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15 April 1987; accepted 25 June 1987

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# Age and Diet of Fossil California Condors in Grand Canyon, Arizona

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**A dozen new radiocarbon dates, together with a thorough review of its fossil distribution, shed new light on the time and probable cause of extinction of the California condor, *Gymnogyps californianus*, in Grand Canyon, Arizona. The radiocarbon data indicate that this species became extinct in Grand Canyon, and other parts of the inland West, more than 10,000 years ago in coincidence with the extinction of megafauna (proboscidians, edentates, perissodactyls). That condors relied on the megafauna for food is suggested by the recovery of food bones from a late Pleistocene nest cave in Grand Canyon. These fossil data have relevance to proposed release and recovery programs of the present endangered population of California condors.**

During the late Pleistocene (Rancholabrean Land Mammal Age) at least two species of large vultures lived in North America. These species were the extinct condor, *Breagyps clarki*, known primarily from Rancho La Brea, California, and the California condor, *Gymnogyps californianus* (*1*), which is near extinction today. These species differed from one another primarily in the bill and cranium; *B. clarki* had an elongated beak that may have allowed it to feed on viscera deep inside carcasses, much as griffon vultures do in Africa today (*2*). Fossils of *G. californianus* have been reported from sites throughout western North America and Florida, of which only two have been radiocarbon dated previously (*3*) (Table 2). The presence of California condor remains on the surface of cave floors, occasionally with archeological artifacts, has led some authors to suggest that until recently *G. californianus* ranged and nested in many areas of the western United States (*4, 5*). This suggestion implies that the condor's decline has occurred only within the past two centuries. With the exception of sites in coastal California and Oregon (*6*) no direct association of condor remains with archeological artifacts are known. Moreover, in dry caves in the western United States it is not unusual to find surface remains of extinct mammals dated at 11,000 to 12,000 years old or older next to artifacts dating from 1,000 to 4,000 years old.

An alternative hypothesis is that the condor was widely extirpated at the close of the Pleistocene in conjunction with the disappearance of many large mammals and birds, but managed to survive in Pacific coastal regions where it still occurs today (*7*). Until now, no reliable method has been available to test either of these hypotheses. The tandem accelerator mass spectrometer (TAMS) provides accurate radiocarbon analysis of very small samples (1 to 3 mg or less) of organic material and provides a means for obtaining dates on many fossil birds. I report the first series of dates completed on a single species of fossil bird in an effort to determine the exact time and cause of the condor's extinction at eight sites in the Grand Canyon of Arizona and at five sites in New Mexico and Texas. This study also provides evidence of the feeding habits of fossil *G. californianus*.

Surface and subsurface fossils of condors were collected from eight caves in Grand Canyon in 1984 (Table 1). Most of these caves are located high on vertical cliffs, inaccessible to all animals except birds and small, cliff-dwelling vertebrates; similar localities are used for nesting by the California condor today (*8*). In all but one cave, only one to four condor bones were found on the surface. The exception, Sandblast Cave (elevation, 900 m), yielded partial skeletons of at least five condors. These remains were deposited in a large packrat midden just inside the entrance of the cave and were found in association with numerous condor eggshell and feather fragments, and bone fragments of large mammals including horse (*Equus* sp.), bison (*Bison* sp.), mammoth (*Mammuthus* sp.), camel (?*Camelops* sp.), and extinct mountain goat (*Oreamnos harringtoni*). Bone porosity indicates young individuals, perhaps near fledgling age. Because the bones are complete and partly articulated, it is reasonable to infer that the condors died in the cave and that this cave was used for nesting by adult condors.

The bones of large mammals associated

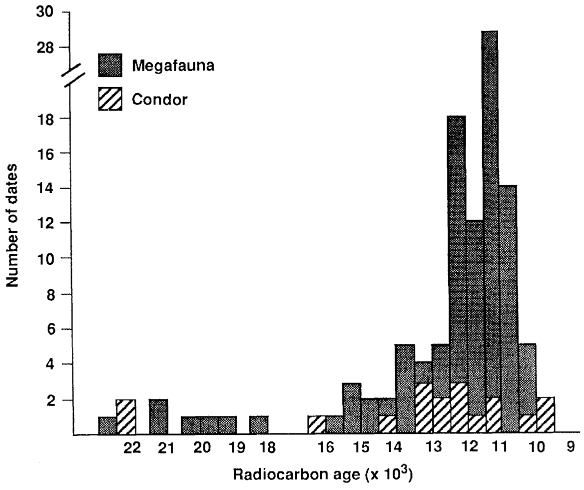

**Fig. 1.** Distribution of radiocarbon dates on Pleistocene megafauna and California condor, *Gymnogyps californianus*. Megafauna dates are from D. J. Meltzer and J. I. Mead (*12*); only those dates considered most reliable [score of 8 or 9 (*12*, figure 1, p. 163)] are plotted. On the basis of their rating system, all dates of condor bone are rated 7 and all those of tissue are rated 9. Note the break on the vertical axis to account for the large number of dates between 11,000 and 11,500 B.P.

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**Table 1.** Caves in Grand Canyon, Arizona, where fossils of *Gymnogyps californianus* have been reported. Sites indicated by an asterisk (*) were discovered in 1983 and 1984.

| Cave | Material | Reference |
|---|---|---|
| Rampart Cave | Carpometacarpus, five phalanges, innominate, synsacrum, ulna fragment, coracoid (immature) | (*17*) |
| Vulture Cave | Tibiotarsus, furculum fragment, quills | (*18*) |
| Stanton's Cave | >70 bones of at least five individuals | (*4, 10*) |
| Tooth Cave | Phalanx and vertebra | (*4*) |
| Tse'an Kaetan Cave | Distal ulna | (*4*) |
| Luka Cave | Ulna or tibiotarsus? | (*4*) |
| Stevens Cave* | Skull, humerus, two pelves | |
| Sandblast Cave* | 64 bones of at least five individuals | |
| Skylight Cave* | Ulna | |
| Bridge Cave* | Carpometacarpus and tibiotarsus fragment | |
| Midden Cave* | Carpometacarpus | |
| Shrine Cave* | Tibiotarsus | |
| Skull Cave* | Carpometacarpus, phalanx | |
| Three Springs Cave* | Cervical vertebra, phalanx | |

with the condor remains possibly represent food bones brought to the cave by the condors. Bone fragments of similar size and skeletal elements including phalanges, carpals, tarsals, teeth, and mandibles of horses, cows, sheep, and deer, are found in nests of *G. californianus* today (*9*). Skeletal elements at Sandblast Cave are an incisor and right upper third molar of horse, a right upper second premolar and horn fragment of bison, a small tooth fragment of mammoth, a canine and mesoectocuneiforme of a camel, a mandible, shaft of radius and tibia, two fragmentary humeri, and a vertebra of extinct mountain goat, and numerous unidentifiable fragments of large mammal bones. Moreover, the cave entrance is not easily accessible to mammalian carnivores, nor were any of their bones or feces found in the deposits.

At Stevens Cave, a complete condor skull was found deep inside and on the cave floor. The specimen is so well preserved that it retains an intact beak and has dried connective tissue; its radiocarbon age was 12,540 years before present (B.P.) (AA-692). Based on its small size the bone from Stanton's Cave resembles modern *G. californianus* and not *G. "amplus"* (*10*).

Radiocarbon dates from Grand Canyon were obtained on five samples of condor tissue and eight of bone. They range in age from 9,585 to 22,180 B.P. and data averaging indicates that this species lived in the canyon up to 10,730 B.P. (Table 2) (*11*). Figure 1 indicates the coincidence between radiocarbon dates recording last occurrences of California condors and those for large mammals in North America. In addition, 37 radiocarbon dates on extinct mountain goat horn sheaths and dung from caves in Grand Canyon indicate that this species became extinct by 11,160 ± 125 B.P., and 41 dates on Shasta ground sloth (*Nothrotheriops shastensis*) dung from Grand Canyon, Nevada, Texas, and New Mexico suggest this species disappeared by 11,000 B.P. (*13*). Moreover, radiocarbon dates on condor bone from four sites in New Mexico and two in Texas (Table 2) suggest that the condor's extirpation occurred throughout the Southwest at that time or soon after.

Among the various groups of late Pleistocene extinctions the most seriously decimated were the raptorial birds, especially scavengers (*14*). The findings at Sandblast Cave provide direct evidence that condors did scavenge carcasses of large animal species that subsequently became extinct. If Pleistocene condors indeed depended on large mammal carcasses, then their disappearance from most areas at the close of the Pleistocene may be traced to loss of food source.

This raises the question as to why the condor survived in its present limited range along the Pacific coast (*7*). It is possible that the Pacific coastal population endured by feeding primarily on beached carcasses of whales, seals, and fish (*9*), marine animals not affected by late Pleistocene extinctions.

These hypotheses may be falsified by the discovery of inland condor remains that significantly postdate 10,000 B.P. Condor

**Table 2.** Radiocarbon (TAMS) dates on bone (collagen) and tissue of *Gymnogyps californianus* from Grand Canyon, Arizona, New Mexico, and Texas.

| Site | Sample and location | Laboratory number | Age (B.P.) |
|---|---|---|---|
| | *Grand Canyon, Arizona* | | |
| Stanton's Cave | Tissue from right coracoid (AO 922); surface | AA-786 | 14,260 ± 170 |
| Sandblast Cave | Bone from distal left femur; surface, area 2 | AA-790 | 9,580 ± 160 |
| Sandblast Cave | Tissue from right femur; trench 1, level 2 | AA-694 | 11,940 ± 520 |
| Sandblast Cave | Tissue from right tibiotarsus; trench 1, level 3 | AA-693 | 13,110 ± 680 |
| Midden Cave | Bone from right carpometacarpus; surface | AA-791 | 22,180 ± 400 |
| Bridge Cave | Bone from right carpometacarpus; surface | AA-697 | 11,140 ± 120 |
| Skylight Cave | Bone from right ulna;* surface | AA-788 | (4,120 ± 90) |
| | Tissue from same specimen | AA-2222 | 11,345 ± 130 |
| Skull Cave | Bone from left carpometacarpus; surface, passage A | AA-789 | 12,210 ± 220 |
| Stevens Cave | Tissue from skull; surface, passage room 2–3 | AA-692 | 12,540 ± 790 |
| Stevens Cave | Bone from pelvis; surface, room 1 | AA-792 | 22,110 ± 370 |
| Stevens Cave | Bone from pelvis; surface, room 3 | AA-793 | 12,320 ± 180 |
| Tse'an Kaetan Cave | Bone from left ulna; surface | AA-851 | 16,290 ± 250 |
| | *New Mexico* | | |
| Howell's Ridge Cave, Grant Co. (*3*) | Unspecified | A-1557 | 13,460 ± 220 |
| U-Bar Cave, Hidalgo Co. | Bone from coracoid, surface spoil | AA-1492 | 13,030 ± 180 |
| Dark Canyon Cave, Eddy Co. | Bone from tibiotarsus (UTEP 75-262) | AA-1490 | 9,585 ± 310 |
| Rocky Arroyo Cave, Eddy Co. | Bone from humerus (USNM 319169) | AA-1491B | 12,180 ± 130 |
| | *Texas* | | |
| Mules Ear Peak Cave, Brewster Co. | Tissue from tibiotarsus (USNM 320806) | AA-1494 | 12,580 ± 135 |
| Maravillas Canyon, Brewster Co. | Bone from humerus | AA-1276 | 10,215 ± 320 |

*Amino acid analysis of bone and tissue from this specimen indicated the bone was contaminated, but the tissue was composed of amino acids most closely matching the collagen molecule. The date on the tissue therefore is considered more reliable than that of the bone (*19*).

bones from Mules Ear Peak Cave, Texas, have been dated at 1,500 to 3,000 B.P. based on nonassociated archeological artifacts (*4*) but a radiocarbon date now indicates a late Pleistocene age (Table 2). Although historic sightings of condors are known from Arizona and Utah in the late 1800s (*5*), it is thought that these represented an early historic range expansion when large herds of cattle, horse, and sheep were introduced by European settlers to the inland West beginning in the 1700s; cattle are the primary food of condors today (*7, 9*). These herds probably allowed the condor to re-expand its range inland by feeding on the carcasses of these animals, just as it had on those of late Pleistocene megafauna. If condors had survived in the inland West prehistorically, their bones should be conspicuous among the many thousands of bird bones now known from archeological sites in Arizona, New Mexico, Colorado, and Utah; none have been reported (*15*). The absence of Holocene, prehistoric records of *G. californianus* in the inland West supports the above hypotheses.

At Grand Canyon, the extinction of condors in the late Pleistocene is relevant to suggestions on releasing condors there as part of the condor recovery program (*5*). Since condors could not survive in the canyon at the close of the Pleistocene, and when modern flora and faunal communities were gradually established by 8,500 B.P. (*16*), it is unlikely that it could survive there today unless supplemental food supplies are provided on a regular basis.

Other questions regarding condor extinctions still remain, such as why it did not survive in coastal regions of Florida and the eastern United States, and why it apparently did not occur in the Great Plains where large herds of bison existed throughout the Holocene. Answers to these questions may relate to habitat, climatic, and temperature limitations for breeding condors that require additional investigation.

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20. This research was funded by grants from the National Geographic Society, Grand Canyon Natural History Association, and Cave Research Foundation. Fossils were collected from caves in Grand Canyon under a permit from Grand Canyon National Park. All material is housed at the University of Arizona Laboratory of Paleoenvironmental Studies, Tucson. I thank rock climbers L. Coats, T. Coats, and D. Dawson for their invaluable assistance and skills in Grand Canyon. Field assistance was also provided by J. and E. Mead, L. Stevens, S. Bassett, S. Heavenrich, R. and J. Raymond, L. Rayburn, R. Haratani, and C. Brown. J. Mead and L. Kiff confirmed identifications of extinct mountain goat bones and condor eggshell fragments, respectively, and T. R. Van Devender kindly allowed publication of radiocarbon data from Maravillas Canyon, Texas. D. Weaver, R. C. Euler, S. Olson, and A. Harris generously provided fossil condor bone and tissue from their institutional collections for use in radiocarbon analysis. I especially thank B. Gore and D. Donahue for their expertise with the radiocarbon analysis. P. S. Martin, D. Steadman and S. David Webb read an earlier draft of the paper and provided many useful suggestions.

5 March 1987; accepted 3 June 1987

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# Sequence of a Probable Potassium Channel Component Encoded at *Shaker* Locus of *Drosophila*

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YUH NUNG JAN, LILY YEH JAN

**Potassium currents are crucial for the repolarization of electrically excitable membranes, a role that makes potassium channels a target for physiological modifications that alter synaptic efficacy. The *Shaker* locus of *Drosophila* is thought to encode a $K^+$ channel. The sequence of two complementary DNA clones from the *Shaker* locus is reported here. The sequence predicts an integral membrane protein of 70,200 daltons containing seven potential membrane-spanning sequences. In addition, the predicted protein is homologous to the vertebrate sodium channel in a region previously proposed to be involved in the voltage-dependent activation of the $Na^+$ channel. These results support the hypothesis that *Shaker* encodes a structural component of a voltage-dependent $K^+$ channel and suggest a conserved mechanism for voltage activation.**

PHYSIOLOGICAL STUDIES OF *Shaker* mutants suggest the the *Shaker* locus of *Drosophila melanogaster* encodes a structural component of a voltage-dependent $K^+$ channel that conducts a transient current, the A current (*1*). We have characterized genomic DNA and several complementary DNA (cDNA) clones from the *Shaker* region (*2*). Two of these cDNA clones, ShA1 and ShA2, differ only in length. They appear to have at least seven exons spread over 65 kilobases (kb) of genomic DNA; molecular rearrangements corresponding to five *Shaker* mutations are found within this same expanse of genomic DNA. These results suggest that the ShA cDNA clones represent a processed transcript that

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