

Dietary controls on extinction versus survival among avian megafauna in the late Pleistocene

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ABSTRACT

The late Pleistocene extinction decimated terrestrial megafaunal communities in North America, but did not affect marine mammal populations. In coastal regions, marine megafauna may have provided a buffer that allowed some large predators or scavengers, such as California condors (*Gymnogyps californianus*), to survive into the Holocene. To track the influence of marine resources on avifaunas we analyzed the carbon, nitrogen, and hydrogen isotope composition of collagen from late Pleistocene vultures and raptors, including species that survived the extinction (condor, bald eagle, golden eagle) and extinct species (teratorn, black vulture). At the Rancho La Brea and McKittrick tar pits of southern California, isotope values for extinct teratorns (*Teratornis merriami*, $n = 10$) and black vultures (*Coragyps occidentalis*, $n = 8$) show that they fed entirely in a terrestrial C_3 ecosystem. In contrast, La Brea condors cluster into two groups, one with a terrestrial diet ($n = 4$), and the other with a strong marine influence ($n = 5$). At localities in the American southwest, Texas, and Florida, where condors became extinct, they have isotope values indicating entirely terrestrial diets ($n = 10$). Our results suggest that dependence upon terrestrial megafaunal carrion as a food source led to the extinction of inland California condor populations and coastal populations of teratorns and black vultures at the Pleistocene–Holocene boundary, whereas use of marine foods allowed coastal condor populations to survive.

Keywords: California condor, paleoecology, stable isotopes, late Pleistocene extinction.

INTRODUCTION

In the late Pleistocene, the skies of North America teemed with a variety of vultures and raptor species, approximately half of which became extinct at the end of the Pleistocene (Grayson, 1977). This avian extinction coincided with a 72% reduction in generic diversity of mammalian megafauna (Koch and Barnosky, 2006; Emslie, 1987). These two extinction events may be linked if avian scavengers were dependent upon megafaunal carrion as a food source.

The paleoecology of late Pleistocene vultures and raptors has been deduced from morphologic analysis (Hertel, 1995; Campbell and Tonni, 1981). A study of feeding morphology within the vulture guild at the La Brea tar pits in southern California indicated that species with intermediate cranial morphologies were more likely to survive into the Holocene than those with extreme morphologies (Hertel, 1994). For example, the California condor (*Gymnogyps californianus*), which has a non-specialized cranial morphology, survived the extinction event along the Pacific coast. Yet this intermediate morphology did not correlate with condor survival elsewhere in North America. Pleistocene condors were distributed

across much of the continent south of the Last Glacial Maximum ice sheets (Steadman and Miller, 1987), but by 10 ka they had disappeared everywhere except the Pacific coast (Koford, 1953; Emslie, 1988). We hypothesize that condors may have survived in western coastal regions if they scavenged both marine and terrestrial mammal carcasses. Whales and seals were not affected by the late Pleistocene extinction, so their carcasses may have provided a consistent food source for condor populations along the Pacific coast (Koford, 1953; Emslie, 1987; Chamberlain et al., 2005).

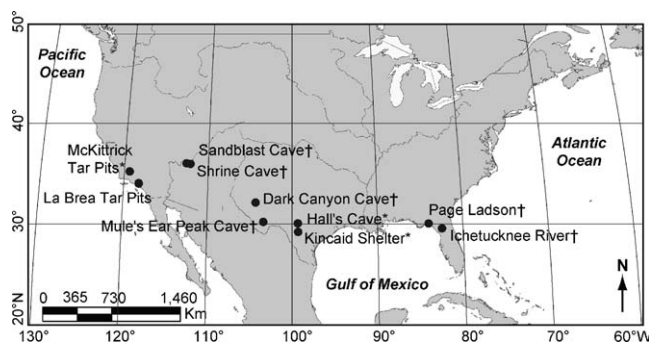
We use the stable carbon ($\delta^{13}C$), nitrogen ($\delta^{15}N$), and hydrogen (δ^2H) isotope composition of bone collagen to quantify terrestrial versus marine resource use by late Pleistocene condors, vultures, and raptors. Carbon and nitrogen in collagen are supplied by an animal's diet, providing a proxy for foraging behavior (following discussion based on Schoeninger and DeNiro, 1984; Koch, 1998; Kelly, 2000). The $\delta^{13}C$ values of terrestrial foodwebs primarily reflect the biomass fractions of C_3 and C_4 plants. The $\delta^{15}N$ values of terrestrial ecosystems are determined by environmental factors, such as aridity, that affect plant and soil nitrogen cycling dynamics. Both $\delta^{13}C$ and

$\delta^{15}N$ values increase with trophic level, though the increase is much stronger for nitrogen. Marine foodwebs are typically enriched in ^{15}N relative to terrestrial foodwebs, and have $\delta^{13}C$ values intermediate between those for C_3 and C_4 terrestrial ecosystems.

While the carbon and nitrogen dual-isotope approach is commonly used to reconstruct the proportions of marine and terrestrial food sources in the diets of top consumers, this system cannot be used to differentiate between an arid C_4 terrestrial diet and a marine diet with high $\delta^{15}N$ and $\delta^{13}C$ values. We use hydrogen isotopes as an additional proxy to further identify marine food sources in the diets of fossil raptors and vultures. Because environmental water represents the source of hydrogen during photosynthesis, the higher δ^2H values of ocean water (0‰) relative to most continental freshwater (growing season precipitation values for North America range from $-150‰$ to $-20‰$) should cause marine ecosystems to be 2H enriched relative to terrestrial ecosystems (Bowen et al., 2005). A significant fraction of the nonexchangeable hydrogen in vertebrate proteins such as collagen comes from dietary protein (Hobson et al., 1999), and as such can be used to identify the presence of marine food in the diets of top consumers.

Using these stable isotopes we examined diets of late Pleistocene avian scavengers (extant—condor; extinct—teratorn [*Teratornis merriami*]; locally extinct—western black vulture [*Coragyps occidentalis*]) and raptors (extant—bald eagle [*Haliaeetus leucocephalus*] and golden eagle [*Aquila chrysaetos*]) from coastal southern California. We use these data to correlate diet with species survival across the late Pleistocene extinction. We then explore the pattern of condor extinction at the continental scale by comparing the diets of condors from La Brea to those of condors and other vultures from late Pleistocene sites across North America where condors went extinct (Fig. 1). The $\delta^{15}N$ and $\delta^{13}C$ values for the La Brea condors were presented in Chamberlain et al. (2005), and here we present δ^2H values and ^{14}C dates for the same nine individuals.

Figure 1. Map showing fossil localities. Dots—fossil vulture and teratorn localities, no condors. Dagger symbols—localities where condors became extinct by 10 ka. Holocene range of condors was restricted to Pacific coastal regions.



METHODS AND MATERIALS

Collagen extraction methods and details of stable isotope analysis are outlined in detail in the GSA Data Repository (Appendix A¹). Stable isotope compositions are reported using delta (δ) notation and are referenced to Vienna Pee Dee belemnite, air, and Vienna standard mean ocean water for carbon, nitrogen, and hydrogen, respectively. Samples were only analyzed in duplicate for their hydrogen isotope ratios, and the mean of the replicate analyses is presented here. A few samples (5) that gave unusually high variability ($1\sigma > 5\text{‰}$) among

replicates were culled from the $\delta^2\text{H}$ data set. As there is no agreed upon calibration curve for the conversion of ^{14}C ages $>21,000$ yr B.P. into calendar years, all ages are presented as uncalibrated ^{14}C dates. Quantitative analyses were done using SYSTAT 10 and JMP 5.0.1a statistical software. Prior to the application of parametric statistics, all data were tested for normal distributions.

VULTURE AND RAPTOR PALEOECOLOGY AT LA BREA

Stable Isotope Results

Means and standard deviations for the La Brea vulture and raptor species and a complete list of specimens and isotope values are supplied in Appendix B (see footnote 1). Carbon and nitrogen isotope distributions differ significantly among species (MANOVA—Pillai's Trace test, $p < 0.0001$), and post-hoc pair wise comparisons are significant between all

species (F -test; $p < 0.05$), except for condors and bald eagles. For the set of species for which we have sufficient data for all three chemical elements (condors, teratorns, and black vultures), isotope distributions also differ significantly among species (MANOVA—Pillai's Trace test, $p < 0.001$).

Background for Dietary Interpretations

We assume that megafauna were the primary terrestrial resource available to avian scavengers from the tar pits. Isotope values for La Brea herbivores and carnivores range on average from -22‰ to -18‰ for carbon, and from 4‰ to 12‰ for nitrogen (Coltrain et al., 2004). These $\delta^{13}\text{C}$ values indicate that the La Brea ecosystem was almost entirely dominated by C_3 plants, as is the case today. Among the herbivore species, grazers have higher $\delta^{15}\text{N}$ values than browsers, and carnivores have higher values than herbivores. To compare isotope data from vultures and raptors to the megafauna they scavenged upon, we assume trophic level ^{13}C and ^{15}N enrichments of 1‰ and 4‰ , respectively (Chamberlain et al., 2005).

Hydrogen isotope ratios of collagen for marine-feeding vertebrates have not been reported in the literature. Therefore we prepared and analyzed bone collagen from two large modern seabird species (*Phalacrocorax penicillatus*—Brandt's cormorant [$n = 2$]; *Pelecanus occidentalis*—brown pelican [$n = 2$]) that are known piscivores from coastal California. The $\delta^2\text{H}$ values of the seabirds range from -14‰ to 28‰ , suggesting that marine feeders are likely to have bone collagen $\delta^2\text{H}$ values greater than $\sim -15\text{‰}$. For comparison, bone collagen $\delta^2\text{H}$ values reported for white-tailed deer (Cormie et al., 1994) range from -91‰ to $+13\text{‰}$. Although these data indicate some overlap between the $\delta^2\text{H}$ values of terrestrial and marine feeders, values greater than -20‰ were only observed for deer in areas where environmental water $\delta^2\text{H}$ values were very high (i.e., similar to ocean water values) due to high $\delta^2\text{H}$ values of precipitation and high levels of evaporation. Because precipitation isotope ratios for modern southern California (annual range -64‰ to -43‰ ; Bowen and Revenaugh, 2003) are much lower than those of ocean water, we expect that La Brea terrestrial feeders should have bone collagen $\delta^2\text{H}$ values lower than the -15‰ value we use as a minimum for marine feeders.

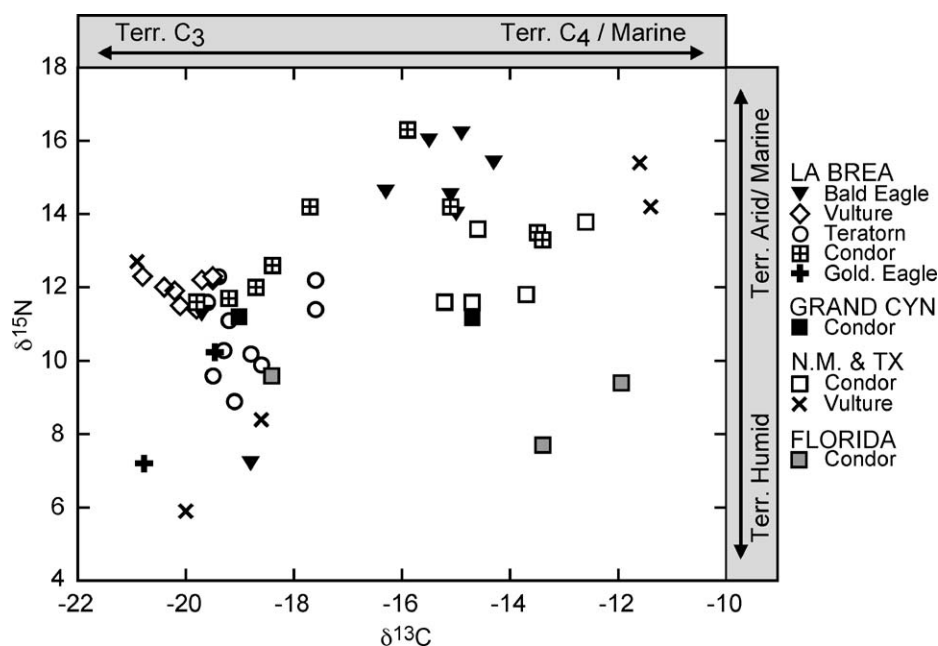


Figure 2. Plot of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (‰) for fossil raptors and vultures from all North American localities. Sources and controls of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ variability in terrestrial and marine ecosystems are given in text. Carbon isotope values vary along two environmental gradients; terrestrial C_3 to marine (La Brea), or terrestrial C_3 to terrestrial C_4 (southwest and Florida). Nitrogen isotope values also vary along two environmental gradients; terrestrial mesic to marine (La Brea), or terrestrial mesic to terrestrial xeric (southwest and Florida). CYN—canyon; N.M.—New Mexico; TX—Texas.

Diets of Pleistocene La Brea Raptors

Morphologic and observational data show that modern bald eagles are opportunistic piscivores and terrestrial scavengers, and our isotope data suggest that Pleistocene bald eagles had similar feeding behaviors (Figs. 2 and 3) (Hertel, 1995). Six individuals have high $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values that are outside the range of local terrestrial values and can most

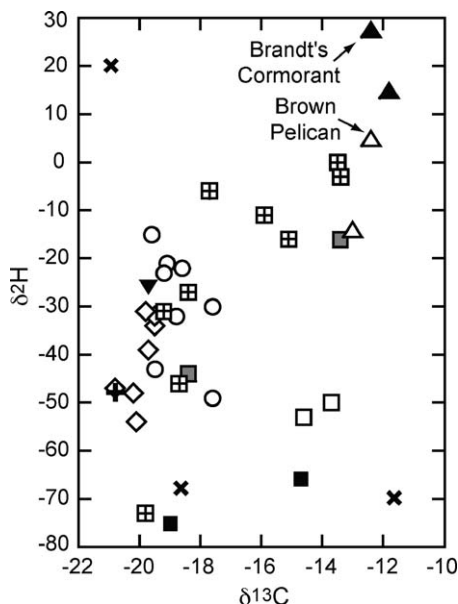


Figure 3. Plot of $\delta^{13}\text{C}$ and $\delta^2\text{H}$ values (‰) for fossil raptors and vultures from all North American localities. $\delta^2\text{H}$ values are not available for all $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ samples. Symbols as in Figure 2. Additional isotope data for two modern piscivorous seabirds are included. To compare these modern data to those from Pleistocene, we normalize $\delta^{13}\text{C}$ values to account for shifts in $\delta^{13}\text{C}$ value of earth surface carbon reservoirs due to natural and anthropogenic processes. We apply ice-core-derived correction of +1.2‰ to modern seabird $\delta^{13}\text{C}$ values (Leuenberger et al., 1992).

likely be explained by marine food sources, though the presence of bald eagles in the tar pits indicates they consumed terrestrial species to some extent. The other two bald eagles and the golden eagles have fully terrestrial $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. It is difficult to determine if the terrestrial eagle isotope values reflect predation on small mammals or scavenging on megafaunal carrion. The $\delta^2\text{H}$ values of the bald eagle and golden eagle that we were able to analyze are low, in agreement with our interpretation of a terrestrial diet for these individuals.

Diets of Pleistocene La Brea Condors and Vultures

The two extinct scavengers from La Brea and McKittrick, the black vulture and teratorn, both have mean $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^2\text{H}$ values consistent with a terrestrial diet. The black vulture has the lowest standard deviations for all three isotopes among the species analyzed, which suggests they had the least variable diet. Their $\delta^{15}\text{N}$ values correspond to the higher (grazer) end of the range in La Brea herbivore $\delta^{15}\text{N}$ values, indicating they were not sampling the full diversity of megafauna at the tar pits. This result conflicts with the results of a morphological analysis (Hertel, 1994), which suggested that Pleistocene black

TABLE 1. LA BREA CONDOR $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, AND $\delta^2\text{H}$ VALUES (‰), AND ^{14}C AGES

Specimen #	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^2\text{H}$	Age (^{14}C yr B.P.)	CAMS #
UCMP 148875	-19.2	11.7	-31.1	24,230 ± 550	104164
UCMP 148876	-15.9	16.3	-11.4	30,900 ± 1300	104165
UCMP 148877	-15.1	14.2	-15.6	19,030 ± 280	104166
UCMP 148878	-13.5	13.5	0.2	22,710 ± 450	104167
UCMP 148879	-19.8	11.6	-73.0	na	
UCMP 148880	-18.7	12.0	-46.2	21,260 ± 370	104168
UCMP 148881	-17.7	14.2	-5.8	30,700 ± 1300	104169
UCMP 148884*	-13.4	13.3	-2.1	31,000 ± 1300	104170
UCMP 148885	-18.4	12.6	-27.1	24,900 ± 600	104171

na—not analyzed; CAMS—Center for Mass Spectrometry, LLNL; UCMP—University of California Museum of Paleontology.

*Analyzed as 4 replicates for $\delta^2\text{H}$. The standard deviation for these replicates was >5‰ (range = -14.2–11.1‰).

vultures were generalized scavengers similar to condors. The specialized diet of La Brea black vultures may have been driven by competition with other species within the diverse vulture guild. Black vulture $\delta^2\text{H}$ values have a maximum of -31‰, confirming that terrestrial feeders in the La Brea ecosystem have relatively low $\delta^2\text{H}$ values that can be used to distinguish them from marine feeders ($\delta^2\text{H}$ > -15‰).

In contrast to the black vulture, the gigantic teratorn has $\delta^{15}\text{N}$ isotope values that correspond to a mixed diet of both browser and grazer megafauna. One individual has a $\delta^2\text{H}$ value that is high enough (-15‰) to suggest a marine food source in the diet. The isotopic variability of the teratorns may reflect the dietary flexibility that is required of such a large terrestrial scavenger. Based on morphology alone the teratorn has been classified both as a small mammal predator (Campbell and Tonni, 1981) and as a piscivore (Hertel, 1995). Although our isotopic data set cannot fully resolve this discrepancy in dietary interpretations, it is clear that teratorns were not obligate piscivores.

The wide ranges in California condor $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^2\text{H}$ values reflect a diet that included both terrestrial and marine food sources (Table 1). Dietary mixing models using carbon and nitrogen isotope results for the La Brea condors with terrestrial and marine dietary end members were presented in Chamberlain et al. (2005). In summary, when compared to terrestrial (horse and bison) and marine (baleen whale and pinniped) food sources, they found that four of the condors had a diet that was >50% marine. We note that three of these putatively marine-feeding condors have $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values that could alternatively be explained by terrestrial diet in an arid C_4 environment. However, the $\delta^2\text{H}$ data clearly divide the condors into marine and terrestrial groups, and resolve the potential ambiguities in dietary interpretations. The five condors with the highest $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values have marine $\delta^2\text{H}$ values; the remaining four condors have terrestrial $\delta^2\text{H}$ values.

We obtained accelerator mass spectrometry ^{14}C dates for eight of the La Brea California

condors to examine temporal patterns in foraging behavior. The condors range in age from 30,900 to 19,030 ^{14}C yr B.P. (Table 1). We found no correlation between ^{14}C yr B.P. and either $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, or $\delta^2\text{H}$ value (General Linear Model; $p > 0.05$). The lack of a temporal pattern in the isotope data indicates that La Brea condors were feeding across the terrestrial-marine interface throughout the late Pleistocene.

CONDOR PALEOECOLOGY ACROSS NORTH AMERICA

Paleontological Context

The $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^2\text{H}$ values of condors from late Pleistocene sites across North America are variable and reflect continent-scale differences in climate, topography, and vegetation (Figs. 2 and 3; Appendix B [see footnote 1]). Taphonomic processes that facilitate the breakdown of collagen have left us with a limited organic record for most Pleistocene sites in southern North America. This data set may represent the only collagen stable isotope values available for late Pleistocene taxa in these regions.

The Pleistocene condors and vultures from the southwest and Florida were all found either in direct association with megafaunal fossils or near contemporaneous sites containing megafauna (Emslie, 1988; Feranec, 2004). There are published direct dates on tissues for three of the condors that range from 13,000 to 9500 ^{14}C yr B.P. (Emslie, 1987), and here we report an age of 11,275 ± 45 ^{14}C yr B.P. for the Shrine Cave condor.

Diets of Pleistocene Southwest and Florida Condors and Vultures

The condors and vultures from both the southwest (Grand Canyon, New Mexico, Texas) and Florida have collagen $\delta^{13}\text{C}$ values that are between the collagen values expected for carnivores living in pure C_3 (-22‰) and pure C_4 (-10‰) ecosystems. They were likely scavenging in open grasslands and mixed forests of these regions. This result agrees with $\delta^{13}\text{C}$ values measured in megafaunal enamel apatite from sites in the southwest and Florida, which also indicate a mix of C_3 and C_4 plants (Connin et al., 1998; Feranec, 2004; Koch et al., 2004).

The $\delta^{15}\text{N}$ values of condors from the southwest are more enriched in ^{15}N than those from Florida condors, which we hypothesize is the result of arid (drier) versus humid (moister) climate conditions. In modern ecosystems mean annual precipitation and the $\delta^{15}\text{N}$ values of C_3 vegetation have a strong inverse relationship due to the preferential loss of ^{15}N -depleted nitrogen-bearing compounds in the soils of drier environments (Swap et al., 2004). Other studies of modern and fossil mammals have found ^{15}N -enriched values in animal collagen from arid regions (Sealy et al., 1987; Gröcke et al., 1997; Stevens and Hedges, 2004). Two condors and two vultures from the southwest have elevated $\delta^{15}\text{N}$ values similar to those of marine-feeding condors at La Brea. Yet these individuals (two analyzed) do not have marine $\delta^2\text{H}$ values, which implies that their $\delta^{15}\text{N}$ values reflect a xeric terrestrial environment and not a >500 km migration to the nearest marine resources at the Gulf of Mexico paleocoastline (Thompson and Schweitzer, 1996).

For two birds, the Ichetucknee River condor and a Kincaid Shelter vulture, $\delta^2\text{H}$ values within the range of marine feeders (greater than -15‰) are contrasted by $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values that are clearly terrestrial. The $\delta^{15}\text{N}$ value of the Florida condor is too low to allow for any marine dietary input, and likewise for the pure C_3 $\delta^{13}\text{C}$ value of the Texas vulture. In contrast to the La Brea birds, these animals lived in areas where precipitation $\delta^2\text{H}$ values today are similar to those of ocean water (Bowen and Revenaugh, 2003) and, in combination with the effects of evaporative concentration of ^2H in surface water and plants, produce $\delta^2\text{H}$ values for deer bone collagen that are within the marine range (Cormie et al., 1994). The results for these two birds suggest that hydrogen isotope ratios are likely to be ambiguous indicators of diet in regions where ecosystem water resources have $\delta^2\text{H}$ values that are similar to those of ocean water.

CONCLUSIONS

Our stable isotope results provide insight into the difference between modern and Pleistocene geographical distributions of condors in North America. The use of marine megafauna by California condors on the Pacific coast likely allowed these populations to survive the extinction of terrestrial megafauna. Inland condor populations, even from regions relatively close (<100 km) to the coast (e.g., northern Florida), primarily consumed terrestrial resources, and all these populations vanished along with terrestrial megafauna. This conclusion is bolstered by the extinction on the Pacific coast of other large scavengers, such as teratorms and black vultures; these animals did not consume marine foods. There is no coastal upwelling of productive Atlantic and Gulf of Mexico waters offshore of Florida

to support the large numbers of marine mammals that are found along the Pacific coast. For this reason, Florida was not another coastal refugium for condors during the megafaunal extinction. Our results highlight the importance of understanding how top consumers forage across the marine-terrestrial interface, and use productive coastal zones as extinction refugia during periods of environmental or ecological change.

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