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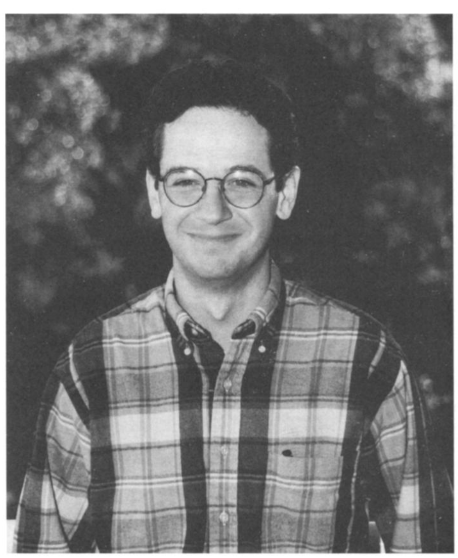
Isotopic Paleoecology and Land Vertebrates: Individuals, Species, and Ecosystems

Many studies of the isotope chemistry of fossils treat them as recording devices. There is growing interest in past changes in temperature, humidity, and Earth surface chemistry, and biogenic materials are a readily available substrate from which to extract environmental data. The influences of physiology, nutrition, and mobility are seen as nasty "vital" effects that must be removed so that we can get down to the environmental business at hand. With a few notable exceptions (Heinz Lowenstam, for example) scientists who were primarily interested in the fossil record have played a small role in the development of isotopic approaches to paleobiology. Rather the field has been pushed forward by isotope geochemists exploring biological systems, modern ecologists and scientists studying earth surface processes who have extended their reach into the historical record, paleoceanographers, and analytical chemists who have developed new methods. The main exception to this pattern has been in paleoanthropology, where much of the trail blazing isotopic research was conducted by scientists whose primary interest was the record of change in hominid diets and ecology. This situation has begun to change over the past fifteen years, as paleobiologists have learned more about isotopic techniques and started to apply them directly to answer questions about the ecology of individual fossil organisms, the evolution of entire species, and the role of vertebrates in ecosystem function. There are two general ways that isotopes are used in paleobiology and paleoecology. Because of subtle mass differences, isotopes of light elements (e.g., H, B, C, N, O, S) are often sorted by chemical, physical and biological processes. Variations in isotope ratios produced by this sorting can be used to monitor the magnitudes and rates of these processes. For example, differences in the processes associated with carbon fixation produce a large difference in carbon isotope composition between plants using the C3 versus the C4 photosynthetic pathway. Alternatively, we can simply use naturally-occurring isotopic differences among substances to trace their flow through biological systems. Isotope chemistry serves as a natural label. This type of research can involve either stable isotopes or variations in heavier elements (e.g., Sr, Nd, Pb) that are produced by radioactive decay. A simple example of this approach is the use of carbon isotopes in vertebrates to track the proportion of C4 plants (warm climate grasses) versus C3 plants (trees, shrubs, cool climate grasses) in animal diets.

Most approaches in paleobiology treat organisms of the same species as equivalent. In vertebrate paleontology, we often infer the diet or habitat preferences of whole species by studying average morphology. Yet different individuals in a population or species have different behaviors, habitats, and histories that must powerfully influence ecological and evolutionary processes. My earliest interest in stable isotopes and vertebrate paleontology came from just such a problem. What time of year did animals die? My graduate advisor, Dan Fisher, had discovered that a number of the late Pleistocene mastodons excavated in the Great Lakes region were butchered by Paleoindians. We were trying to evaluate whether or not these butchered



Due to the tolerance of colleagues at museums and Earth science departments around the nation, Paul Koch has been vaporizing small parts of fossils for isotopic studies since his days as a graduate student at the University of Michigan. His research activities in isotope chemistry have been divided among three areas: vertebrate paleobiology, continental paleoclimatology, and modern large mammal ecology. He gained the skills necessary for this work through undergraduate studies at the University of Rochester, his graduate work at Michigan, and post-doctoral fellowships at the Geophysical Laboratory and in the Department of Paleobiology at the Smithsonian Institution. Following several years as a faculty member in geological sciences at Princeton University, Paul moved to the Department of Earth Sciences at the University of California, Santa Cruz in 1996. Being so close to the ocean has led to his first serious foray into studies of marine ecosystems, though there are connections to his previous work on land vertebrates. Like his past work on elephants, this new work also involves large gray animals with unusual snouts: elephant seals.

individuals were scavenged natural deaths or deaths caused by hunting. The oxygen isotope composition of precipitation varies seasonally, and mastodons recorded this seasonal shift in growth laminations in their tusks. By tracking these isotopic oscillations, we demonstrated that butchered individuals tended to die in the late fall, whereas non-butchered individuals died in the late winter/early spring, supporting the notion that different processes (hunting versus natural death) were responsible for mortality. Recent studies have investigated many attributes at the level of individuals within fossil populations. Carbon isotopes provide a quantitative measure of the diet of individuals, allowing study of the variability in resource use within a species, as well as the pattern of resource partitioning among species. Carbon isotope analysis has shown that patterns of resource use among late Pleistocene herbivores in North America were remarkably stable, despite large changes in vegetation. The radiogenic isotope composition of vertebrates is largely controlled by the composition of local soils, providing a label of animal location. Studies of human remains by Doug Price and colleagues have begun to tease apart the role of migration versus resident population growth in the expansion and decline of local populations. Nitrogen isotopes are enriched at higher levels in food webs, and nursing infants are effectively "carnivores", feeding one trophic level higher than their parents. Nitrogen isotope differences among the skeletons of adults provide a monitor of differences in the amount of meat in the diet. Differences among the skeletons (or within the teeth) of juveniles relate to the age of weaning. Marilyn Fogel and colleagues have studied changes in the age of weaning in North American human populations before and after the introduction of corn in order to test hypotheses about the effects of nutrition on population growth. The "nursing effect" on nitrogen isotopes is present in mammals other than humans but, to date, the signal has not been exploited to test ecological or evolutionary hypotheses.

At the next level in the taxonomic hierarchy, isotopic studies have been used to characterize aspects of the biology or ecology of entire species. An example is the work of Barrick and colleagues, using oxygen isotopes to evaluate whether different dinosaur species were homeotherms or heterotherms. Similarly, Hervè Bocherens and I demonstrated that the oxygen isotope composition of hippopotamus was lower than that of land mammals from the same ecosystem. Fossil hippos are also "light," and Bruce MacFadden has applied the method to study the habitat preferences of putatively aquatic rhinoceros species from the Miocene and Pliocene. At the species level, carbon isotopes could be used to determine the relationship between behavioral change, morphologic evolution, and faunal turnover.

How, precisely, do changes in morphology take place in response to change in resources? Do animals begin to incorporate the new food item into their diet, then subsequently change in morphology to process the new resource more efficiently? Or do preadaptations allow some organisms to monopolize and exploit a new resource as soon as it appears? Because carbon isotopes provide a label for grass consumption (at least in area with a warm growing season), they provide a tool for examining evolutionary lags during transitions between browsing and grazing. In addition, while vertebrate herbivores have been a vital source of information about the expansion of C4 grasses in the late Miocene, the response of herbivores to this major change in vegetation has scarcely been considered. C4 plants differ from C3 plants in protein content, digestibility, and levels of defense by secondary metabolites. The late Miocene was marked by a major vertebrate extinction, but the selectivity of this extinction in relation to dietary preference, the breadth of resources utilized, or digestive physiology has not been explored. This is obviously a fertile area for future research.

Finally, vertebrate isotope geochemistry has the potential to illuminate terrestrial ecosystem structure and process, and how these features change through earth history. Here, the questions most often concern the heterogeneity of vegetation and the flow of carbon and nitrogen through ecosystems. For example, at many fossil sites in Texas and Florida, I've found co-occurring organisms that have mutually exclusive diets, either 100% C4 grass or 100% C3 trees and shrubs. If these deposits represent an ecological snapshot, then isotopic data indicate that a vegetational mosaic existed on the distance scale characteristic of the home range of these animals. Alternatively, if these deposits are time-averaged over thousands of years, we may be documenting the passage of an ecotone over the location. Another aspect of vegetation amenable to study in canopy structure. In closed woodlands, forest floor plants are enriched in "light" carbon due to the fixation of trapped carbon dioxide derived from the decay of plants and to the effects of low light levels on photosynthesis. Strong carbon isotope gradients between the forest floor and the top of the canopy indicate a dense forest with closely spaced trees. Carbon isotope gradients could be reconstructed by comparing forest floor and canopy dwelling herbivores, though the approach has not been used extensively to date.

Because of differences in food web structure and photosynthesis between marine and freshwater ecosystems, carnivorous marine fish tend to have higher carbon and nitrogen isotope compositions than their freshwater counterparts. Coupled with radiogenic isotope tracers, these isotopic differences could be used as to assess which fish in a freshwater fauna were anadromous, undertaking lifetime migrations between fresh water and the sea. More surprising still, we can use these isotopic differences to monitor the source of carbon and nitrogen supporting primary production in fresh water streams. Because the bodies of adult salmon are composed of "heavy" marine carbon and nitrogen, they are isotopically distinct from the local sources of carbon and nitrogen to the freshwater streams in which salmon spawn prior to death. Isotopic analysis of stream-side vegetation, fresh water invertebrates, and even the young salmon that grow to maturity in these streams reveals that a large portion of the carbon and nitrogen in these systems is marine in origin. It is supplied by the decaying bodies of adult salmon. The implications of this finding are profound. Reductions in the number of adults reaching the stream, due to over fishing or damming of rivers, negatively impacts the reproductive potential of the salmon who do survive to reach the spawning sites. To my knowledge, no one has studied the historical record of this system of marine fertilization of fresh water ecosystems.

The isotope systems and techniques used today in ecology and paleobiology were often developed by geochemists interested in non-biological problems. As the job market in more traditional areas, such as economic, metamorphic, and igneous geochemistry, has weakened in recent years, scientists trained in these disciplines are using their talents to attack environmental and biological questions. I don't blame them. Problems in paleoecology, evolution, and ecosystem function are exciting, societally-relevant, and probably easier to explain to parents and non-scientists than oxygen fugacity or eutectics. And the geochemical talents of these recruits can light up the field in expected ways. In my opinion, the most comprehensive and biologically-realistic treatment of the controls on oxygen isotopes in vertebrates was produced by a scientist (Matt Kohn) who was trained as a high-temperature isotope geochemist. Yet I would argue that paleontologists, at least those with strong backgrounds in biochemistry, physiology and ecology, are uniquely suited to make important contributions in this field. In the process, because they use the language and tools of geology, but apply them to problems that require a deep understanding of biological systems, isotopic studies can help to bridge the intellectual distance between these disciplines.

—PAUL L. KOCH