTER, R. N. HOLDAWAY, M. L. HALE, E. MCLAY, C. OSKAM, M. T. P. GILBERT, P. SPENCER, E. WILLERSLEV, AND M. BUNCE. 2009. Identification of microsatellites from an extinct moa species using high-throughput (454) sequence data. *Biotechniques*, 46(3):195-200.
- ALROY, J. 1996. Constant extinction, constrained diversification, and uncoordinated stasis in North American mammals: New perspectives on faunal stability in the fossil record. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 127(1-4):285-311.
- ALROY, J. 2000. New methods for quantifying macroevolutionary patterns and processes. *Paleobiology*, 26(4):707-733.
- ALROY, J. 2001. A multispecies overkill simulation of the end-Pleistocene megafaunal mass extinction. *Science*, 292:1893-1896.
- ALTER, S. E., E. RYNES, AND S. R. PALUMBI. 2007. DNA evidence for historic population size and past ecosystem impacts of gray whales. *Proceedings of the National Academy of Sciences of the United States of America*, 104(38):15162-15167.
- ANDERSON, C. N. K., U. RAMAKRISHNAN, Y. L. CHAN, AND E. A. HADLY. 2005. Serial SimCoal: A population genetics model for data from multiple populations and points in time. *Bioinformatics*, 21(8):1733-1734.
- ARENS, N. C., AND I. D. WEST. 2008. Press-pulse: A general theory of mass extinction? *Paleobiology*, 34(4):456-471.
- ASARA, J. M., M. H. SCHWEITZER, L. M. FREIMARK, M. PHILLIPS, AND L. C. CANTLEY. 2007. Protein sequences from mastodon and *Tyrannosaurus rex* revealed by mass spectrometry. *Science*, 316(5822):280-285.
- ATKINSON, Q. D., R. D. GRAY, AND A. J. DRUMMOND. 2008. mtDNA variation predicts population size in humans and reveals a major southern Asian chapter in human prehistory. *Molecular Biology and Evolution*, 25(2):468.
- AVISE, J. C., AND D. WALKER. 1998. Pleistocene phylogeographic effects on avian populations and the speciation process. *Proceedings of the Royal Society of London, B*, 265:457-463.
- AVISE, J. C., D. WALKER, AND G. C. JOHNS. 1998. Speciation durations and Pleistocene effects on vertebrate phylogeography. *Proceedings of the Royal Society of London B*, 265:1707-1712.
- BARNES, I., P. MATHEUS, B. SHAPIRO, D. JENSEN, AND A. COOPER. 2002. Dynamics of Pleistocene population extinctions in Beringian brown bears. *Science*, 295:2267-2270.
- BARNES, I., B. SHAPIRO, A. LISTER, T. KUZNETSOVA, A. SHER, D. GUTHRIE, AND M. G. THOMAS. 2007. Genetic structure and extinction of the woolly mammoth, *Mammuthus primigenius*. *Current Biology*, 17(12):1072-1075.
- BARNES, S. S., E. MATISOO-SMITH, AND T. L. HUNT. 2006. Ancient DNA of the Pacific rat (*Rattus exulans*) from Rapa Nui (Easter Island). *Journal of Archaeological Science*, 33(11):1536-1540.
- BARNOSKY, A. D. 1986. "Big game" extinction caused by late Pleistocene climatic change: Irish Elk (*Megaloceros giganteus*) in Ireland. *Quaternary Research*, 25(1):128-135.
- BARNOSKY, A. D. 2004a. Climate change, biodiversity, and

- ecosystem health: The past as a key to the future, p. 3-5. *In* A. D. Barnosky (ed.), *Biodiversity Response to Environmental Change in the Early and Middle Pleistocene: The Porcupine Cave Fauna from Colorado*. University of California Press, Berkeley, California.
- BARNOSKY, A. D. 2004b. Faunal dynamics of small mammals through the Pit Sequence, p. 318-326. *In* A. D. Barnosky (ed.), *Biodiversity Response to Climate Change in the Early and Middle Pleistocene: The Porcupine Cave Fauna from Colorado*. University of California Press, Berkeley, California.
- BARNOSKY, A. D. 2008. Megafauna biomass tradeoff as a driver of Quaternary and future extinctions. *Proceedings of the National Academy of Sciences of the United States of America*, 105:11543-11548.
- BARNOSKY, A. D. 2009. *Heatstroke: Nature in an Age of Global Warming*. Island Press, Washington, DC, 269 p.
- BARNOSKY, A. D., AND A. B. SHABEL. 2005. Comparison of species richness and ecological structure in historic and middle Pleistocene Colorado mountain mammal communities. *Proceedings of the California Academy of Sciences, Series 4*, 56(Suppl. 1):50-61.
- BARNOSKY, A. D., C. J. BELL, S. D. EMSLIE, H. T. GOODWIN, J. I. MEAD, C. A. REPENNING, E. SCOTT, AND A. B. SHABEL. 2004a. Exceptional record of mid-Pleistocene vertebrates helps differentiate climatic from anthropogenic ecosystem perturbations. *Proceedings of the National Academy of Sciences of the United States of America*, 101:9297-9302.
- BARNOSKY, A. D., E. A. HADLY, AND C. J. BELL. 2003. Mammalian response to global warming on varied temporal scales. *Journal of Mammalogy*, 84(2):354-368.
- BARNOSKY, A. D., E. A. HADLY, B. A. MAURER, AND M. I. CHRISTIE. 2001. Temperate terrestrial vertebrate faunas in North and South America: Interplay of ecology, evolution, and geography with biodiversity. *Conservation Biology*, 15(3):658-674.
- BARNOSKY, A. D., P. L. KOCH, R. S. FERANEC, S. L. WING, AND A. B. SHABEL. 2004b. Assessing the causes of late Pleistocene extinctions on the continents. *Science*, 306:70-75.
- BEHRENSMEYER, A. K., C. T. STAYTON, AND R. E. CHAPMAN. 2003. Taphonomy and ecology of modern avifaunal remains from Amboseli Park, Kenya. *Paleobiology*, 29(1):52-70.
- BELLE, E. M. S., P. A. LANDRY, AND G. BARBUJANI. 2006. Origins and evolution of the Europeans' genome: Evidence from multiple microsatellite loci. *Proceedings of the Royal Society, B*, 273(1594):1595-1602.
- BLOIS, J. L. 2009. *Ecological Responses to Paleoclimatic Change: Insights from Mammalian Populations, Species, and Communities*. Unpublished Ph.D. dissertation, Stanford University.
- BLOIS, J. L., AND E. A. HADLY. 2009. Mammalian response to Cenozoic climatic change. *Annual Review of Earth and Planetary Sciences*, 37:181-208.
- BROOK, B. W. 2008. Synergies between climate change, extinctions and invasive vertebrates. *Wildlife Research*, 35:doi: 10.1071/wr07116.
- BROOK, B. W., AND D. M. J. S. BOWMAN. 2002. Explaining the Pleistocene megafaunal extinctions: Models, chronologies, and assumptions. *Proceedings of the National Academy of Sciences of the United States of America*, 99(23):14624-14627.
- BROOK, B. W., D. M. J. S. BOWMAN, D. A. BURNEY, T. F. FLANNERY, M. K. GAGAN, R. GILLESPIE, C. N. JOHNSON, A. P. KERSHAW, J. W. MAGEE, P. S. MARTIN, G. H. MILLER, B. PEISER, AND R. G. ROBERTS. 2007. Would the Australian megafauna have become extinct if humans had never colonised the continent? *Quaternary Science Reviews*, 26:560-564.
- BROOK, B. W., N. S. SODHI, AND C. J. A. BRADSHAW. 2008. Synergies among extinction drivers under global change. *Trends in Ecology and Evolution*, 23:453-460.
- BUNCE, M., M. SZULKIN, H. R. L. LERNER, I. BARNES, B. SHAPIRO, A. COOPER, AND R. N. HOLDAWAY. 2005. Ancient DNA provides new insights into the evolutionary history of New Zealand's extinct giant eagle. *PLoS Biology*, 3(1):44-46.
- CALVIGNAC, S., S. HUGHES, C. TOUGARD, J. MICHAUX, M. THEVENOT, M. PHILIPPE, W. HAMDINE, AND C. HANNI. 2008. Ancient DNA evidence for the loss of a highly divergent brown bear clade during historical times. *Molecular Ecology*, 17(8):1962-1970.
- CARDINALE, B. J., M. A. PALMER, AND S. L. COLLINS. 2002. Species diversity enhances ecosystem functioning through interspecific facilitation. *Nature*(6870):426-428.
- CARO, T. 2007. The Pleistocene re-wilding gambit. *Trends in Ecology and Evolution*, 22(6):281-283.
- CARRASCO, M. A., B. P. KRAATZ, E. B. DAVIS, AND A. D. BARNOSKY. 2007. The Miocene mammal mapping project (MIOMAP): An online database of Arikareean through Hemphillian fossil mammals. *Bulletin of the Carnegie Museum of Natural History*, 39:183-188.
- CEBALLOS, G., P. R. EHRLICH, J. SOBERÓN, I. SALAZAR, AND J. P. FAY. 2005. Global mammal conservation: What must we manage? *Science*, 309:603-607.
- CHAN, Y. L., C. N. K. ANDERSON, AND E. A. HADLY. 2006. Bayesian estimation of the timing and severity of a population bottleneck from ancient DNA. *PLoS Genetics*, 2(4):451-460.
- CHAN, Y. L., E. A. LACEY, O. P. PEARSON, AND E. A. HADLY. 2005. Ancient DNA reveals Holocene loss of genetic diversity in a South American rodent. *Biology Letters*, 1(4):423-426.
- CHAPRON, G. 2005. Re-wilding: Other projects help carnivores stay wild. *Nature*, 437(7057):318-318.

- DALEN, L., V. NYSTROM, C. VALDIOSERA, M. GERMONPRE, M. SABLIN, E. TURNER, A. ANGERBJORN, J. L. ARSUAGA, AND A. GOTHERSTROM. 2007. Ancient DNA reveals lack of postglacial habitat tracking in the arctic fox. *Proceedings of the National Academy of Sciences of the United States of America*, 104(16):6726-6729.
- DAVIDSON, A. D., M. J. HAMILTON, A. G. BOYER, J. H. BROWN, AND G. CEBALLOSA. 2009. Multiple ecological pathways to extinction in mammals. *Proceedings of the National Academy of Science of the United States of America*, 106(26):10702-10705.
- DAVIS, E. B. 2005. Comparison of climate space and phylogeny of *Marmota* (Mammalia: Rodentia) indicates a connection between evolutionary history and climate preference. *Proceedings of the Royal Society, B*, 272:519-526.
- DI MICHELE, W. A., A. K. BEHRENSMEYER, T. D. OLSZEWSKI, C. C. LABANDEIRA, J. M. PANDOLFI, S. L. WING, AND R. BOBE. 2004. Long-term stasis in ecological assemblages: Evidence from the fossil record. *Annual Review of Ecology, Evolution, and Systematics*, 35:285-322.
- DINERSTEIN, E., AND W. R. IRVIN. 2005. Re-wilding: No need for exotics as natives return. *Nature*, 437(7058):476-476.
- DONLAN, C. J. 2005. Re-wilding North America. *Nature*, 436(7053):913-914.
- DONLAN, C. J., J. BERGER, C. E. BOCK, J. H. BOCK, D. A. BURNEY, J. A. ESTES, D. FOREMAN, P. S. MARTIN, G. W. ROEMER, F. A. SMITH, M. E. SOULÉ, AND H. W. GREENE. 2006. Pleistocene rewilding: An optimistic agenda for twenty-first century conservation. *American Naturalist*, 168(5):660-681.
- DRUMMOND, A. J., A. RAMBAUT, B. SHAPIRO, AND O. G. PYBUS. 2005. Bayesian coalescent inference of past population dynamics from molecular sequences. *Molecular Biology and Evolution*, 22:1185-1192.
- ELITH, J., C. H. GRAHAM, R. P. ANDERSON, M. DUDIK, S. FERRIER, A. GUISAN, R. J. HIJMANS, F. HUETTMANN, J. R. LEATHWICK, A. LEHMANN, J. LI, L. G. LOHMANN, B. A. LOISELLE, G. MANION, C. MORITZ, M. NAKAMURA, Y. NAKAZAWA, J. M. OVERTON, A. T. PETERSON, S. J. PHILLIPS, K. RICHARDSON, R. SCACHETTI-PEREIRA, R. E. SCHAPIRE, J. SOBERON, S. WILLIAMS, M. S. WISZ, AND N. E. ZIMMERMANN. 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, 29(2):129-151.
- FAUNMAP WORKING GROUP. 1996. Spatial response of mammals to the late Quaternary environmental fluctuations. *Science*, 272(5268):1601-1606.
- FLESSA, K. W., AND S. T. JACKSON. 2005. Forging a common agenda for ecology and paleoecology. *Bioscience*, 55(12):1030-1031.
- GILPIN, M. E., AND M. E. SOULÉ. 1986. Minimum viable populations: The processes of species extinctions, p. 13-34. *In* M. E. Soulé (ed.), *Conservation Biology: The Science of Scarcity and Diversity*. Sinauer Associates, Sunderland, Massachusetts.
- GRAHAM, R. W. 1976. Late Wisconsin mammalian faunas and environmental gradients of the eastern United States. *Paleobiology*, 2(4):343-350.
- GRAHAM, R. W. 1984. Paleoenvironmental implications of the Quaternary distribution of the Eastern chipmunk (*Tamias striatus*) in central Texas. *Quaternary Research*, 21(1):111-114.
- GRAHAM, R. W. 1997. The spatial response of mammals to Quaternary climate changes, p. 153-162. *In* B. Huntley, W. Cramer, A. V. Morgan, H. C. Prentice, and J. R. M. Allen (eds.), *Past and Future Rapid Environmental Changes: The Spatial and Evolutionary Responses of Terrestrial Biota*. Springer-Verlag, Berlin.
- GRAHAM, R. W., AND E. C. GRIMM. 1990. Effects of global climate change on the patterns of terrestrial biological communities. *Trends in Ecology and Evolution*, 5(9):289-292.
- GRAHAM, R. W., AND J. I. MEAD. 1987. Environmental fluctuations and evolution of mammalian faunas during the last deglaciation in North America, p. 371-402. *In* W. F. Ruddiman, and H. E. Wright (eds.), *The Geology of North America, Volume K-3, North America and Adjacent Oceans During the Last Deglaciation*. Geological Society of America, Boulder, Colorado.
- GRAHAM, R. W., E. L. LUNDELIUS, M. A. GRAHAM, E. K. SCHROEDER, R. S. TOOMEY, E. ANDERSON, A. D. BARNOSKY, J. A. BURNS, C. S. CHURCHER, D. K. GRAYSON, R. D. GUTHRIE, C. R. HARRINGTON, G. T. JEFFERSON, L. D. MARTIN, H. G. McDONALD, R. E. MORLAN, H. A. SEMKEN, S. D. WEBB, L. WERDELIN, AND M. C. WILSON. 1996. Spatial response of mammals to late Quaternary environmental fluctuations. *Science*, 272(5268):1601-1606.
- GRAYSON, D. K. 1998. Moisture history and small mammal community richness during the latest Pleistocene and Holocene, northern Bonneville Basin, Utah. *Quaternary Research*, 49:330-334.
- GRAYSON, D. K. 2005. A brief history of Great Basin pikas. *Journal of Biogeography*, 32(12):2103-2111.
- GRAYSON, D. K. 2006. The Late Quaternary biogeographic histories of some Great Basin mammals (western USA). *Quaternary Science Reviews*, 25(21-22):2964-2991.
- GRAYSON, D. K., AND D. B. MADSEN. 2000. Biogeographic implications of recent low-elevation recolonization by *Neotoma cinerea* in the Great Basin. *Journal of Mammalogy*, 81(4):1100-1105.
- GUGERLI, F., L. PARDUCCI, AND R. J. PETIT. 2005. Ancient plant DNA: Review and prospects. *New Phytologist*, 166(2):409-418.
- GUILDAY, J. E. 1971. The Pleistocene history of the Appalachian mammal faunas, p. 233-262. *In* P. C. Holt, R. A. Paterson, and J. P. Hubbard (eds.), *The Distributional History of the Biota of the Southern Appalachians*.

- Part III: The Vertebrates. Research Division Monograph 4. Virginia Polytechnic Institute and State University, Blacksburg, Virginia.
- GUILDAY, J. E. 1984. Pleistocene extinction and environmental change: Case study of the Appalachians, p. 250-258. *In* P. S. Martin and R. G. Klein (eds.), *Quaternary Extinctions: A Prehistoric Revolution*. University of Arizona Press, Tucson, Arizona.
- HADLY, E. A. 1996. Influence of late-Holocene climate on northern Rocky Mountain mammals. *Quaternary Research*, 46(3):298-310.
- HADLY, E. A. 1999. Fidelity of terrestrial vertebrate fossils to a modern ecosystem. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 149(1-4):389-409.
- HADLY, E. A. 2003. The interface of paleontology and mammalogy: Past, present, and future. *Journal of Mammalogy*, 84(2):347-353.
- HADLY, E. A., AND B. A. MAURER. 2001. Spatial and temporal patterns of species diversity in montane mammal communities of western North America. *Evolutionary Ecology Research*, 3(4):477-486.
- HADLY, E. A., M. H. KOHN, J. A. LEONARD, AND R. K. WAYNE. 1998. A genetic record of population isolation in pocket gophers during Holocene climatic change. *Proceedings of the National Academy of Sciences of the United States of America*, 95(12):6893-6896.
- HADLY, E. A., U. RAMAKRISHNAN, Y. L. CHAN, M. VAN TUINEN, K. O'KEEFE, P. A. SPAETH, AND C. J. CONROY. 2004. Genetic response to climatic change: Insights from ancient DNA and phylochronology. *PLoS Biology*, 2(10):1600-1609.
- HADLY, E. A., P. A. SPAETH, AND C. L. LI. In press. Niche conservatism above the species level. *Proceedings of the National Academy of Sciences of the United States of America*.
- HANDT, O., M. HOSS, M. KRINGS, AND S. PAABO. 1994. Ancient DNA: Methodological challenges. *Experientia*, 50(6):524-529.
- HILL, M. G., JR., M. G. HILL, AND C. C. WIDGA. 2008. Late Quaternary Bison diminution on the Great Plains of North America: Evaluating the role of human hunting versus climate change. *Quaternary Science Reviews*, 27:1752-1771.
- HIJMANS, R. J., AND C. H. GRAHAM. 2006. The ability of climate envelope models to predict the effect of climate change on species distributions. *Global Change Biology*, 12:2272-2281.
- HOELZEL, A. R., J. HALLEY, S. J. O'BRIEN, C. CAMPAGNA, T. ARNBOM, B. LEBOEUF, K. RALLS, AND G. A. DOVER. 1993. Elephant seal genetic-variation and the use of simulation-models to investigate historical population bottlenecks. *Journal of Heredity*, 84: 443-449.
- HOFREITER, M. 2008a. Mammoth genomics. *Nature*, 456(7220):330-331.
- HOFREITER, M. 2008b. Long DNA sequences and large data sets: Investigating the Quaternary via ancient DNA. *Quaternary Science Reviews*, 27:2586-2592.
- HOFREITER, M., C. CAPELLI, M. KRINGS, L. WAITS, N. CONARD, S. MUNZEL, G. RABEDER, D. NAGEL, M. PAUNOVIC, G. JAMBRESIC, S. MEYER, G. WEISS, AND S. PAABO. 2002. Ancient DNA analyses reveal high mitochondrial DNA sequence diversity and parallel morphological evolution of late pleistocene cave bears. *Molecular Biology and Evolution*, 19(8):1244-1250.
- HOFREITER, M., S. MUENZEL, N. J. CONARD, J. POLLACK, M. SLATKIN, G. WEISS, AND S. PAABO. 2007. Sudden replacement of cave bear mitochondrial DNA in the late Pleistocene. *Current Biology*, 17(4):R122-R123.
- HOFREITER, M., D. SERRE, H. N. POINAR, M. KUCH, AND S. PAABO. 2001. Ancient DNA. *Nature Reviews, Genetics*, 2:353-359.
- HOFREITER, M., D. SERRE, N. ROHLAND, G. RABEDER, D. NAGEL, N. CONARD, S. MUNZEL, AND S. PAABO. 2004. Lack of phylogeography in European mammals before the last glaciation. *Proceedings of the National Academy of Sciences of the United States of America*, 101(35):12963-12968.
- HUGHES, T. P., A. H. BAIRD, D. R. BELLWOOD, M. CARD, S. R. CONNOLLY, C. FOLKE, R. GROSBURG, O. HOEGH-GULDBERG, J. B. C. JACKSON, J. KLEYPAS, J. M. LOUGH, P. MARSHALL, M. NYSTROM, S. R. PALUMBI, J. M. PANDOLFI, B. ROSEN, AND J. ROUGHGARDEN. 2003. Climate change, human impacts, and the resilience of coral reefs. *Science*, 301(5635):929-933.
- HUYNEN, L., I. LISSONE, S. SAWYER, AND D. LAMBERT. 2008. Genetic identification of moa remains recovered from Tiniroto, Gisborne. *Journal of the Royal Society of New Zealand*, 38(4):231-235.
- HUYNEN, L., C. D. MILLAR, R. P. SCOFIELD, AND D. M. LAMBERT. 2003. Nuclear DNA sequences detect species limits in ancient moa. *Nature*, 425(6954):175-178.
- IPCC. 2007. *Climate Change 2007*. Cambridge University Press, Geneva, 210 p.
- IUCN. 2009. *IUCN Red List of Endangered Species, 2009.1*. Available from: <http://www.iucnredlist.org>.
- JABLONSKI, D., AND W. G. CHALONER. 1994. Extinctions in the fossil record. *Philosophical Transactions of the Royal Society, B*, 344:11-17.
- JACKSON, J. B. C., AND D. ERWIN. 2006. What can we learn about ecology and evolution from the fossil record? *Trends in Ecology and Evolution*, 21:322-328.
- JOHNS, G. C., AND J. C. AVISE. 1998. A comparative summary of genetic distances in the vertebrates from the mitochondrial cytochrome *b* gene. *Molecular Biology and Evolution*, 15(11):1481-1490.
- KOCH, P. L., AND A. D. BARNOSKY. 2006. Late Quaternary extinctions: State of the debate. *Annual Review of Ecology, Evolution, and Systematics*, 37:215-250.

- LALUEZA-FOX, C., J. KRAUSE, D. CARAMELLI, G. CATALANO, L. MILANI, M. L. SAMPIETRO, F. CALAFELL, C. MARTINEZ-MAZA, M. BASTIR, A. GARCIA-TABERNEIRO, M. DE LA RASILLA, J. FORTEA, S. PAABO, J. BERTRANPETIT, AND A. ROSAS. 2006. Mitochondrial DNA of an Iberian neandertal suggests a population affinity with other European neandertals. *Current Biology*, 16(16):R629-R630.
- LALUEZA-FOX, C., M. L. SAMPIETRO, D. CARAMELLI, Y. PUDER, M. LARI, F. CALAFELL, C. MARTINEZ-MAZA, M. BASTIR, J. FORTEA, M. DE LA RASILLA, J. BERTRANPETIT, AND A. ROSAS. 2005. Neandertal evolutionary genetics: Mitochondrial DNA data from the Iberian Peninsula. *Molecular Biology and Evolution*, 22(4):1077-1081.
- LEONARD, J. A. 2008. Ancient DNA applications for wildlife conservation. *Molecular Ecology*, 17:4186-4196.
- LEONARD, J. A., R. K. WAYNE, J. WHEELER, R. VALADEZ, S. GUILLEN, AND C. VILA. 2002. Ancient DNA evidence for Old World origin of New World dogs. *Science*, 5598:1613-1616.
- LEOPOLD, A. S., S. A. CAIN, C. M. COTTAM, I. N. GABRIELSON, AND T. KIMBALL. 1963. *Wildlife Management in the National Parks: The Leopold Report*. The National Park Service. Available from: http://www.nps.gov/history/history/online_books/leopold/leopold.htm.
- LINDAHL, T. 2000. Quick guide: Fossil DNA. *Current Biology*, 10(17):R616-R616.
- LYMAN, R. L. 1998. *White Goats, White Lies: The Misuse of Science in Olympic National Park*. University of Utah Press, Salt Lake City, Utah, 278 p.
- LYMAN, R. L. 2006. Paleozoology in the service of conservation biology. *Evolutionary Anthropology*, 15:11-19.
- LYMAN, R. L., AND K. P. CANNON. 2004. *Zooarchaeology and Conservation Biology*. University of Utah Press, Salt Lake City, Utah, 266 p.
- LYONS, S. K., F. A. SMITH, AND J. H. BROWN. 2004. Of mice, mastodons, and men: Human mediated extinctions on four continents. *Evolutionary Ecology Research*, 6:339-358.
- MACPHEE, R. D. E. 1999. *Extinctions in Near Time: Causes, Contexts, and Consequences*. Kluwer Academic/Plenum Publishers, New York, London, 394 p.
- MACPHEE, R. D. E., AND C. FLEMING. 1999. Requiem Aeternam: The last five hundred years of mammalian species extinctions, p. 333-371. *In* R. D. E. MacPhee (ed.), *Extinctions in Near Time: Causes, Contexts, and Consequences*. Kluwer Academic/Plenum Publishers, New York.
- MACPHEE, R. D. E., AND P. A. MARX. 1997. The 40,000 year plague: Humans, hyperdiseases, and first-contact extinctions, p. 169-217. *In* S. M. Goodman and B. R. Patterson (eds.), *Natural Change and Human Impact in Madagascar*. Smithsonian Institution Press, Washington, D. C.
- MARTIN, P. S. 2005. *Twilight of the Mammoths: Ice Age Extinctions and the Rewilding of America*. University of California Press, Berkeley, California, 269 p.
- MARTIN, P. S., AND R. G. KLEIN. 1984. *Quaternary Extinctions: A Prehistoric Revolution*. University of Arizona Press, Tucson, Arizona, 892 p.
- MARTIN, P. S., AND H. E. WRIGHT, JR. 1967. *Pleistocene Extinctions: The Search for a Cause*. Volume 6 of the Proceedings of the VII Congress of the International Association for Quaternary Research. Yale University Press, New Haven, Connecticut, 453 p.
- MARTINEZ-MEYER, E., A. TOWNSEND PETERSON, AND W. W. HARGROVE. 2004. Ecological niches as stable distributional constraints on mammal species, with implications for Pleistocene extinctions and climate change projections for biodiversity. *Global Ecology and Biogeography*, 13(4):305-314.
- MCGILL, B. J., E. A. HADLY, AND B. A. MAURER. 2005. Community inertia of quaternary small mammal assemblages in North America. *Proceedings of the National Academy of Sciences of the United States of America*, 102(46):16701-16706.
- MCLACHLAN, J. S., AND J. J. HELLMANN. 2007. A framework for the debate of assisted migration in an era of climate change. *Conservation Biology*, 21:297-302.
- MCMENAMIN, S. K., E. A. HADLY, AND C. K. WRIGHT. 2008. Climatic change and wetland desiccation cause amphibian decline in Yellowstone National Park. *Proceedings of the National Academy of Sciences of the United States of America*, 105(44):16988-16993.
- MEINE, C., M. SOULÉ, AND R. F. NOSS. 2006. "A mission-driven discipline": The growth of conservation biology. *Conservation Biology*, 20(3):631-651.
- MENOTTI-RAYMOND, M., AND S. J. O'BRIEN. 1993. Dating the genetic bottleneck of the African cheetah. *Proceedings of the National Academy of Sciences of the United States of America*, 90:3172-3176.
- MILLER, F. J., F. L. ROSENFELDT, C. ZHANG, A. W. LINNANE, AND P. NAGLEY. 2003. Precise determination of mitochondrial DNA copy number in human skeletal and cardiac muscle by a PCR-based assay: Lack of change of copy number with age. *Nucleic Acids Research*, 31:e61.
- MIOMAP. 2009. MIOMAP Database. Available from: <http://www.ucmp.berkeley.edu/>.
- MITTERMEIER, R., C. GOETTSCHE-MITTERMEIER, P. R. GIL, G. FONSECA, T. BROOKS, J. PILGRIM, AND W. R. KONSTANT. 2003. *Wilderness: Earth's Last Wild Places*. University of Chicago Press, Chicago, Illinois, 576 p.
- NEOTOMA. 2009. NEOTOMA Paleobiology Database, Plio-Pleistocene to Holocene. Available from: <http://www.neotomadb.org/>.
- NEWSOME, S. D., M. A. ETNIER, D. GIFFORD-GONZALEZ, D. L. PHILLIPS, M. VAN TUINEN, E. A. HADLY, D. P. COSTA, D. J. KENNETT, T. P. GUILDERSON, AND P. L. KOCH. 2007. The shifting baseline of northern fur seal ecology in the northeast Pacific Ocean. *Proceedings of the National*

- Academy of Sciences of the United States of America, 104(23):9709-9714.
- NGS. 2006. World Parks. National Geographic, October. Available from: <http://ngm.nationalgeographic.com/ngm/0610/feature0611/map.html>.
- NOGUES-BRAVO, D., J. RODRIGUEZ, J. HORTAL, P. BATRA, AND M. B. ARAUJO. 2008. Climate change, humans, and the extinction of the woolly mammoth. *PLoS Biology*, 6(4):685-692.
- NOW. 2009. Neogene of the Old World Database. Available from: <http://www.helsinki.fi/science/now>.
- NRC (NATIONAL RESEARCH COUNCIL). 2002. Ecological Dynamics on Yellowstone's Northern Range. The National Academies Press, Washington, D. C., p. 198.
- ORLANDO, L., D. BONJEAN, H. BOCHERENS, A. THENOT, A. ARGANT, M. OTTE, AND C. HANNI. 2002. Ancient DNA and the population genetics of cave bears (*Ursus spelaeus*) through space and time. *Molecular Biology and Evolution*, 19(11):1920-1933.
- ORLANDO, L., D. MALE, M. T. ALBERDI, J. L. PRADO, A. PRIETO, A. COOPER, AND C. HANNI. 2008. Ancient DNA clarifies the evolutionary history of American late Pleistocene equids. *Journal of Molecular Evolution*, 66(5):533-538.
- ORLANDO, L., M. MASHKOUR, A. BURKE, C. J. DOUADY, V. EISENMANN, AND C. HANNI. 2006. Geographic distribution of an extinct equid (*Equus hydruntinus*: Mammalia, Equidae) revealed by morphological and genetical analyses of fossils. *Molecular Ecology*, 15(8):2083-2093.
- OWEN, P. R., C. J. BELL, AND E. M. MEAD. 2000. Fossils, diet, and conservation of black-footed ferrets (*Mustela nigripes*). *Journal of Mammalogy*, 81(2):422-433.
- PANDOLFI, J. M. 2002. Coral community dynamics at multiple scales. *Coral Reefs*, 21(1):13-23.
- PANDOLFI, J. M. 2006. Ecology - Corals fail a test of neutrality. *Nature*, 440(7080):35-36.
- PAWLOWSKI, J., I. BOLIVAR, J. F. FAHRNI, C. DEVARGAS, M. GOUY, AND L. ZANINETTI. 1997. Extreme differences in rates of molecular evolution of foraminifera revealed by comparison of ribosomal DNA sequences and the fossil record. *Molecular Biology and Evolution*, 14(5):498-505.
- PBDB. 2009. Paleobiology Database. Available from: <http://paleodb.org/cgi-bin/bridge.pl>.
- PEAKALL, R., D. EBERT, L. J. SCOTT, P. F. MEAGHER, AND C. A. OFFORD. 2003. Comparative genetic study confirms exceptionally low genetic variation in the ancient and endangered relictual conifer, *Wollemia nobilis* (Araucariaceae). *Molecular Ecology*, 12:2331-2343.
- POINAR, H. N., M. HOFREITER, W. G. SPAULDING, P. S. MARTIN, B. A. STANKIEWICZ, H. BLAND, R. P. EVERSLED, G. POSSNERT, AND S. PAABO. 1998. Molecular coproscopy: Dung and diet of the extinct ground sloth *Nototheriopsis shastensis*. *Science*, 281(5375):402-406.
- POINAR, H. N., M. KUCH, G. McDONALD, P. MARTIN, AND S. PAABO. 2003. Nuclear gene sequences from a late Pleistocene sloth coprolite. *Current Biology*, 13(13):1150-1152.
- PORDER, S., A. PAYTAN, AND E. A. HADLY. 2003. Mapping the origin of faunal assemblages using strontium isotopes. *Paleobiology*, 29(2):197-204.
- RAMAKRISHNAN, U., AND E. A. HADLY. In press. Using phylochronology to reveal cryptic population histories: Review and synthesis of four ancient DNA studies. *Molecular Ecology*.
- RAMAKRISHNAN, U., E. A. HADLY, AND J. L. MOUNTAIN. 2005. Detecting past population bottlenecks using temporal genetic data. *Molecular Ecology*, 14(10):2915-2922.
- ROMPLER, H., N. ROHLAND, C. LALUEZA-FOX, E. WILLERSLEV, T. KUZNETSOVA, G. RABEDER, J. BERTRANPETIT, T. SCHONEBERG, AND M. HOFREITER. 2006. Nuclear gene indicates coat-color polymorphism in mammoths. *Science*, 313(5783):62-62.
- ROSENZWEIG, M. L. 1995. *Species Diversity in Space and Time*. Cambridge University Press, New York, 436 p.
- RUBENSTEIN, D. R., D. I. RUBENSTEIN, P. W. SHERMAN, AND T. A. GAVIN. 2006. Pleistocene park: Does re-wilding North America represent sound conservation for the 21st century? *Biological Conservation*, 132(2):232-238.
- SCHLAEPFER, M. A. 2005. Re-wilding: A bold plan that needs native megafauna. *Nature*, 437(7061):951-951.
- SEMKEN, H. A., JR., AND R. W. GRAHAM. 1996. Paleoecologic and taphonomic patterns derived from correspondence analysis of zooarcheological and paleontological faunal samples, a case study from the North American prairie/forest ecotone, p. 477-490. In A. Nadachowski and L. Werdelin (eds.), *Neogene and Quaternary Mammals of the Palaearctic*. *Acta Zoologica Cracoviensia* 39.
- SHAPIRO, B., A. J. DRUMMOND, A. RAMBAUT, M. C. WILSON, P. E. MATHEUS, A. V. SHER, O. G. PYBUS, M. T. P. GILBERT, I. BARNES, J. BINLADEN, E. WILLERSLEV, A. J. HANSEN, G. F. BARYSHNIKOV, J. A. BURNS, S. DAVYDOV, J. C. DRIVER, D. G. FROESE, C. R. HARRINGTON, G. KEDDIE, P. KOSINTSEV, M. L. KUNZ, L. D. MARTIN, R. O. STEPHENSON, J. STORER, R. TEDFORD, S. ZIMOV, AND A. COOPER. 2004. Rise and fall of the Beringian steppe bison. *Science*, 306(5701):1561-1565.
- SHAY, S. 2005. Re-wilding: Don't overlook humans living on the plains. *Nature*, 437(7058):476-476.
- SMITH, C. I. 2005. Re-wilding: Introductions could reduce biodiversity. *Nature*, 437(7057):318-318.
- SORENSEN, M. D., A. COOPER, E. E. PAXINOS, T. W. QUINN, H. F. JAMES, S. L. OLSON, AND R. C. FLEISCHER. 1999. Relationships of the extinct moa-nalos, flightless Hawaiian waterfowl, based on ancient DNA. *Proceedings of the Royal Society of London, B*, 266(1434):2187-2193.
- SOULÉ, M. E. 1987. Where do we go from here?, p. 175-183. In M. E. Soulé (ed.), *Viable Populations for Conservation*. Cambridge University Press, Cambridge.

- SPAETH, P. A., M. VAN TUINEN, Y. L. CHAN, D. TERCA, AND E. A. HADLY. 2009. Phylogeography of *Microtus longicaudus* in the tectonically and glacially dynamic central Rocky Mountains. *Journal of Mammalogy*, 90(3):571–584.
- SPIELMAN, D., B. W. BROOK, AND R. FRANKHAM. 2004. Most species are not driven to extinction before genetic factors impact them. *Proceedings of the National Academy of Sciences of the United States of America*, 101:15261–15264.
- STEADMAN, D. W., P. S. MARTIN, R. D. E. MACPHEE, A. J. T. JULL, H. G. McDONALD, C. A. WOODS, M. ITURRALDEVINENT, AND G. W. L. HODGINS. 2005. Asynchronous extinction of late Quaternary sloths on continents and islands. *Proceedings of the National Academy of Sciences of the United States of America*, 102(33):11763–11768.
- TERRY, R. C. 2007. Inferring predator identity from small-mammal remains. *Evolutionary Ecology Research*, 9:199–219.
- TERRY, R. C. 2008. Modeling the effects of predation, prey cycling, and time averaging on relative abundance in raptor-generated small mammal death assemblages. *Palaeos*, 23(6):402–410.
- VALDIOSERA, C. E., J. L. GARCIA-GARITAGOITIA, N. GARCIA, I. DOADRIO, M. G. THOMAS, C. HANNI, J. L. ARSUAGA, I. BARNES, M. HOFREITER, L. ORLANDO, AND A. GOTHERSTORM. 2008. Surprising migration and population size dynamics in ancient Iberian brown bears (*Ursus arctos*). *Proceedings of the National Academy of Sciences of the United States of America*, 105(13):5123–5128.
- VAN TUINEN, M., K. O'KEEFE, U. RAMAKRISHNAN, AND E. A. HADLY. 2008. Fire and ice: Genetic structure of the Uinta ground squirrel (*Spermophilus armatus*) across the Yellowstone hotspot. *Molecular Ecology*, 17(7):1776–1788.
- WAKE, D. B., AND V. T. VREDENBURG. 2008. Are we in the midst of the sixth mass extinction? A view from the world of amphibians. *Proceedings of the National Academy of Sciences of the United States of America*, 105:11466–11473.
- WEAVER, T. D., AND C. C. ROSEMAN. 2005. Ancient DNA, late Neanderthal survival, and modern-human-Neanderthal genetic admixture. *Current Anthropology*, 46(4):677–683.
- WEINSTOCK, J., E. WILLERSLEV, A. SHER, W. F. TONG, S. Y. W. HO, D. RUBENSTEIN, J. STORER, J. BURNS, L. MARTIN, C. BRAVI, A. PRIETO, D. FROESE, E. SCOTT, X. L. LAI, AND A. COOPER. 2005. Evolution, systematics, and phylogeography of Pleistocene horses in the New World: A molecular perspective. *PLoS Biology*, 3(8):1373–1379.
- WESTERN, D., AND A. K. BEHRENSMEYER. 2009. Bone assemblages track animal community structure over 40 years in an African savanna ecosystem. *Science*, 324(5930):1061–1064.
- WIENS, J. J., AND C. H. GRAHAM. 2005. Niche conservatism: Integrating evolution, ecology, and conservation biology. *Annual Review of Ecology, Evolution, and Systematics*, 36:519–539.
- WILLERSLEV, E., E. CAPPELLINI, W. BOOMSMA, R. NIELSEN, M. B. HEBGAARD, T. B. BRAND, M. HOFREITER, M. BUNCE, H. N. POINAR, D. DAHL-JENSEN, S. JOHNSEN, J. P. STEFFENSEN, O. BENNIKE, J.-L. SCHWENNINGER, R. NATHAN, S. ARMITAGE, C.-J. D. HOOG, V. ALFIMOV, M. CHRISTL, J. BEER, R. MUSCHELER, J. BARKER, M. SHARP, K. E. H. PENKMAN, J. HAILE, P. TABERLET, M. THOMAS, P. GILBERT, A. CASOLI, E. CAMPANI, AND M. J. COLLINS. 2007. Ancient biomolecules from deep ice cores reveal a forested southern Greenland. *Science*, 317:111–114.
- WILLERSLEV, E., AND A. COOPER. 2005. Ancient DNA. *Proceedings of the Royal Society, B*, 272:3–16.
- WOOD, D. L., AND A. D. BARNOSKY. 1994. Middle Pleistocene climate change in the Colorado Rocky Mountains indicated by fossil mammals from Porcupine Cave. *Quaternary Research*, 41(3):366–375.
- WROE, S., J. FIELD, R. FULLAGAR, AND L. S. JERMIIN. 2004. Megafaunal extinction in the late Quaternary and the global overkill hypothesis. *Alcheringa*, 28(1):291–331.
- ZIMMER, C. 2009. As climate warms, species may need to migrate or perish. *Yale environment360*, 20 April 2009. Available from: <http://www.e360.yale.edu/content/feature.msp?id=2142>.