Pleistocene to recent dietary shifts in California condors

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We used carbon and nitrogen isotopes to investigate changes in the diet of California condors from the Pleistocene to the recent. During the Pleistocene, condors from California fed on both terrestrial megafauna and marine mammals. Early accounts reported condors feeding on the carcasses of marine mammals, but by the late 1700s, condor diets had shifted predominantly to terrestrial animals, following the commercial harvesting of marine mammals and the development of cattle ranching on land. At present, dairy calves provided by humans significantly augment condor diet, constituting an artificial support of the current population. Reestablishing a marine mammal component in the condor diet may be an effective strategy for fostering viable condor populations independent of direct human subsidies.

carbon isotopes | nitrogen isotopes | paleodiet

During the Pleistocene, California condors (*Gymnogyps californianus*) ranged from the Pacific coast of North America across the southern U.S. to Florida and north to western New York (1, 2). Historical records show that by the 17th century, condors were restricted to the west coast of North America, from Baja California to British Columbia (3, 4). At present, small reintroduced populations live in California, Arizona, and Baja California. Paleontological evidence suggests that populations of these obligate scavengers were associated with the carcasses of large animals (1). After the late Pleistocene extinction of most large terrestrial mammals in North America (5), condors appear to have been restricted to the west coast, where stranded marine mammals offered the only remaining abundant source of large animal carcasses (1).

There is little direct evidence that marine mammals were a significant component of condor diets, however, beyond scattered historical observations. In 1806, Lewis and Clark observed condors feeding on whales near the mouth of the Columbia River (6). Captain Clark wrote on February 16, 1806: "This bird fly's very clumsily, nor do I know whether it ever seizes it's prey alive, but am induced to believe it does not. We have seen it feeding on the remains of the whale and other fish which have been thrown up by the waves on the sea coast. These I believe constitute their principal food, but I have no doubt but that they also feed on flesh." In 1855, Taylor found hundreds of condors feeding on sea lion carcasses on the California coast (7). He wrote: "During the early part of the present month, large quantities of sea lions have been killed on the southern coast for the oil; the carcasses of these animals on the beach may be seen at times surrounded by hundreds of the Condors. A friend of ours informed us that he saw a few days ago, as many as three hundred of these creatures near such feeding ground, within a distance of a league." (7). In the 1860s, Cooper reported on condors feeding on seal and whale carcasses in California, although he never directly observed them doing so (8).

To investigate changes in condor diets, we determined the stable carbon (^{12}C, ^{13}C) and nitrogen (^{14}N, ^{15}N) isotope ratios of bone collagen and keratin from condors and their potential food sources. Isotopic variations in collagen and keratin have been used to study animal diets (9), including the balance between marine and terrestrial food sources (10, 11). We determined the carbon and nitrogen isotope composition of feathers from 12 modern (i.e., those that died in the wild from 1993 to 2001) and 50 historical condors (i.e., those from museums collected between 1797 and 1965). We analyzed bone collagen from 10 Pleistocene condors from the Rancho La Brea tar pits (≈11,000–36,000 years ago) (12), 10 historical birds (1904–1965), and 10 modern birds (1993–2001). With respect to potential food sources for condors, we measured or compiled isotopic data from the literature. For collagen, we measured Pleistocene bison (*Bison antiquus*) and horse (*Equus occidentalis*) from La Brea and used published data for Holocene pinnipeds (13) and 20th century whales from the California coast (10). For keratin, we measured hair from 20th century mule deer from California, feral pigs, range-fed and feedlot cattle, and California pinnipeds.

Materials and Methods

Isotopic Methods. Isotope ratios for N and C are presented as δ values, where $\delta = 1{,}000[(R_{sample}/R_{standard})-1]$, and $R = {}^{15}N/{}^{14}N$ and ${}^{13}C/{}^{12}C$, respectively. The isotopic reference standards are atmospheric N_2 for nitrogen and Vienna–PeeDee belemnite for carbon. Isotopic measurements were made on 0.3–0.7 mg of feather, hair, or collagen. Isotopic values were determined by using a Costech (Valencia, CA) ECS 4010 elemental analyzer coupled in continuous flow to a Finnigan (Bremen, Germany) Delta Plus XL mass spectrometer located at Stanford University. The precision of the isotopic analysis for keratin was determined to be $\pm 0.1‰$ and $\pm 0.2‰$ for $\delta^{15}N$ and $\delta^{13}C$ (1 SD, $n = 200$), respectively.

All feather samples were washed in a light detergent and a 3:1 chloroform/methanol solution before analysis. Collagen samples from Rancho La Brea were prepared following procedures outlined elsewhere (14, 15). Bone was cleaned to remove visible tar and then ground to a fine powder. One hundred-milligram samples of powder were placed in heat-sealed Ankom (Macedon, NY) filter bags and then refluxed with petroleum ether and acetone in a soxhlet extractor to remove hydrocarbons and lipids. Samples were decalcified by using 0.5 M HCl for 48–72 h at 4°C. Samples were subsequently rinsed in water, lyophilized, and then gelatinized in 0.01 M HCl at 65°C for 12–15 h. The gelatin extract was then filtered through a 0.45-μm glass-fiber filter before analysis. To isolate collagen from modern and historical bone samples, specimens were cleaned of adhering soft tissue, and lipids were removed with a 3:1 chloroform/methanol solution. Samples were demineralized in 1.0 M HCl at room temperature for 72 h. Collagen extracts were rinsed with distilled water and

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dried under vacuum. Measured atomic C/N ratios for all collagen samples fell in the range of 2.3–3.4.

Carbon isotope values were corrected for the global decrease in the ^{13}C content of atmospheric carbon dioxide, due largely to fossil fuel burning over the last 150 years (16–18). Based on ice core records (16), we applied a time-dependent correction of $-0.005‰$ per year between 1860 and 1960 and $-0.022‰$ per year since 1960, for a total correction of $-1.2‰$ for Pleistocene samples (17) and $-1.5‰$ for Holocene samples (18) (see Table 2, which is published as supporting information on the PNAS web site).

We also examined the variability in $\delta^{13}C$ and $\delta^{15}N$ isotope values within individual feathers for both modern and historical condors. Both $\delta^{13}C$ and $\delta^{15}N$ isotope values can vary within individual feathers (19) and depend upon the diet of the condor during the period of feather growth (9). Most primary feathers of condors are shed between February and September and are replaced over a period of 4 months (20). Thus, we would expect some degree of isotopic variability within a given feather, particularly because the scavenging diet of condors can be highly variable. Indeed, individual feathers for some condors show a wide range of $\delta^{13}C$ and $\delta^{15}N$ isotope values (see Table 2), but this variability is significantly less than the range of isotope values observed within or among populations of modern, historical, and Pleistocene condors.

We did not include any samples from feathers that may have been grown in a zoo before release. Our criteria for selecting feathers was: (*i*) we used only growing feathers or the portions of these feathers that were generated after release or (*ii*) we used fully grown feathers from birds that had been in the wild for at least 850 days. This criterion assumes that feathers are replaced every 2 years and it takes ≈4 months to form a full primary feather (20).

Isotopic Characterization of Potential Condor Diets. To explore the causes of the dietary shifts in condors, we measured the $\delta^{13}C$ and $\delta^{15}N$ values of possible food sources. These included: bone collagen from 14 bison (*B. antiquus*) and 8 horses (*E. occidentalis*), both from Pleistocene deposits at Rancho La Brea; hair keratin from 53 mule deer (*Odocoileus hemionus*) collected from 1907–2003 in California; hair from 15 modern feral pigs (*Sus scrofa*); 21 pinnipeds (northern elephant seal, *Mirounga angustirostris*); northern fur seal (*Callorhinus ursinus*); California sea lion (*Zalophus californianus*); Steller sea lion (*Eumetopias jubatus*) dating from 1907–2003; and 33 range and feedlot cattle (*Bos taurus*) (Table 2). We also used published isotopic values of collagen from Holocene and modern pinnipeds from California (13) and from modern baleen and toothed whales from California (10). These animals were chosen for analysis, because condors are known to prefer to feed on large mammals, and cattle and deer make up a major component of condor diets today (4, 21).

The isotopic differences among potential food sources reflect a combination of the trophic levels of these animals and how carbon and nitrogen enter the food web. In terrestrial settings, the $\delta^{13}C$ values of animal tissue, for the most part, are controlled by the relative abundance of C_3 ($\delta^{13}C = -26.7 \pm 2.7‰$) vs. C_4 ($\delta^{13}C = -12.5 \pm 1.1‰$) plants (22). This difference is apparent in the $\delta^{13}C$ values of feedlot cattle fed C_4 plants (corn) and all other terrestrial herbivores, which eat almost exclusively C_3 plants in California (23). Marine mammals, in contrast, have high $\delta^{13}C$ values relative to terrestrial mammals, because marine plants tend to have higher $\delta^{13}C$ value than terrestrial C_3 plants. This occurs because of greater diffusional limitation on CO_2 supply and/or carbon-concentrating mechanisms in marine photosynthesis, which tend to reduce the expression of the large biochemical isotope fractionation by RUBSICO, the enzyme central to carbon fixation (24). This ≈7‰ difference is particularly useful in discriminating between marine and terrestrial food sources in condors. In addition, marine food webs tend to be longer than terrestrial food webs. As a consequence, animals that feed near the top of these food webs, such as piscivorous pinnipeds, tend to have higher $\delta^{13}C$ values than animals that feed at lower trophic levels, such as plankton-feeding baleen whales. The enrichment in ^{15}N observed in the more carnivorous animals within both terrestrial and marine food webs (e.g., pinnipeds vs. baleen whales) result from trophic level effects on $\delta^{15}N$ discussed above. There are several possible causes for $\delta^{15}N$ differences among herbivores at La Brea, such as differences in dietary sources (grass vs. shrubs) and digestive physiology (hind gut vs. fore gut) (25).

Statistical Analysis. Statistical tests were calculated by using the software program SIGMASTAT (version 2.0, Systat Software, Point Richard, CA). Differences in keratin and collagen isotopic composition between temporal groups were assessed by using a multivariate ANOVA. Significant differences in keratin isotopic composition between modern and historical groups were found by using an exact F test (F value = 2.512; $F < 0.0001$). Significant differences in bone collagen isotopic composition between modern, historical, and Pleistocene groups were also found by using two approximate multivariate F tests, Pillai's trace (F value = 1.436; $F < 0.0001$), and Wilks' λ (F value = 0.069; $F < 0.0001$).

Trophic Isotope Shifts. In general, consumer tissues are enriched in ^{15}N and ^{13}C relative to their diet by ≈3‰ and ≈1‰, respectively (26). However, controlled isotopic studies of diet and bird tissues show that these isotopic fractionations can vary significantly among tissue types and bird species (9, 27, 28). Although there are no controlled feeding studies of condors, recent work suggests that, as the protein content of diet rises, the diet-to-tissue fractionation increases for both carbon and nitrogen (28, 29). Trophic ^{15}N enrichments of 4‰ are common for birds on high-protein diets (27–29). Some of these studies also show diet-to-keratin ^{13}C enrichments of ≥3‰ for birds on high protein diets (27, 29). In many cases, however, these diets contain substantial amounts of lipid, which is ^{13}C depleted relative to bulk diet and dietary protein. Because we are comparing diet keratin (or collagen) with condor keratin (or collagen), we expect smaller ^{13}C enrichments. For our isotopic modeling, we use trophic isotope shifts of +4‰ and +1‰ for $\delta^{15}N$ and $\delta^{13}C$ values, respectively, but examine the impact of uncertainties in these values with sensitivity tests. The choice of different fractionation factors does change the relative proportion of food sources, in some cases by as much as ≈15% (Tables 3 and 4, which are published as supporting information on the PNAS web site). However, these changes do not affect the conclusions drawn in this paper that Pleistocene condors had a significant component of marine mammals in their diet, that historical condors switched to a predominantly C_3 terrestrial-sourced diet, and calves of C_4 fed cattle provided by humans are a significant component of modern condor diet.

Isotope Mixing Models. To quantify the relative proportions of C_3, marine and C_4 components in the diets of historical and modern condors, we used the IsoError model (30). We chose to use IsoError rather than IsoSource (31), because the five possible prey items statistically group into three end-member food sources. IsoError is better suited for analyses of three sources with two isotopes or two sources with one isotope (32), and it yields means ±95% confidence intervals on estimates of source contributions. The IsoError model inputs include the average (±1 SD) $\delta^{13}C$ and $\delta^{15}N$ values for condors that have been corrected for trophic isotope shifts. In addition, the model requires isotopic values (±1 SD) for end-member diets: C_3 terrestrial herbivores, C_4 feedlot cattle, and marine mammals.

The C_3 food source is a pooled average of $\delta^{13}C$ and $\delta^{15}N$ values of deer, feral pigs, and range cattle collected from California. The C_4 food source is an average of isotope values for feedlot cattle. Last, the marine food source is the average of isotope values for pinnipeds, toothed, and baleen whales (see Table 2 for end-member values for collagen and keratin).

The diets of modern condors were modeled by using $\delta^{13}C$ data from keratin and end-member C_3 and C_4 food sources (Table 2). This strategy builds upon the observation that these condors, which are all from southern California, have never been observed feeding on marine mammals, and they have been monitored closely. Nevertheless, we did a sensitivity test using a two-component model (C_3 and C_4; see Table 3).

For historical condors, results of the IsoError model are presented in Table 4. Our sensitivity test consists of recalculating model results for different combinations of trophic isotope shifts that are 1‰ higher and lower than our preferred values. We did a sensitivity test using a three-component model (C_3, C_4, and marine food sources). As discussed above, the choice of reasonable fractionation factors between diet and tissue do not affect the conclusions of this study.

The diets of the Pleistocene condors were modeled by using isotope data from bone collagen and the end-member dietary sources in Fig. 1*B*. Because there is no evidence for C_4 plants in the late Pleistocene near Rancho La Brea (25), we used an IsoError mixing model with two end-member food sources: a C_3 terrestrial food source consisting of Pleistocene bison and horses and a marine food source consisting of modern and Holocene pinnipeds, toothed, and baleen whales. We modeled carbon and nitrogen isotopes separately, and each model gave similar results (i.e., the mean source contribution of each food source was within the 95% confidence interval for each model) (Table 5, which is published as supporting information on the PNAS web site). Again, we conducted sensitivity tests by considering trophic isotope shifts that are 1‰ higher and lower than our preferred values.

Results and Discussion

Our isotopic data suggest that the condors have undergone two major dietary shifts, one from Pleistocene to historical times and the other between historical and modern times. For both keratin and collagen, modern and historical condors have similar $\delta^{15}N$ values, whereas $\delta^{13}C$ values are lower in historical than in modern birds (Fig. 1). For keratin, modern and historical condors are isotopically distinct [multivariate ANOVA (MANOVA); F test, F value = 2.512, $F < 0.0001$). Pleistocene condor bone collagen is enriched in ^{13}C and ^{15}N relative to historical condors (Fig. 1*B*). These differences in isotopic composition are highly significant (MANOVA; Pillai's trace, F value = 1.436, $F < 0.0001$).

After comparing condor isotope values with those from potential food sources, we conclude that marine mammals were an important component of the diets of Pleistocene condors, and that historical condors ate terrestrial land animals. Furthermore, our results confirm that the diets of recently released condors include a substantial component of domestic cattle from dairy farms or feedlots. Three types of food in condor diets are isotopically distinct: (*i*) native or range-fed terrestrial herbivores, such as deer, range-fed cattle, and, in the Pleistocene, megafauna (bison, horse, etc.); (*ii*) domestic terrestrial herbivores in dairy farms or cattle raised on feedlots; and (*iii*) marine mammals. These three types of food segregate cleanly in bivariate $\delta^{13}C$-$\delta^{15}N$ space (Fig. 1). Marine food webs are strongly enriched in ^{15}N relative to most terrestrial food webs and are enriched in ^{13}C relative to food webs based on C_3 plants. Thus, terrestrial herbivores feeding in C_3-dominated ecosystems, such as California with its cool growing season, should also have lower $\delta^{15}N$ and $\delta^{13}C$ values than marine mammals. Herbivores from dairy farms and feedlots, which have diets supplemented by corn, a C_4 plant, should have higher $\delta^{13}C$ values than C_3 feeders.

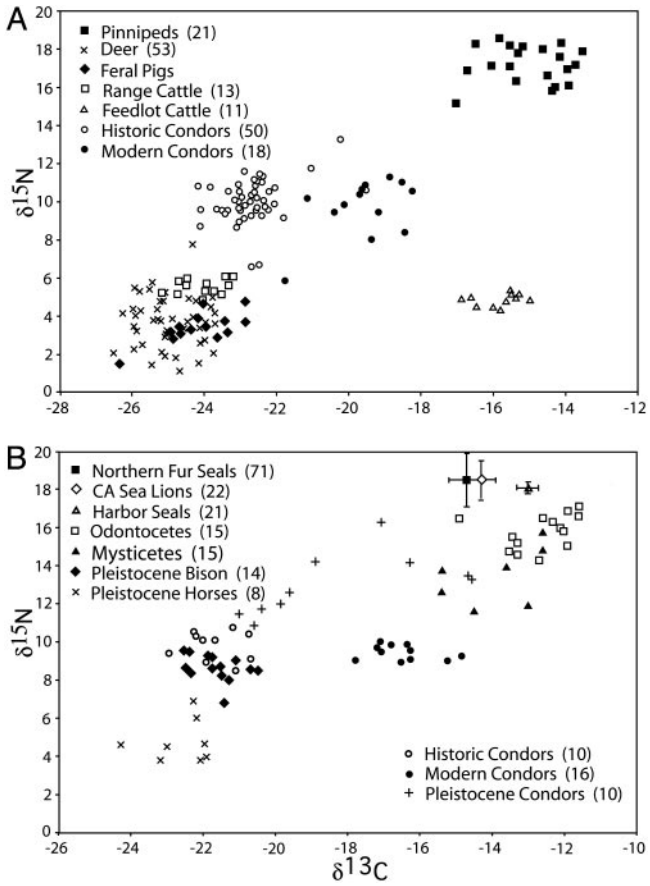

Fig. 1. $\delta^{13}C$ and $\delta^{15}N$ measurements from condor populations. (*A*) $\delta^{13}C$ and $\delta^{15}N$ of feather keratin from modern and historical California condors. These values are the mean of 2–23 analyses on a given feather. Also shown are $\delta^{13}C$ and $\delta^{15}N$ values for hair keratin of pinnipeds, deer, feral pigs, and range and feedlot cattle. $\delta^{13}C$ values are corrected to modern atmospheric $^{13}CO_2$ content. (*B*) $\delta^{13}C$ and $\delta^{15}N$ of bone collagen from modern, historical, and Pleistocene condor populations. Also shown are isotope values of collagen for Pleistocene bison and horses, pinnipeds [mean and 1 SD (25)], and modern *Odontocete* (toothed) and *Mysticete* (baleen) whales (10). $\delta^{13}C$ values are corrected to modern atmospheric $^{13}CO_2$ content.

The wide range of $\delta^{13}C$ and $\delta^{15}N$ values for bone collagen from Pleistocene condors demonstrates that these birds had a highly variable diet that included both C_3 terrestrial and marine sources. The Pleistocene condors segregate into two groups, with one group more dependent on marine food sources (4 of 10 individuals; Fig. 1*B*). Other sources of ^{15}N and ^{13}C enriched food, principally scavenged carnivorous animals and herbivores feeding on C_4 vegetation, can be excluded. None of the Pleistocene herbivores at La Brea have high $\delta^{13}C$ values that would indicate a diet rich in C_4 plants (25). Although carnivores from La Brea do have higher $\delta^{15}N$ and $\delta^{13}C$ values than herbivores (25), these values are not high enough to explain the heavy isotope enrichments seen in the condors we interpret as marine feeders. The other six Pleistocene birds have isotope values consistent with feeding on terrestrial mammals in a C_3 dominated ecosystem. One of these more terrestrial feeders could have had a mixed marine and terrestrial diet. When the population is modeled as a whole, marine mammals represent ≈25% of the diets of Pleistocene condors (Table 1).

The $\delta^{13}C$ and $\delta^{15}N$ values of keratin and collagen from the 1790s to the mid-1900s reveal that condors had diets dominated by terrestrial food sources. With the establishment of missions and ranches in California, a large amount of cattle and sheep

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Table 1. Mean proportions (±95% confidence intervals shown in parentheses) of C_3, marine and C_4 dietary sources for modern, historical, and Pleistocene California condors based on the IsoError mixing model (31)

Condor tissue	C3	Marine	C4
Modern feathers (via δ^{13}C data)	52.3 (45.5–59.1)	NA	47.7 (40.9–54.6)
Historical feathers	85.2 (79.7–91.1)	13.9 (9.6–19.6)	0.9 (0.0–1.7)
Pleistocene bone collagen (via δ^{13}C data)	68.2 (47.6–88.7)	31.8 (11.3–52.4)	NA
(via δ^{15}N data)	80.0 (64.6–95.3)	20.0 (4.7–35.3)	NA

Trophic-level fractionations of +1 and +4 for C and N, respectively, have been applied to the condor data for use in the model. Isotope values for dietary sources and an explanation of modeling protocols are provided as Tables 2–5.

carrion was available to condors. Cattle were introduced in the 1770s, when California was under Spanish control; cattle populations exploded to 75,000 by 1800, resulting in many stray and feral animals (33). During the period when California was under Mexican control (1822–1848), cattle were raised largely for leather and tallow (33), yielding a large bounty of carcasses. It has been argued this livestock served as a principal food supply for condors (4), which is consistent with our modeling results showing that ≈85% of the historical population had a diet dominated by herbivores that ate C_3 vegetation. Three condors, collected between 1877 and 1885 near the ocean in the Columbia River area of Washington and Monterey, CA, have high δ^{13}C values and, in one case, high δ^{15}N values (Fig. 1*A*), in accord with early observations of condors in these areas feeding on whale, seal, and salmon carcasses (6, 8).

To reduce the possibilities of poisoning by lead fragments in hunter-killed carcasses, modern condors are provided with an unlimited quantity of stillborn dairy calves (34). Indeed, our data show that modern condors rely substantially on dairy calves, provided by humans to supplement their diet. The ≈4‰ increase in δ^{13}C values of modern over historical birds cannot be accounted for with a diet consisting of herbivores that consume mostly C_3 vegetation, such as deer, range cattle, or feral pigs (Fig. 1*A*). Nor can the increase in δ^{13}C values be the result of proliferation of C_4 vegetation during the last century. There are few native C_4 plants in California, and our isotope data for range-fed cattle indicate that C_3 vegetation is their principal food. Corn, a C_4 plant, is a principal food of the dairy cattle that are the source of the stillborn calves provided to the condors. Mass balance calculations indicate that ≈45% of the diet of the condors that were the source of the feathers analyzed had a C_4 source. The dairy calves provided to the condors constitute a substantial artificial support of the current population.

Conclusion

The dietary shifts we have documented have important implications for understanding the past distribution of condors. Our data demonstrate that marine mammals were an important component of the diet of condors in coastal California during the Pleistocene, even when large terrestrial mammals were relatively abundant. It is highly unlikely that Pleistocene condors living in interior regions had marine-dominated diets, as observed for 40% of the animals in our small sample from the La Brea tar pits. Thus, our results support the hypothesis (1) that the restriction of the range of condors to the Pacific coast after the Pleistocene megafaunal extinction was largely controlled by the presence of a "fall-back" food source, marine mammals, which at least some of the population was already using. The switch to terrestrial foods in historical condor populations may reflect the reduction of pinnipeds and whale populations due to commercial hunting in the late 1700s through the early 1900s (35). At the same time, however, the expansion of cattle ranching in California and elsewhere in the American west offered condors a new source of abundant large terrestrial carcasses that allowed them to shift eastward, away from coastal refugia. Historical accounts of condor feeding patterns in the 1800s show that cattle and deer comprised the major component of their diet (36). Our isotope data indicate that a combination of range livestock and wild ungulates remain a component of the diet of the birds sampled, but a significant portion of their diet was provided by humans in the form of stillborn calves of corn (C_4) fed cattle.

The development of conservation strategies for viable condor populations requires that adequate and safe food supplies exist for these birds in the wild. Coastal regions lack abundant carcasses of large land mammals and, throughout the former and present range of the condors in southern and central California, this food supply is likely to become increasingly scarce. Efforts to establish a self-sustaining condor population may be enhanced, however, by the widespread availability of marine mammals as an additional food source. This strategy is particularly attractive, in that pinniped populations are reestablishing along the coast of California (refs. 38 and 39; U.S. National Oceanic and Atmospheric Administration Stock Assessments).

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