THE ISOTOPIC ECOLOGY OF FOSSIL VERTEBRATES AND CONSERVATION PALEOBIOLOGY

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ABSTRACT.—Over the past 50,000 years, global ecosystems have experienced substantial shifts in composition and function as a result of climate change and the direct and/or indirect impact of humans. Studies of how species and ecosystems responded to these changes and characterization of the ecology of past ecosystems provide unique perspectives for conservation biology and restoration ecology. Stable isotope analysis is a powerful tool for such studies, as it can be used to trace energy flow, the strength of species interactions, animal physiology, and movement patterns. Here, we provide a brief summary of the isotopic systems used to study ecology and physiology, past and present. We highlight four examples in which isotopic data have played a central role in characterizing ecological shifts in marine and terrestrial faunas over the past 50,000 years, and end by discussing the role isotopic paleoecology could play in characterizing interactions among extinct Pleistocene megafauna. Such data would be integral to assessing the viability of Pleistocene 'rewilding' of North America.

INTRODUCTION

OVER ROUGHLY the past one million years, ecosystems have experienced dramatic shifts between glacial and interglacial climates as well as a host of disturbances set in motion by members of the genus *Homo*. The past 40,000 years have been especially eventful. Earth entered then exited one of the most profound glacial periods of the Plio-Pleistocene icehouse, and a wave of extinctions engulfed terrestrial communities as modern humans spread around the planet. These extinctions, which preferentially eliminated large, slow-breeding species on continents, and all types of species on islands, were set in motion by human impacts (especially hunting and introduced species), though regional climate change likely affected the timing and pace of extinction for particular populations or species (Barnosky et al., 2004; Burney and Flannery, 2005; Koch and Barnosky, 2006). Paleobiological exploration of how extinct and extant species responded to these changes in their physical and biological environment can produce unique theory and data of use in conservation biology and restoration ecology.

Biogeography has received the greatest attention, including issues such as how fast geographic ranges can shift, or how, mechanistically, a species or biome shifts its range. Paleobiological research has roles to play on four additional fronts. First, it provides examples of actual ecosystems, some of which persisted for millions of years or existed under different climatic regimes. If we can understand the functional links in such ecosystems, they offer targets for restoration ecology unlike those adopted from the historical record, and they can be modeled to determine if they have attributes that make them more resilient to change than our current defaunated ecosystems (Berlow et al., 2008). Second, it offers a sound ecological baseline against which to judge ongoing ecological shifts. Third, paleobiology can reveal behaviors of species and species interactions that are not occurring today, either because of very recent disturbance or some event earlier in the Holocene or Pleistocene. Finally, it reveals how aspects of species' ecology besides geographic range (e.g., trophic interactions, reproductive strategies, growth dynamics) respond to the typical perturbations of the glacial-interglacial world, as well as the unusual perturbation of Quaternary extinctions.

Here, we'll explore the purchase on such issues that can be gained through study of the isotopic biogeochemistry of fossils and sub-fossils. Our focus will be on the isotopic ecology and conservation biology of vertebrates. We'll begin by briefly describing an isotopic tool kit—the types of tissues that can be used for isotopic analysis and the aspects of animal ecology that

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can be deduced from isotopic data. Then we'll turn to case studies that use isotopic data to answer different types of questions in conservation biology.

There are many reasons why isotopic methods are useful for studies at the intersection between paleobiology and conservation biology. Similar approaches can be applied to newly collected specimens, materials in zoological collections, and fossils, forming a seamless temporal bridge from the present to the past. Isotopic composition often serves as a natural label of mass flow, yielding quantitative data on interaction strengths in trophic studies. Most importantly, isotopic methods can provide information on the behavior and physiology of individuals. Consider, for example, what we might mean when we say that a species is a dietary 'generalist', which might make it more resilient in the face of environmental change. If we imagine that the species can consume three types of prey, being a generalist might mean that all individuals in a species consume roughly equal amounts of the three foods, or that different populations specialize on different mixes, or that different individuals within the same population have different diets, or even that an individual consumes different foods at different times (seasonally, ontogenetically). All these situations can (potentially) be discriminated through isotopic analysis. More generally, many questions central to conservation biology require an understanding of how a species' niche does (or does not) change in space and time. Isotopic data are amenable to conversion into niche axes, including both bionomic (defined by resources an animal uses) and scenopoetic (defined by bio-climatic limits) dimensions (Newsome et al., 2007a).

Before proceeding, we want to emphasize three points. While we are concerned with whole ecosystems and species interactions, many of our case studies are autecological. In some cases, we are looking at top carnivores (e.g., seals, wolves), so changes in their ecology may indicate shifting conditions lower in the trophic chain, or they have important top-down impacts; in other instances, we are looking at species of great value economically (e.g., salmon) or culturally (e.g., condors). Second, we would never advocate for an exclusive reliance on isotopic data in studies of conservation paleobiology. Several of the studies we discuss are vastly more powerful because they couple data from isotopes, morphology, ancient DNA, etc. Finally, perhaps more so than for other types of paleobiological research, the starting point in conservation paleobiology should be an extremely careful analysis of modern systems. This conservative approach is warranted when the information being gathered may be used to

Table *1*.—Summary information on materials used as substrates for isotopic analysis of vertebrates.

Tissue	Molecule	Temporal window*	Isotope systems in material	Preservation window (years)
Hair	Keratin	Accretion	H, C, N, O, S	10^4
Feather	Keratin	Accretion	H, C, N, O, S	10^4
Bone	Bioapatite	Years	CO_3 - C, O; PO_4 - O Sr, Nd, Pb	10^3 - 10^8? 10^3
Bone	Collagen	Years	H, C, N, O, S	10^5-10^6 (10^8?)
Bone	Lipid	Weeks-months	H, C	
Enamel	Bioapatite	Accretion	CO_3 - C, O; PO_4 - O	10^8
Dentin	Bioapatite	Accretion	Same as bone	Same as bone
Dentin	Collagen	Accretion	H, C, N, O, S	Same as bone
Egg shell	Carbonate	Days-weeks	C, O	10^7-10^8
Egg shell	Protein	Days-weeks	C, N	10^4

Compound	Signal window	Isotope systems	Preservation window
Amino acid	Depends on tissue type	H, C, N	10^6?
Cholesterol	Weeks-months	H, C	10^7?
Fatty acid	Weeks-months	H, C	10^4?

*Materials that grow by accretion have the potential for offering either short or long temporal windows, depending on how they are sampled.

set policy or develop conservation strategies.

AN ISOTOPIC TOOL KIT FOR CONSERVATION PALEOBIOLOGY

Conventions

The isotopic ratio of an element (X) is expressed as the ratio of the heavy (H) to light (L) isotope using the delta (δ) notation through comparison of samples to international standards: $\delta^{H}X = ((^{H}X/^{L}X_{sample} \div {}^{H}X/^{L}X_{standard})-1) \times 1000$ (Sharp, 2007). We will consider the following systems: hydrogen ($^{2}H/^{1}H$), carbon ($^{13}C/^{12}C$), nitrogen ($^{15}N/^{14}N$), oxygen ($^{18}O/^{16}O$), sulfur ($^{34}S/^{32}S$), and strontium ($^{87}Sr/^{86}Sr$). Units are parts per thousand (per mil, ‰). The fractionation of isotopes between two substances, A and B (e.g., diet and animal, or tissue A and tissue B within an animal), is expressed in many ways. Most common are 1) the fractionation factor: $\alpha_{A\text{-}B} = (1000 + \delta^{H}X_{A})/(1000 + \delta^{H}X_{B})$; 2) difference or discrimination: $\Delta_{A\text{-}B} = \delta^{H}X_{A} - \delta^{H}X_{B}$; and 3) enrichment or epsilon: $\varepsilon_{A\text{-}B} = 1000(\alpha_{A\text{-}B} - 1)$. Note that the sign (for Δ or ε) or magnitude (for α) of these terms depends on the order of the subscripts, and that $\Delta_{A\text{-}B} \approx \varepsilon_{A\text{-}B}$.

Isotopic substrates.—Vertebrate bodies offer many substrates for analysis (unless otherwise noted, this section is based on Kohn and Cerling, 2002; Koch, 2007). Tissues differ in their macromolecular and elemental compositions, styles of growth, and preservation potential (Table 1). Soft tissues such as hair and feathers contain protein and lipids and may persist for 10^{3} to 10^{4} years in unusual settings (e.g., mummification, permafrost). Mineralized tissues such as bone, tooth enamel and dentin, eggshell, and otoliths last much longer. Bone, enamel, and dentin are composites of mineral, protein, and lipid. The mineral is a form of hydroxyapatite ($Ca_{10}[PO_{4}]_{6}[OH]_{2}$) we refer to as bioapatite. Bioapatite has a few weight percent (wt %) carbonate and various cations (e.g., Sr) substituting for calcium. Bone is composed of tiny bioapatite crystals intergrown with an organic matrix (chiefly the protein collagen) that makes up ~30% of its dry weight. Enamel is much less porous, has <5 wt % organic matter, and has much larger crystals. The crystal size and organic content of dentin resemble bone, but its porosity is intermediate between enamel and bone. Bird eggshells are composed of tiny crystals (chiefly calcite) secreted around a honeycomb of fibrous organic sheets (~3 wt %, chiefly protein). Otoliths, the mineralized structures in the vertebrate inner ear, vary in mineralogy—aragonite occurs in jawed fish and amphibians, and calcite occurs in amniotes. Various isotopic analyses can be performed on both the organic and mineral components of vertebrate tissues (Table 1). Regarding the former, a great deal of information can be obtained if isotopic analysis can be conducted on individual organic molecules (amino acids, sterols, fatty acids), rather than bulk tissue (reviewed by Evershed et al., 2007).

The time interval integrated within an isotopic sample (Table 1) depends on the mode of growth and turnover rate of each tissue (or the pools from which tissues are synthesized). Experiments and models focusing on soft tissues (blood, muscle) suggest that the rates of isotopic incorporation (i.e., the time it takes for a tissue to equilibrate after a change in input) depend on rates of tissue growth and turnover, as well as on body mass (Martínez del Rio et al., 2009). Bone growth is complex, involving cartilage ossification, accretion, and remodeling, so a bulk sample of bone mineral or collagen has material that is time-averaged over months to years. Dentin grows by accretion with little remodeling and can be microsampled to generate time series. Enamel also has incremental features, but time lags in its maturation lead to substantial time averaging. In all mammals except those with ever-growing teeth, enamel mineralization takes place early in life, over a period of months to years. All other vertebrates replace their teeth throughout life, so teeth collected from a dead individual formed over the last year or two of life, depending on replacement rate. Eggshells form rapidly, so their carbonate and protein represent short time intervals (days to weeks). Growth of feathers and hair may be continuous or episodic, and depending on sampling strategy can represent weeks to about a year. Otoliths have incremental laminae that can be microsampled for time series or bulk sampled for a lifetime average.

Isotopic studies of animal ecology require an understanding of the controls on fractionation between diet and tissue or drinking water and tissue. This complex topic has been reviewed by Koch (2007) and Martínez del Rio et al. (2009). Briefly, C, N and S in tissues are supplied by diet, O and H in tissues and body water (from which biominerals form) are supplied by diet, water, and O_{2}, and cations (Sr, Pb, etc.) are ingested as food and water. Animal soft tissues show only slight enrichments in ^{13}C and ^{34}S isotopes relative to diet, whereas ^{15}N enrichment is stronger and more consistent. Enrichment magnitude depends on tissue type

TABLE *2*.—A summary of common isotope systems and expected patterns in δ-values used to examine scenopoetic and bionomic dimensions of ecological niche space (from Newsome et al., 2007a).

Gradient	Isotopes	High δ-values	Low δ-values	Sce.	Bio.
Trophic level	C, N	High levels	Low levels		✓
C3 vs. C4 plants	C, O, H	C4	C3	✓	✓
C3 vs. C4 animals	C	C4	C3		✓
C3 functional types	C	Thick cuticle (e.g., evergreen trees)	Thin cuticle (e.g., deciduous forbs)		✓
Canopy position	C, O	High canopy	Forest floor	✓	✓
Plant fungal symbioses	N	Non-mycorrhizal	Mycorrhizal		✓
N_2-fixation - terrestrial	N	Typically indicates little N fixation, but so do values much less than 0‰	Strong fixation when values near 0‰		✓
Marine plants/ consumers	C	Seagrass, kelp	Planktonic algae	✓	✓
Marine plants	N	Most marine 1° producers	N-fixers	✓	
Benthic-pelagic	C, S	Benthic	Pelagic	✓	✓
Marine-terrestrial	H, C, O, N	Marine	Terrestrial	✓	✓
Marine-terrestrial	S, Sr	Variable	Variable	✓	✓
Latitude - terrestrial	H, O	Low latitude	High latitude	✓	
Latitude - marine	C	Low latitude	High latitude	✓	
Latitude - marine	N	Low latitude (except areas with N_2 fixers)	High latitude	✓	
Altitude	H, O	Low altitude	High altitude	✓	
Altitude (C3 ecosystems)	C	High altitude	Low altitude	✓	
Aridity	H, O, C, N	Xeric	Mesic	✓	
Nearshore-Offshore	C	Nearshore, Upwelling	Offshore	✓	
Temperature - terrestrial	H, O	High temperature	Low temperature	✓	
Geologic substrate	Sr	Old rocks, granite	Young rocks, basalt	✓	
Methanogenesis	C	Photosynthetic carbon	Methanogenic carbon	✓	✓
Denitrification	N	Strong denitrification	Little/no denitrification	✓	
N_2-fixation - marine	N	Little fixation	Strong fixation	✓	

(especially for C), digestive physiology, diet quality, and physiological state (anabolic vs. catabolic). Carbon in bioapatite is derived from body water bicarbonate. It reflects bulk dietary C but shows strong ^{13}C-enrichment associated with carbonate equilibria, as well as variation related to microbial fermentation of food. Oxygen in biominerals is ^{18}O-enriched relative to body water by the amount expected for systems near isotopic equilibrium. Fractionation of O and H isotopes between diet, water, and soft tissues is a current topic of study; it is too early to summarize. It is usually asserted that Sr, Pb and other heavy isotopes are incorporated from diet with no fractionation.

Diet

Table 2 summarizes the vertebrate niche dimensions that can be discriminated using different isotopic systems (discussion based on Koch, 2007; Newsome et al., 2007a). Carbon in land plants is supplied by the well-mixed atmospheric CO_2 reservoir, so there is a degree of uniformity in $\delta^{13}C$ values across ecosystems. $\delta^{13}C$ values are commonly used to distinguish consumption of C3 versus C4 plants (or animals that feed on C3 versus C4 plants). C3 photosynthesis occurs in all trees, most shrubs and herbs, and grasses in regions with a cool growing season. C4 photosynthesis occurs in grasses where the growing season is warm, and in some sedges and dicots. C3 plants have lower $\delta^{13}C$ values than C4 plants. Crassulacean acid metabolism (CAM) occurs in succulent plants, producing $\delta^{13}C$ values that range between those for C3 and C4 plants, but are often similar to C4 plants. There are consistent $\delta^{13}C$ differences among C3 plants related to light level, moisture, position in the canopy, and other factors that affect the rate of photosynthesis and stomatal resistance to CO_2 diffusion into the plant. Within C3 ecosystems, $\delta^{13}C$ values differ among plant functional types in relation to stomatal resistance, which correlates with cuticle thickness. For example, in a boreal system Brooks et al. (1997) found that $\delta^{13}C$ values in evergreen trees > shrubs/deciduous trees > moss > deciduous forbs.

The substrates for H, O, N and S in the plants and waters at the base of terrestrial food webs vary spatially, so care must be taken when comparing consumer isotope values among ecosystems. Within ecosystems, leaf water and dry matter $\delta^{2}H$ and $\delta^{18}O$ values vary with water stress, canopy height, and plant functional type, chiefly because of differences in evaporation, which tend to leave the plant enriched in the heavy isotope. For example, for leaf water and tissue $\delta^{2}H$ values, C3 < C4 < CAM, and for leaf water $\delta^{18}O$ values, C3 dicots < C3 grass < C4 grass. Because of strong ^{15}N-enrichment moving up food webs, $\delta^{15}N$ values are used to study trophic level. Within ecosystems, plants from wetter habitats have lower $\delta^{15}N$ values than those from dry habitats, and they show $\delta^{15}N$ differences among functional types related to rooting depth, symbioses with nitrogen-fixing bacteria (which shift plant values to 0‰), and mycorrhizal associations. In boreal ecosystems, non-mycorrhizal plants (graminoids, forbs) have higher $\delta^{15}N$ values than mycorrhizal plants (trees and shrubs), mosses and lichens.

In marine ecosystems, $\delta^{13}C$ values vary among plant functional types (and their consumers) such that phytoplankton < macroalgae < sea grass, which translates into a difference between pelagic vs. benthic production. These differences are ultimately related to diffusional limitations on CO_2 supply to plants, and are affected by factors such as algae size, shape, and, most importantly, photosynthetic rate. In some case, CO_2 limitations are severe enough that plants take up HCO_3^{2-}, rather than CO_2, leading to higher tissue, $\delta^{13}C$ values. Benthic-pelagic differences are also present in $\delta^{34}S$ values, but otherwise marine $\delta^{34}S$ values are relatively invariant compared to terrestrial and freshwater values. Marine plants do not differ greatly in $\delta^{15}N$ value by functional type. In most systems, they have values ≥5‰ (the signature of deep water nitrate), though N_2-fixing cyanobacteria have values close to 0‰. Because marine food webs are often long, however, $\delta^{15}N$ values are a powerful tool for studying trophic level. Freshwater submerged aquatic plants have variable $\delta^{13}C$ values, depending on the mix of CO_2 from the atmosphere, plant decomposition, and oxidation of bacterially-generated methane (a source of ^{13}C-depleted nutrients). Finally, because most isotope systems differ between marine and terrestrial/freshwater ecosystems, they are useful for discriminating between the consumption of such resources at the interface of these systems (estuaries, coastal sites).

Habitat preferences and migratory patterns

Isotopic systems that differ within and among biomes provide information on habitat preferences and migration (discussion based on Koch, 2007; Newsome et al., 2007a; Hobson, 2008). Dietary isotope differences sometimes translate cleanly into habitat differences. For example, C4 feeding is a sign that an animal spends time on grasslands. In dense forests, $\delta^{13}C$ and $\delta^{18}O$ values of plant biomass increase from the forest floor to the top of the canopy, and as such can reveal the height at which an herbivore spends time feeding. Foraging location is also revealed by isotopic systems that discriminate consumption of marine versus terrestrial resources. In other cases, isotopic gradients among habitats are controlled by climatic or oceanographic factors (wholly scenopoetic niche dimensions; Table 2). $\delta^{2}H$ and $\delta^{18}O$ of precipitation and hence body water are lower in colder and higher altitude terrestrial habitats. Evaporation causes higher $\delta^{2}H$ and $\delta^{18}O$ values in plants, and water stress increases stomatal resistance, raising δ^{13}C values. Soil and plant δ^{15}N values also increase with decreasing rainfall. Thus for all these systems, increasing aridity leads to higher isotopic values in plants that cascade up food webs to consumers. In marine systems, higher photosynthetic rates in nearshore plants lead to higher δ^{13}C values relative to those offshore. Low δ^{15}N values occur where N-fixation is important (e.g., nutrient-poor tropical gyres), whereas high values occur where denitrification is active (e.g., highly productive regions with well developed oxygen minimum zones). In areas where primary production is limited by other factors (light, micronutrients, etc.), marine δ^{15}N and δ^{13}C values are low because of incomplete nitrate utilization and low photosynthetic rates, respectively, which may explain low δ^{13}C and δ^{15}N values in marine plants at high latitude relative to those at middle latitudes.

All these isotopic systems that vary by habitat, biome, or climate can be used to assess animal migration. The greatest amount of work has been done on bird migration, tracking latitudinal treks against δ^{2}H and δ^{18}O landscapes (isoscapes), supplemented with δ^{13}C and δ^{15}N values (Bowen and West, 2008). Other studies have examined time series of samples collected from teeth, otoliths, and other accreted materials (e.g., Koch et al., 1995; Kennedy et al., 2000). Elements such as Sr or Pb, which vary in relation to geologic factors, offer isotopic gradients uncorrelated to climatic or biome differences and are, therefore, extremely useful in migration studies in the terrestrial realm, or between marine and terrestrial systems.

In marine systems, movements of mammals, birds, teleosts, and sharks have all been tracked isotopically. In general, differences in isotopic composition at the base of the food web due to oceanographic differences map out very large regions that can be used to discriminate foraging zones among marine consumers. For example, there is a 2 to 3‰ decrease in food web δ^{13}C and δ^{15}N values from temperate (30 to 35ºN) to high-latitude (>50ºN) northeast Pacific pelagic ecosystems (discussion based on Graham et al., in press). Higher temperatures and upwelling lead to higher phytoplankton growth rates (and higher δ^{13}C values of phytoplankton and higher level consumers) in the California Current relative to the Gulf of Alaska. Higher productivity in coastal systems along the entire eastern Pacific Ocean and southern Bering Sea lead to higher ecosystem δ^{13}C values when compared to offshore systems, and zooplankton δ^{13}C and δ^{15}N values decrease from east to west across the shelf-slope break in the southeastern Bering Sea. These regional gradients have been used to characterize migration patterns for modern and fossil marine mammals and birds in the region. Note that for expected gradients in marine δ^{13}C values, we have focused on the organic carbon fixed by primary producers. Expected patterns in the δ^{13}C value of dissolved inorganic carbon are complex, related to the balance between atmospheric and oceanic mixing, remineralization, and local productivity. These variations are not very relevant to studies of vertebrates, because with the exception of fish otoliths, most C in vertebrates is supplied by diet (organic carbon), not inorganic carbon.

Reproductive biology

Three aspects of reproductive biology have been studied using isotopic methods: nutrient allocation to reproduction, nursing/weaning, and pregnancy. Inger and Bearhop (2008) reviewed avian studies using isotopes to quantify the roles of endogenous reserves (capital) versus recently ingested nutrients (income) in forming eggs and chicks. This approach works best if there is a sharp isotopic contrast between female foraging zones immediately before nesting and those surrounding the nesting sites. Koch (2007) reviewed isotopic studies of nursing, lactation, and pregnancy in mammals. If lactating mothers catabolize their own tissues to make milk, δ^{15}N and δ^{13}C values from nursing offspring should indicate they are feeding at a higher trophic level than their mothers. As expected, nursing young are ^{15}N-enriched by 3 to 5‰ relative to their mothers in many extant terrestrial and marine mammals. The prediction is complicated for C by the fact that milk is rich in lipids, and lipids are ^{13}C-depleted relative to proteins. Weaning age can be reconstructed by assessing age at the transition from nursing to weaned isotope values by sampling tissues that turn over rapidly or by microsampling tissues that grow by accretion, or by sampling bone from growth series (though the latter turns over more slowly). The isotopic consequences of lactation and pregnancy are not as well understood. In a study of pregnant humans, Fuller et al. (2004) found no significant effects of pregnancy on δ^{13}C values, but that δ^{15}N values dropped from conception to birth, and that the magnitude of the drop correlated positively to the baby's birth weight as well as the amount of weight gained by the mother. If the patterns associated with pregnancy and lactation are common among mam-

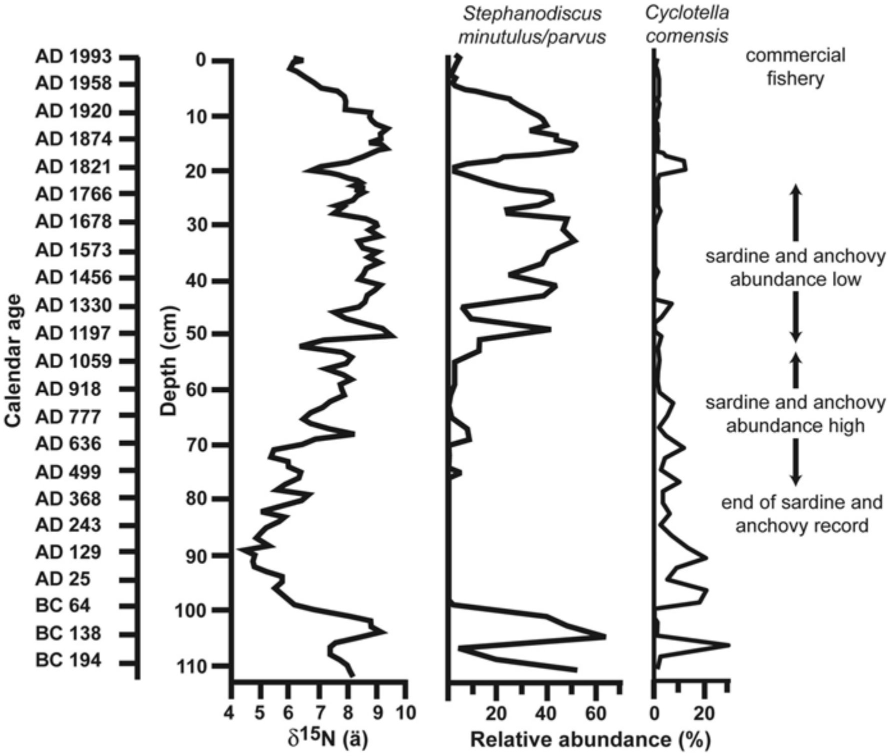

FIGURE *1*.—Temporal variations in sedimentary $\delta^{15}N$ values and the relative abundances of *Stephanodiscus minutulus/parvus* (a mesotrophic to eutrophic diatom) and *Cyclotella comensis* (an oligotrophic diatom) from Karluk Lake, Alaska (modified from Finney et al., 2002).

mals, they offer the potential to study inter-birth interval, neonatal survival rate, and other critical aspects of reproductive biology.

Nutritional state

It has long been argued that during fasting or nutritional 'stress', $\delta^{15}N$ values in consumers might rise (Hobson et al., 1993; reviewed in Koch 2007; Martínez del Rio et al., 2009). Trophic fractionation of N is thought to relate to excretion of nitrogenous wastes that are ^{14}N-enriched relative to the body N pool by enzymatic effects associated with transamination and deamination. Mass balance models imply that, at steady state, the greater the fraction of N lost as ^{14}N-enriched waste, the higher the body ^{15}N-content (i.e., $\Delta^{15}N_{body\text{-}diet}$ increases). The models are supported by experi-ments showing that $\Delta^{15}N_{body\text{-}diet}$ increases with increasing protein content in the diet of individual species, and by the fact that $\Delta^{15}N_{body\text{-}diet}$ is slightly higher for carnivores than herbivores. When animals are out of N balance, $\Delta^{15}N_{body\text{-}diet}$ values may decrease for animals in anabolic states (growth) and increase for animals in catabolic states (fasting, starvation). If we assume that the $\delta^{15}N$ value of their diets didn't change following conception, then Fuller et al.'s (2004) observation that pregnant women have lower $\delta^{15}N$ values supports this view; lower values signal a proportionally reduced loss of ^{14}N-enriched urine as pregnant females achieve positive N balance. Fuller et al. (2005) studied pregnant women with morning sickness who lost weight early in their pregnancies and found strong ^{15}N-enrichment (consistent with a rise in $\Delta^{15}N_{body\text{-}diet}$ value), as expected given these models. Differences in $\delta^{15}N$ values based on diet protein quantity or growth vs. starvation have yet to be extensively exploited in ecological or paleoecological research.

CASE STUDIES IN CONSERVATION PALEOBIOLOGY

We will explore four case studies that use isotopic data to illuminate the autecology of extant species. In the first, isotopic data are used to reconstruct Holocene fluctuations in the abundance of an economically and

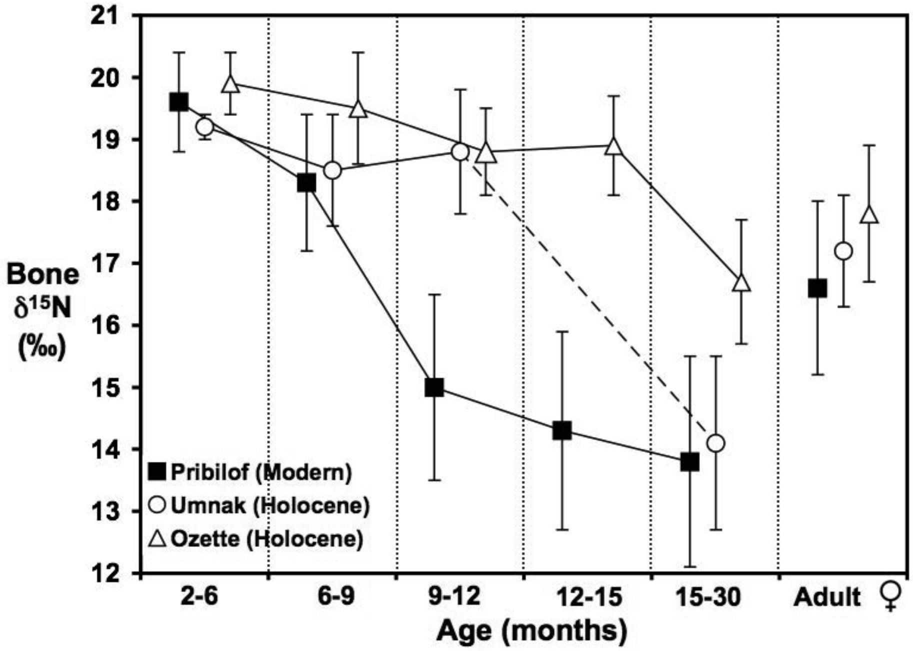

FIGURE 2.—Nitrogen isotope evidence from bone collagen for a large change in weaning age in northern fur seals. $\delta^{15}N$ values (mean ± one standard deviation) are presented for animals in different age classes from a modern rookery on the Pribilof Islands, and Holocene populations from the Olympic Peninsula (Ozette), and the Aleutians (Umnak) (modified from Newsome et al., 2007b).

environmentally critical species, sockeye salmon, in relation to climatic change. In the second, we again explore Holocene abundance variations, but this time in a pinniped, the northern fur seal. Isotopic data are used to understand the foraging, migratory, and reproductive ecology of the species; they point to recent changes in behavior that have ramifications for the conservation biology of the species. The third study focuses squarely on feeding ecology, using isotopic data from fossils of the highly endangered California condor to understand how it survived the late Pleistocene extinction, and to consider what this understanding might imply for the ongoing restoration of the species. The fourth study also examines feeding ecology, this time for of one of the few large terrestrial mammals to survive the late Pleistocene extinction in North America, the grey wolf. Paleogenetic data reveal unsuspected dynamics for the wolves of Alaska, and isotopic and morphological data show how the species evolved behaviorally and physically to respond to its shifting prey base. The final example is a thought exercise. We consider how these different types of information might help scientists identify ecological analogs for extinct megafauna. Overall, the case studies illuminate how isotopic data, when coupled with other sources of information, can reveal the ecological roles and responses of species, as well as the existence and magnitude of important species interactions that occurred in past ecosystems.

Shifting baselines in animal abundance: Alaskan sockeye

Paleobiology can reveal whether abundance shifts documented by wildlife biologists are typical or unusual. Among large vertebrates, some of the most dramatic changes have been at higher latitudes, such as the decline of marine mammal species in the north Pacific and Bering Sea (Springer et al., 2003), and shifts in penguin abundance around Antarctica (Ainley et al., 2005). The roles of climate change (anthropogenic or natural) vs. top-down forcing by industrial whaling is debated in both cases (Ainley et al., 2007; Springer et al., 2008). The context supplied by paleobiological records, both for estimates of the magnitude of past oscillations and about the relationship between abundance shifts and environmental factors, is needed to disentangle this nexus of causes. In Antarctica, ancient

DNA analysis, geochronological studies, and sedimentary isotope records are being used to reconstruct abundance changes in pinnipeds and sea birds (Baroni and Orombelli, 1994; Liu et al., 2004; Hall et al., 2006; Emslie et al., 2007).

Work on sockeye salmon abundance in Alaska over the past several millennia is an elegant example of the way that isotopic paleoecology contributes to such questions (Finney et al., 2000, 2002). Salmon are crucial components of northern Pacific ecosystems, and are important economical and cultural resources. After hatching, juvenile sockeye (*Oncorhyncus nerka*) forage for one to three years in their natal lakes or streams. They then migrate to the ocean, where they forage for one to four years and put on 99% of their adult mass before returning to their natal lakes and streams to spawn and die. Nitrogen isotope data have shown that marine-derived nutrients from salmon carcasses are very significant in some freshwater systems. A drop in salmon-derived nutrients due to overfishing or environmental factors can set in motion a negative feedback, leading to lower freshwater productivity and further reductions in salmon recruitment.

In nursery lakes on Kodiak Island and the Alaska Peninsula, Finney et al. (2000) found a positive linear relationship between salmon abundance and the $\delta^{15}N$ values of zooplankton, salmon smolts, and sediments. Given this modern calibration, Finney et al. (2000, 2002) reconstructed long-term variations in sockeye abundance by analyzing sedimentary $\delta^{15}N$ values and compared their results to historical records of catch and abundance, to shifts in benthic diatom assemblages, and to basin-scale shifts in fish abundance in relation to climate regime changes (Fig. 1). Over the last 300 years, they discovered regionally coherent shifts in sockeye abundance on decadal time scales that point to large-scale forcing from the ocean-atmosphere system. In Karluk Lake, where salmon contribute a large fraction of the nutrients, a drop in sockeye abundance in the early 1800s was followed by a swift recovery at a time when the natural feedback was operating, whereas the dramatic loss of salmon-derived nutrients associated with commercial fishing in the late 20th century seems to have had a strongly negative impact on lake productivity that may be preventing a similar recovery today.

On longer time scales, Finney et al. (2002) found that eutrophic diatom species dominated when $\delta^{15}N$ values were high (i.e., when salmon-derived nutrients

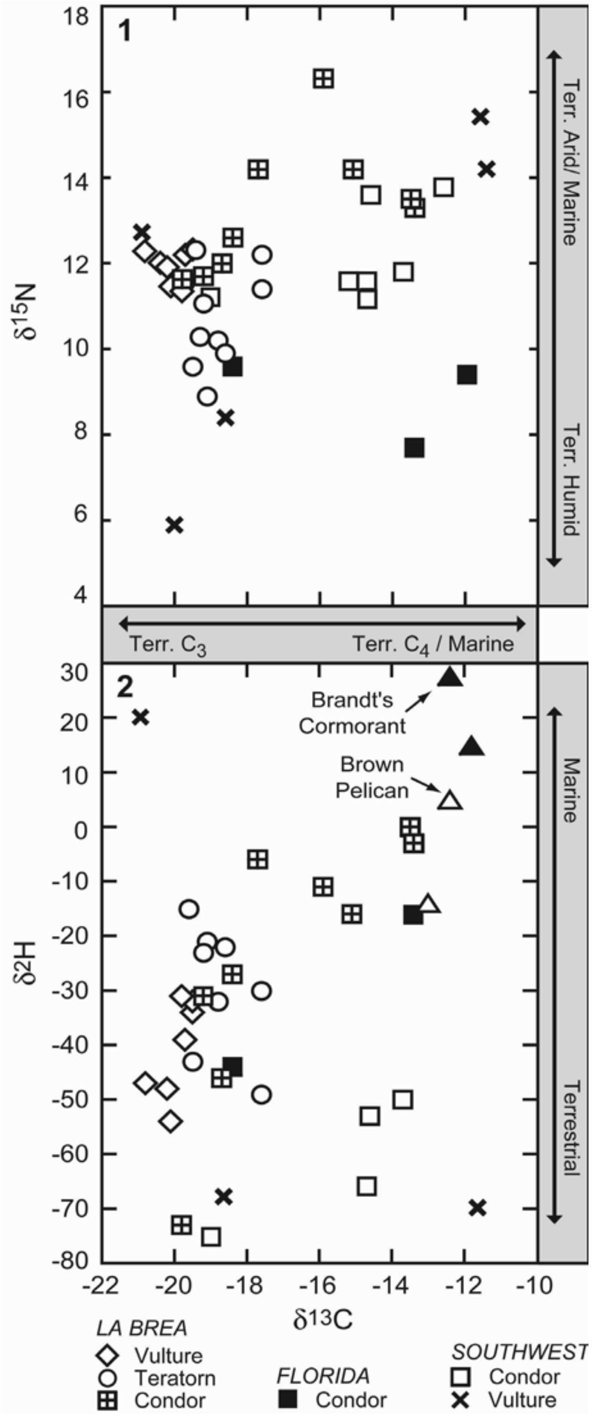

FIGURE 3.—Isotopic variations in Pleistocene condors and associated avifauna in North America; *1*, Collagen $\delta^{13}C$ versus $\delta^{15}N$ values; *2*, Collagen $\delta^{13}C$ versus $\delta^{2}H$ values (including modern marine birds). Environmental axes corresponding to isotopic axes are labeled (modified from Fox-Dobbs et al., 2006).

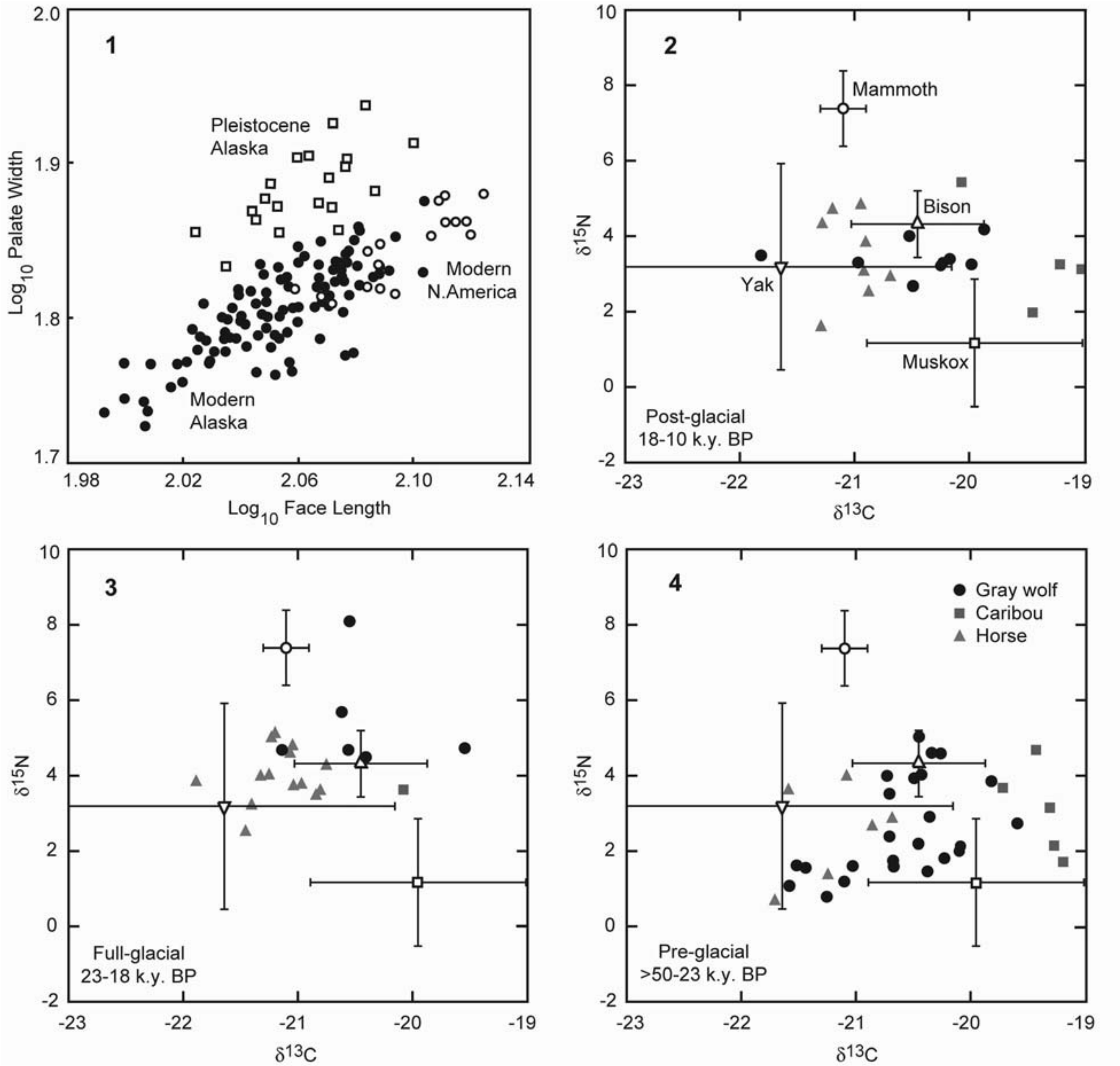

Figure *4*.—Morphology and isotopic data for Beringian and modern wolves and their prey; *1*, Palate width versus face length for late Pleistocene Alaskan (Beringian) and modern grey wolves. Beringian wolves had shorter and broader palates than modern wolves, indicative of a more robust skull and stronger jaws (modified from Leonard et al., 2007); 2 to 4, Collagen δ^{13}C versus δ^{15}N values for Beringian wolves and megafaunal prey. Wolf δ^{13}C and δ^{15}N values have been corrected for trophic isotope differences (-1.3 and -4.6, respectively). Each panel presents individual data for wolves (filled circle), caribou (filled square), and horses (filled triangle) for three time intervals. Bison, yak, muskox and mammoth data are not interval-specific and are presented as means (± one standard deviation) in each panel (modified from Leonard et al., 2007; Fox-Dobbs et al., 2008).

were abundant), and that cycles in salmon abundance were greater than in the observational record in the period before the establishment of commercial fisheries. Historical records over the last century suggest that climate forces salmon production and abundance, but the isotopic abundance record points to contrasting patterns at different time scales. In the twentieth century, there were antagonistic oscillations in marine productivity in the eastern Pacific Ocean to the north and south of the North Pacific Current (~45°N). On a decadal time scale, Alaskan salmon abundance covaries with that of sardines from off the California coast, whereas both are out of phase with anchovy abundance from California. These shifts have been attributed to oceanic regime shifts that affect the entire north Pacific Basin. Yet on the millennial time-scale, isotope data suggest much larger shifts in abundance of all taxa, and salmon abundance is negatively correlated with the abundance of both sardines and anchovies. These shifts are coherent with regional paleoclimatic data, pointing to basin-scale shifts in the ocean-atmosphere system as the driver. The nature of these links is complex, since the millennial abundance patterns don't match those on decadal or centennial time-scales. Given these data, it would clearly be difficult to extrapolate from the response of species to the small-scale fluctuations in decades-long historical records to predict their response to large-scale climatic or anthropogenic change. Longer time-scale records are essential to ground-truth models of the dynamics of these fisheries.

Shifting abundance and changing behavior: northern fur seals

Archaeological remains yield data at lower temporal resolution than the sedimentary cores used to study fish abundance, and the data have been through an anthropogenic filter. Yet such remains are proving a rich trove for all manner of information of relevance to conservation biology (Lyman, 2006). An example is recent work on northern fur seals (*Callorhinus ursinus*) from the northeastern Pacific Ocean (Burton et al., 2001; Gifford-Gonzalez et al., 2005; Moss et al., 2006; Newsome et al., 2007b). This species is common in archaeological middens greater than 500 years old from southern California to the Aleutian Islands. Yet today it breeds almost exclusively on high-latitude offshore islands, with the largest rookeries on the Pribilof Islands (Bering Sea). Animals occupy rookeries for four months, and mothers give birth and wean their pups in this interval. Pribilof breeders are highly migratory for their eight months at sea, foraging pelagically as far south as Baja. These behaviors would have made the species relatively inaccessible to native human hunters. Paleobiological study has revealed why they were more available in the past.

Prehistoric adult female northern fur seals have lower $\delta^{13}C$ values than nearshore-foraging harbor seals, suggesting that they were feeding offshore over their entire range, as they do today. These observations falsify the hypothesis that fur seals were available to prehistoric humans because they foraged closer to shore in the past. Furthermore, prehistoric female fur seals cluster into three groups isotopically: a southern group (California), a northern group (Pacific Northwest to eastern Aleutians), and a western Aleutian group. Isotopic distinctions among seals from different regions suggest that these prehistoric females were less migratory than modern Pribilof females and confirm that fur seals from California were year-round residents. Archaeometric evidence for very young pups at sites in California, the Pacific Northwest, and the eastern Aleutians confirm the presence of temperate-latitude breeding colonies. In bone growth series from modern Pribilof seals, there is a rapid drop in $\delta^{15}N$ values between the 2-6 and 6-9 month age classes, consistent with rapid weaning when animals switch from feeding on maternally-produced tissue to foraging independently at a lower trophic level (Fig. 2). In contrast, $\delta^{15}N$ values of bone growth series from ancient temperate-latitude rookeries indicate that pups were weaned at 12 months or more, not in 4 months as today. Ancient DNA analysis confirms that slower weaning seals were not a separate species. Northern fur seals were more available to ancient human hunters because they had rookeries all along the eastern Pacific margin and because females and pups spent a much greater amount of time on land.

The relative roles of human hunting versus climatic change in explaining these ecological and behavioral shifts are unclear and are the focus of ongoing research. Whatever the cause, by 500 years ago northern fur seals were largely restricted to breeding in the Arctic, where severe winter conditions favored rapid weaning. Paleobiological analysis reveals that in the absence of this strong selection, later weaning was adaptive at rookeries outside the Bering Sea. Most other eared seals wean at a later age, as inferred for ancient northern fur seals. Later weaning is thought to buffer against inter-annual resource fluctuations (like those due to El Niño events) that negatively affect productivity in temperate and tropical marine ecosystems.

Northern fur seals provide a clear example that extant populations with relictual distributions may have experienced major ecological and behavioral changes. Over the past several decades, fur seal migrants from high-latitude rookeries have reestablished colonies at temperate latitudes, despite declines in the source population in the Bering Sea. Establishment of temperate-latitude rookeries may buffer the global population through diversification of population and genetic structure and by diffusing potential threats to viability over a larger geographical area. Yet the restriction of the species to high-latitude rookeries over the past 500 years may have eliminated the behavioral plasticity needed to respond to temperate-latitude conditions. As they re-establish rookeries across their ancient range, northern fur seals may need to 're-evolve' their ancient reproductive strategy. This study highlights the importance of understanding pre-exploitation biogeography and behavior of species whose current ecology may be shaped by recent exploitation and/or environmental change.

Dietary flexibility and post-Pleistocene survival: California condors

The California condor (*Gymnogyps californianus*) is a species of exceptional conservation concern. It is the largest survivor of the once diverse Pleistocene avian megafauna of North America, and it exists in the wild in only a few reintroduced populations. Their current existence is in stark contrast to the continent-wide distribution of condors just 10,000 years ago (Grayson, 1977; Emslie, 1987). Stable isotope data provide insight into the role of marine versus terrestrial resources in the extinction patterns of avian scavengers at the Pleistocene-Holocene boundary, and the types of resources that might sustain condors in the future.

The large-bodied avian scavengers that co-existed in North America for tens of thousands of years suffered extinction and extirpation at the Pleistocene-Holocene boundary coincident with the mass extinction of terrestrial mammalian megafauna. The $\delta^{13}C$ and $\delta^{15}N$ values in bone collagen from two extinct scavengers in southern California, the teratorn (*Teratornis merriami*) and western black vulture (*Coragyps occidentalis*), indicate that both species were dependent upon terrestrial carrion (Fig. 3.1) (Fox-Dobbs et al., 2006). In contrast, isotope values for fossil condors from the region point to a diet that contained terrestrial (C3) and marine resources. Marine megafauna (whales and seals) survived the late Pleistocene extinction and are abundant in the productive eastern boundary current of the northeastern Pacific Ocean; they apparently provided a source of carrion for Pacific coast condor populations that carried them through the loss of terrestrial megafauna. Isotope mixing models indicate that many condors had diets that were >50% marine (Chamberlain et al., 2005), and ^{14}C chronologies reveal no temporal patterns; Pacific coast condors fed across the terrestrial-marine interface throughout the late Pleistocene (Fox-Dobbs et al., 2006).

The loss of condors elsewhere in North America versus their survival on the Pacific coast can be explained by dietary differences between the two groups (Fox-Dobbs et al., 2006). Extirpated condors from the southwestern U.S. and Florida are found in association with mammalian megafauna, and these animals have $\delta^{13}C$ values that fall between those expected for scavengers living in pure-C_3 and pure-C_4 ecosystems. The $\delta^{15}N$ values are more ambiguous; some individuals with high $\delta^{13}C$ values also have $\delta^{15}N$ values extending into the range interpreted as indicative of marine feeding on the Pacific coast. Yet high $\delta^{13}C$ and $\delta^{15}N$ values are common in arid, C_4-plant dominated ecosystems. Thus with only C and N isotope data it is possible that the specimens with high values in coastal California were immigrants from arid regions, not marine-feeders, or conversely, that the animals with high values in the southwest were immigrants from coastal regions. This conundrum was resolved through H isotope analysis, which provides an independent proxy for consumption of terrestrial (typically low $\delta^{2}H$ values) versus marine resources (high $\delta^{2}H$ values). $\delta^{2}H$ data confirm that high $\delta^{15}N$ values for Pacific coast condors were associated with marine feeding, whereas animals with high values in the southwest were completely terrestrial (Fig. 3.2).

Accounts from the 1800's report condors scavenging on beached marine mammals. Condors seem to have thrived during the period of Spanish and subsequent Mexican control of the west coast of the United States, as cattle ranching for leather created an abundance of terrestrial carrion, effectively recreating their lost Pleistocene resource base, which included both marine and terrestrial megafauna. Condors ate terrestrial food during their period of decline from the 1850s to the 1970s, perhaps because marine mammal abundances were low at this time as well because of sealing, whaling, and persecution from fisherman (Chamberlain et al., 2005). With the rise in marine mammal populations on the California coast following passage of the Marine Mammal Protection Act in 1972, condors reintroduced to coastal California, Baja California, or the Channel Islands have the possibility of returning to their 'ancient' coastal foraging strategy. There are anecdotal reports of condors again feeding on seals and whales, so they retain the behavioral plasticity to expand their diet

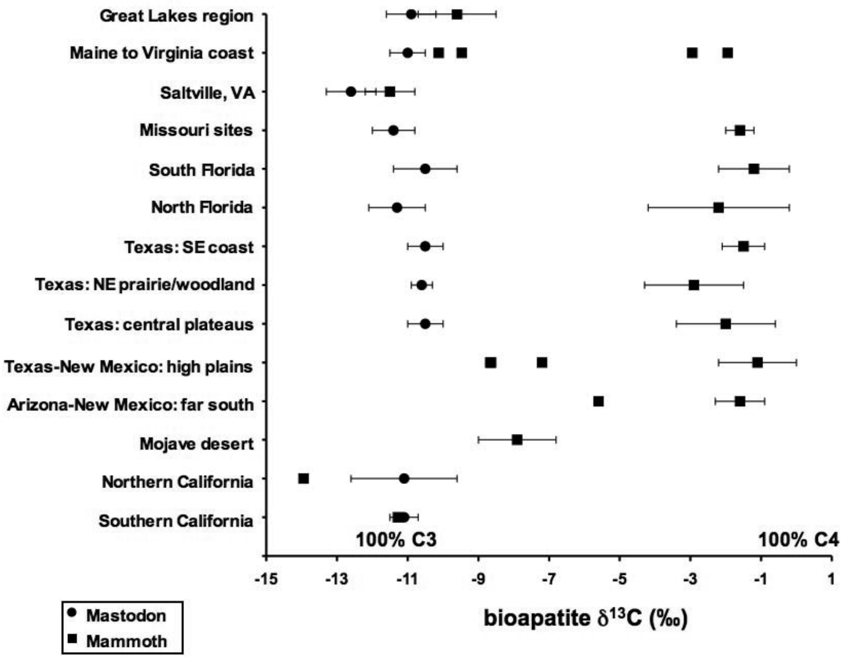

FIGURE 5.—Bioapatite δ^{13}C values for Pleistocene mastodons (filled circles) and mammoths (filled squares) from different regions across North America (means ± one standard deviation or data for individual specimens if no error bars are presented). Samples span the entire late Pleistocene. Collagen δ^{13}C values were converted to bioapatite values by adding +9.2‰. Expected δ^{13}C values for animals on 100% C3 and 100% C4 diets are presented (data for compilation available from PLK).

to marine mammal carrion. Unfortunately reintroduced condors are accumulating toxic lead loads, which have been traced via lead isotopes to ammunition (Church et al., 2006). Condors may be ingesting lead shot in gut piles left by hunters, or in the carcasses of fatally wounded animals that eluded their hunters. Whether or not consumption of marine carrion would reduce condor lead loads or induce other problems (e.g., organic contaminants) is an important open question. In any case, given the likely role of marine carrion in sustaining condor populations after the collapse of terrestrial megafauna, ecological niche modeling to prioritize areas for reintroduction (e.g., Martínez-Meyer et al., 2006) should factor in marine resource use.

Cryptic extinction and change in morphology and behavior: Alaskan grey wolves

First-order patterns of species presence and absence in the fossil record or current phylogeography do not always accurately reflect past population dynamics or diversity. Alaskan grey wolves (*Canis lupus*) are an excellent example. Grey wolves were widely distributed across Pleistocene and historic North America. Intuitively, this geographic pattern might be thought to reflect the survival of wolves across their ancient range. Within the North American mammalian carnivore guild, two factors generally correlate negatively with survival across the Pleistocene-Holocene boundary: body size and degree of hypercarnivory (reliance upon a pure-meat diet) (Koch and Barnosky, 2006). Based solely on these criteria, grey wolves are unexpected survivors, but if Pleistocene wolves were prey-generalists or scavengers, they might have been able to accommodate a shifting prey-base (e.g., Romanuk et al., 2006).

However, combined stable isotope, ^{14}C, genetic, and morphologic data from Pleistocene and modern grey wolves reveal a cryptic extinction of grey wolves in Beringia (Alaska and Yukon) (Leonard et al., 2007). Ancient DNA analyses show that modern Alaskan grey wolves are not descended from Pleistocene residents, but rather from Eurasian wolves that migrated into Alaska during the Holocene. To understand the defining features of the Beringian wolf ecomorph, and the ecological clues isotopic analyses can provide to explain its extinction, it is important to put the animal into paleoenvironmental context. For most of the glacial period from 60,000 to 10,000 years ago (including the very cold Last Glacial Maximum), the Beringian landscape was an open mosaic of steppe grassland and shrub tundra vegetation. A range of megafaunal prey was present at various times in the late Pleistocene (horse, yak, bison, caribou, muskox, and mammoth). The rapid reorganization of Beringian ecosystems at the end of the Pleistocene, which resulted in the establishment of modern tundra and boreal forest habitats, was temporally associated with the loss of most megafaunal species. The Beringian large carnivore guild was diverse and included grey wolf, American lion (*Panthera atrox*), scimitar-tooth sabercat (*Homotherium serum*), brown bear (*Ursus arctos*), and short-faced bear (*Arctodus simus*). Of these five, only gray wolves were present continuously through the entire late Pleistocene in Beringia (Fox-Dobbs et al., 2008).

Craniodental morphologic analysis suggests that Beringian wolves were either generalist large animal predators or scavengers (Fig. 4.1) (Leonard et al., 2007). They had a more robust craniodentral morphology and exhibited greater tooth wear and fracture than modern wolves, suggesting that they ate more bone and perhaps took down larger prey. All morphologic indices point to heavy carcass utilization, indicating intense competition within the carnivore guild and perhaps within species. Dietary reconstructions from bone collagen $\delta^{13}C$ and $\delta^{15}N$ values are consistent with the interpretation that Beringian wolves were not specialized predators (Figs. 4.2-4.4). Wolves ate a wider range of prey than other large carnivores in each time period, matched only by lions in the late-glacial period (Fox-Dobbs et al., 2008).

Why didn't their generalized diets, which presumably contributed to their persistence through prior climatic and ecologic shifts, allow Beringian wolves to survive into the Holocene? Isotopic data from Beringian wolves and other carnivores provide an important clue. While wolves were the most generalized predators, none of the large-bodied carnivores except short-faced bear were single-prey specialists during the late Pleistocene. There was a high level of trophic overlap and interspecific competition for prey within the megafaunal carnivore guild. Brown bear, the sole survivor within the guild (Barnes et al., 2002), is the only species in which some individuals engage in substantial omnivory. Omnivory may have been the only adequate buffer when megafaunal herbivore populations crashed. Modern grey wolves are less robust than extinct Beringian conspecifics, and they appear to exhibit greater specialization on particular prey, especially cervids, which may have experienced irruptions following the extinction of other, large herbivores. Overall, the study points to the vulnerability of highly connected, carnivore communities to food web perturbations, something that should be explored via food web modeling, and it indicates that the route to survival for modern wolves involved both morphological and behavioral evolution, as well as recolonization of range from which they had been extirpated.

Defining ecological analogs for rewilding

Janzen and Martin (1982) offered a powerful idea that is only now fully reverberating in ecology and conservation biology. They argued that the loss of Pleistocene megafauna disrupted species interactions, such as the dispersal of seeds, leaving behind organisms that are anachronisms, shaped by co-evolution for interactions that no longer occur (Barlow, 2001). We've discussed one such anachronism, the California condor, whose success at sites away from the Pacific coast was dependent on the carrion of extinct or extirpated terrestrial megafauna. As a deeper understanding has grown about the roles of megaherbivores as environmental engineers (Owen-Smith, 1988), and the roles of top carnivores in regulating terrestrial ecosystems (Terborgh et al., 1999), ecologists are beginning to speculate on the impacts of missing species on ecosystem diversity and function.

Donlan et al. (2006) followed this line of reasoning to a provocative conclusion. They suggested that missing ecological function and evolutionary potential can be restored to North America through the introduction of extant conspecifics or taxa related to extinct megafauna (Pleistocene rewilding). They envision this as a carefully managed ecosystem manipulation in which costs and benefits are measured on a case-by-case and locality-by-locality basis. The proposal has, unsurprisingly, raised a debate in conservation biology about the feasibility and wisdom of such manipulations. Would they restore lost function and interactions, or merely create potentially problematic new ones, as often results from non-native species introductions and invasions (Rubenstein et al., 2006)? We side-step this debate, and focus on a pressing matter should such experiments be attempted. What interactions were occurring in Pleistocene communities, and which modern taxa make the best analogs for missing Pleistocene species?

As an example, Levin et al. (2002) examined the indirect effects of horse grazing on salt marsh faunas to explore the types of impacts that late Pleistocene grazers might have had on coastal communities. They pointed to isotopic evidence that Pleistocene equids at coastal sites ate C4 plants, such as *Spartina* (cord-grass) in salt marshes, as do modern horses in these settings. Inadvertent re-introduction of equids to North America may have re-established species interactions and processes that had been present in North America for millions of years, but absent for the past 13,000 years. More information will be needed to confirm the hypothesis that Pleistocene horses actually ate *Spartina*, rather than upland C4 plants. Such information could come from phytoliths or plant fragments in coprolites or in dental calculus, or from δ^{15}N and δ^{34}S analysis (Peterson and Howarth, 1987).

The situation is more complex when the animal to be introduced is not conspecific or even congeneric with the extinct taxon. From the standpoint of safeguarding global species diversity and recreating important ecosystem functions, introduction of proboscideans to North America would be a top priority. In the latest Pleistocene, North America had at least three proboscidean species: *Mammuthus columbi*, the Columbian mammoth; *Mammuthus primigenius*, the woolly mammoth; *Mammut americanum*, the American mastodon. *Mammuthus columbi* and *M. americanum* were common in Pleistocene faunas south of the Laurentide ice sheet, with extensive range overlap across North America, though mammoths were more rare in eastern woodlands, and mastodon were absent from some regions on the central plains and prairies. Tooth morphology suggests that these proboscideans had different diets. Mastodon molars had blunt cusps arrayed in transverse ridges across the tooth, whereas mammoth teeth were high-crowned with flat occlusal surfaces and numerous enamel ridges. Based on these characters and rare gut content and coprolite analysis, mammoths have been reconstructed as grazers (grass eaters), whereas mastodons were considered browsers (animals that eat leaves, twigs, fruit, etc. of shrubs and trees). A growing δ^{13}C database (Koch, unpublished) reveals that the diets of these animals were, in fact, highly focused (Fig. 5). Wherever they occurred, mastodons ate a C3 plant diet, even in sites where C4 grass was available and being consumed by other taxa (e.g., Texas, Florida, Missouri). Likewise, in areas where both C4 grass and C3 browse were available, mammoths were strongly focused on grazing. In other regions, where C4 plants are absent (e.g., northern regions, California), mammoths ate C3 plants, but δ^{13}C values cannot easily distinguish between C3 grass and C3 browse.

Would surviving elephant species be appropriate analogs for these extinct taxa? Observational and isotopic data reveal that African elephants (*Loxodonta africana*, savanna elephants; *Loxodonta cyclotis*, forest elephants) have catholic diets (Koch et al., 1995; Cerling et al., 1999). While the fraction of grass versus browse in the diet varies in relation to the resources available, both species have diets focused on browse (Cerling et al., 1999). Asian elephants (*Elephas maximus*) have a dentition more similar to mammoths, and have diets richer in grass, though still with a substantial amount of browse (Cerling et al., 1999). Perhaps *L. cyclotis* would be a reasonable ecological analog for mastodons, but *L. africana* and *E. maximus* are not as focused on grazing as mammoths were. Of course, introduced elephants might evolve to a more grass-rich diet if placed on the North American prairie, as isotopic data suggest that the browse-rich diets of modern elephants are relatively recent acquisitions. Prior to one million years ago, most proboscideans in African and Asia ate C4 grass (Cerling et al., 1999). Isotopic data would be one part of any evaluation of the match between extinct species and their potential introduced replacements. Other taxa that should be examined closely are the extinct camelids (*Camelops, Hemiauchenia, Paleolama*) and the carnivores (*Smilodon*, *Homotherium*, and *Canis dirus*).

CONCLUSION

Isotopic data have an important role to play in conservation paleobiology because they can provide information on individuals and populations, as well as entire species. They offer proxies for abundance shifts that reveal the response of taxa to processes not operating at present, as seen in the studies on sockeye salmon. They illuminate the autecology of extinct species or extirpated populations (diet, habitat preferences, home range, reproductive ecology, etc.), documenting the full ecological potential of species that are currently in relictual distributions. Sometimes they confirm longstanding hypotheses, as was the case for the discovery of the seafood ‘buffer’ for coastal condors. Sometimes they reveal major surprises, such as the dramatic change in reproductive ecology in northern fur seals, or the fact that grey wolves became extinct in eastern Beringia and evolved a new diet and morphotype as they reoccupied the area. Finally, when coupled with other types of information (tooth wear, taphonomic, genetic, demographic, palynological, etc.) they can reveal the existence and magnitude of important species interactions that occurred in past ecosystems. Such information can also be used to parameterize models to test the function and stability of ecosystems following reintroductions of extirpated species or their ecological analogs. These are all essential services that isotopic paleoecology provides for conservation biology and restoration ecology, and they reinforce the conclusion that a deep temporal perspective is essential to effective and long-term conservation.

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