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FAUNAL REMAINS IN CALIFORNIA CONDOR NEST CAVES[1]

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Abstract: Studies of faunal remains in California Condor (*Gymnogyps californianus*) nests in the 1980s yielded bones and hair of a variety of small, medium-sized, and large mammals, and a near absence of avian and reptilian materials. A prevalence of small to medium-sized species may reflect ease of penetration of hides of such carrion and a relative abundance of ingestible bone from such species. Remains also included metal, plastic, and glass artifacts, likely mistaken for bone materials by condors. Size distributions of bone materials and percentage artifacts among hard remains suggest an overall absence of severe calcium-supply problems for condors.

Key words: calcium supplies, California Condor, carrion preferences, Gymnogyps californianus.

As an obligate scavenger, the California Condor (*Gymnogyps californianus*) has long been known to feed heavily on carcasses of large mammals. Recorded food items include cattle, horses, burros, mules, pigs, sheep, goats, domestic dogs, domestic cats, jackrabbits, deer, elk, coyotes, bobcats, mountain lions, grizzly bears, skunks, ground squirrels, kangaroo rats, whales, sea lions, and salmon (Koford 1953, Miller et al. 1965, Wilbur 1978). Yet despite the frequency of sight records of condors at large carcasses, such as those of cattle, there have been some indications from choice situations that condors may prefer smaller carcasses, such as rabbits, when they are available (Miller et al. 1965). Such a preference is plausible because it is presumably relatively easy for the birds to penetrate the hides of small carcasses and easy for them to obtain needed bone material from such carcasses. Scott and Boshoff (1990) similarly reported a potential preference for small carcasses, especially light-colored small carcasses, in the condor-sized Cape Vulture (*Gyps coprotheres*) in Africa.

Because of a variety of factors, such as the ease of seeing condors in open rangeland habitats, historical sight records of feeding condors may be inherently biased toward large carcasses and may not be fully representative of overall diet of the species. One way to circumvent some of the observational biases in sight records is to examine remains of food found in condor nests, primarily bone material, but also hair and feathers. However, food remains in nests also are subject to biases (Errington 1932, Schipper 1973). Although they can yield useful qualitative data on breadth of diet, food remains, like sight records, cannot be assumed to give quantitatively accurate estimates of various diet components. Presumably, not all food items have the same probability of preservation as food remains in nests, and furthermore, the presence of food remains in condor nests is not absolute proof that they were brought in by the condors. Nevertheless, food remains in nests can give useful insights into condor food hab-

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its, provided a number of methodological constraints are observed in analyses.

Previous studies of food remains in condor nests were conducted by Koford (1953) and Emslie (1987, 1988). Koford examined 15 nests in California in the late 1930s and early 1940s. Emslie analyzed bone fragments in two apparent Pleistocene condor nests in the Grand Canyon of Arizona. In the latter study, Emslie found evidence that condor diet once included now extinct forms such as mammoths, camels, mountain goats, and native horses. He suggested it was plausible that condors may have disappeared from the inland West as a consequence of the loss of such species at the end of the Pleistocene.

In this paper we report on faunal remains and man-made artifacts found in a substantial sample of California Condor nests studied in California in the 1980s. These remains reinforce many earlier conclusions as to the diet of the species, but indicate a somewhat broader range of small–medium species taken than was known earlier. They also suggest that the California Condor has not been severely stressed by a scarcity of calcium sources in recent times, contrary to the proposal of Cowles (1967).

METHODS

Between 1980 and 1985, Snyder et al. (1986) studied 72 recently or formerly active condor nest sites in southern California. Recently-active sites were documented as condor nests by observing activities of the birds at the sites. Formerly active sites were confirmed as condor sites either by historical records or by characteristic "bathtub rings" of excrement on cave walls and presence of distinctive condor eggshell fragments in substrates of the sites. The physical nest-site characteristics determined in the nest survey were described in Snyder et al. (1986).

Substrates in the positions where eggs were laid and nestlings were reared were thoroughly sifted with fine-mesh window screen to collect all eggshell, bone, and pellet materials of greater size than approximately 1 mm^2. The materials collected were deposited at the Western Foundation for Vertebrate Zoology, Camarillo, California (eggshell fragments) and the Santa Barbara Museum of Natural History, Santa Barbara, California (bone, feather, fur, and man-made materials).

Identifications of all bone, fur, and feather material collected were made by comparing samples to the reference collections of faunal specimens at the Santa Barbara Museum of Natural History. Identification as to species was not always possible, in particular with respect to small fragments of long bones, but the majority of materials were identifiable at least to genus. Bone materials were identified by the senior author, hair materials by Gretchen Sibley, feather remains by John Schmitt, and mollusc shells by Paul Scott.

The nests studied in the survey included eight that, judging from shell materials and other remains, had also been utilized for nesting by other avian species, especially Turkey Vultures (*Cathartes aura*), Red-tailed Hawks (*Buteo jamaicensis*), and Common Ravens (*Corvus corax*). The materials in these multiple-use nests could as easily have been brought in by these other species as by condors, so these nests were excluded from the analyses presented below. Other sites contained no food remains. Altogether, 40 condor nests contributed food remains suitable for analysis.

All bone and shell materials that were judged likely brought in by condors were measured for maximum length, to allow comparison of their size distribution with the size distributions of bones found in Cape Vulture nests by Plug (1978) and Pleistocene condor nests by Emslie (1988).

RESULTS

Table 1 presents the identifiable faunal remains believed of condor origin in the 40 nests that qualified for analysis. For each species, we present the number of nest sites in which it occurred and the minimum number of individuals represented in the total. In the table footnotes, we note total numbers of various man-made artifacts and the number of individuals of species considered of non-condor origin found in the same sites.

In a large fraction of nests, we found numerous bones of woodrats (*Neotoma fuscipes, lepida,* or sp.), but because woodrats (packrats) commonly nested in the caves used by condors, we suspect that the large majority, if not all, of the woodrat bones were not brought in by the condors. The same may be true of the bones of other small rodents, especially *Peromyscus,* and the small squirrels *Tamias* and *Glaucomys.* The only site containing *Glaucomys* bones was a natural cavity nest high in a giant sequoia (*Sequoia gigantea*), possibly used as a squirrel nest or roost when not occupied by condors. In addition, some of the small mammal materials could conceivably have been pellet material cast by large owls occasionally roosting in the caves. No sites clearly used by owls for nesting were included in the sample.

Condor nests were generally distant from normal habitat of ground squirrels (*Spermophilus*) and kangaroo rats (*Dipodomys*), and condors have been observed directly feeding on these species in the field, especially after 1080-poisoning campaigns (Koford 1953, Miller et al. 1965). Accordingly, we have considered the remains of these species as likely of condor origin.

Sites were highly variable in the amount of material they contained, with some sites lacking any food remains. The site containing the largest volume of both condor eggshell and bone material was a nest 30 m from the ground in a giant sequoia cavity in which a condor chick was reared in 1984. Possibly the great volume of material in this site was due in part to many previous condor nestings in the site and to the fact that there was almost no evidence of potential woodrat use of the site. We suspect that woodrats are responsible for the loss of many bone and shell materials in sites over time. In one cave frequented by woodrats (not a condor nest), we monitored the fate of chicken eggshell fragments we deliberately placed on the floor and determined that these shells disappeared relatively rapidly over a period of a few months.

The species most frequently represented in the remains considered of condor origin was cattle (*Bos taurus*), a result also found by Koford (1953). Other species represented included a variety of large and me-

TABLE 1. Identifiable faunal remains believed deposited by California Condors in 40 recent nests.[a]

Species	Number of sites	Minimum number of individuals[b]
Artiodactyla		
Cattle (*Bos taurus*)	17	23
Mule deer (*Odocoileus hemionus*)	2	2
Sheep (*Ovis aries*)	2	2
Carnivora		
Coyote (*Canis latrans*)[c]	2	2
Gray fox (*Urocyon cinereoargenteus*)[c]	2	2
Long-tailed weasel (*Mustela frenata*)[c]	2	2
Lagomorpha		
Black-tailed jackrabbit (*Lepus californicus*)	1	1
Brush rabbit (*Sylvilagus bachmani*)[c]	1	1
Sylvilagus sp.[c]	4	4
Rodentia		
California ground squirrel (*Spermophilus beecheyi*)	7	7
Belding's ground squirrel (*Spermophilus beldingi*)	1	1
Golden-mantled ground squirrel (*Spermophilus lateralis*)	1	1
Botta's pocket gopher (*Thomomys bottae*)[c]	3	4
Agile kangaroo rat (*Dipodomys agilis*)[c]	1	1
Dipodomys sp.[c]	1	1
Reptilia		
Coachwhip (*Masticophis flagellum*)[c]	1	1
Mollusca		
Pismo clam (*Tivela stultorum*)	3	3
Common californian venus (*Chione californiensis*)	1	1
Moon shell (*Polinices* sp.)[c]	1	1
Indeterminate marine mollusc	3	3
Crustacea		
Barnacle (*Balanus* sp.)[c]	1	1
Aves		
Indeterminate grebe[c]	1	1

[a] Remains found in nests also included man-made artifacts (45 pieces of plastic, 10 fragments of aluminum cans, 5 pieces of glass, 2 metal bottle caps, 1 pop top from a beverage can, 1 aluminum foil ball, 1 lead bullet, 1 plastic comb fragment, and several photographic flashbulbs) and faunal elements believed to be of non-condor origin (4 *Tamias merriami*, 3 *Glaucomys sabrinus*, 13 *Neotoma fuscipes*, 12 *Neotoma lepida*, 19 *Neotoma* sp., 6 *Peromyscus californicus*, 2 *Peromyscus truei*, 8 *Peromyscus maniculatus*, 1 *Peromyscus* sp., 4 unidentified passerines, and 3 *Helminthoglypta* sp.).

[b] Minimum number of individuals assumes different individuals in different sites.

[c] Items not reported as condor food remains in nest caves by Koford (1953). Note: none of the faunal elements classified above as of non-condor origin were reported by Koford.

dium-sized mammals typical of the region, including a reasonable number of ground squirrels. Perhaps the most surprising result was a relative dearth of remains of mule deer (*Odocoileus hemionus*), as many of the sight records of feeding condors in the 1980s were of deer.

In addition to vertebrate remains, we found frequent fragments of marine molluscs, as had Koford (1953). The species found included pismo clam, common californian venus, and moon shell (Table 1). We also found remains of one barnacle. Land snails (*Helminthoglypta* sp.) were found in several sites, but were judged to have probably entered the sites on their own.

The bones and shells considered likely brought in by condors were mostly of small size (1 to 6 cm). Only 1 of 459 such objects exceeded 10 cm in length and only 4 exceeded 6 cm in length.

In addition to faunal remains, we found man-made artifacts to be reasonably common in sites—primarily small pieces of glass, plastic, and metal. In this respect, condor nests were very similar to nests of Cape Vultures and White-backed Vultures (*Gyps africanus*) studied by Mundy and Ledger (1976), Plug (1978), and Richardson et al. (1986).

DISCUSSION

The ages of remains found in recent and historic condor nests were undetermined. Some materials could have been decades, if not centuries, old, as condor nests were known to have long lifetimes and in some cases to have had long histories of use (Snyder et al. 1986). Materials in substrates did not sort into obvious layers, and we knew from direct observations that the birds continuously churned the substrates with their bills in an apparent search for bone objects, presumably as calcium sources. Some bone objects may have been ingested and regurgitated repeatedly by condors, and presumably many others may have been lost completely over the years to digestion by condors and woodrats. The deposition of remains in nests was clearly a dynamic process, with progressive additions of some materials and losses of others, and with con-

FIGURE 1. California Condor mandibulating plastic cup along shore of Pyramid Lake, Los Angeles County, California, May 11, 1982. One pair of condors frequently "beachcombed" at this location in 1981–1982 in apparent search for bone materials. Photo by Jack Ingram.

tinual mixing of materials from different eras. In such a system there could easily be major biases as to what might be found in substrates at any particular time, and we make no claims that the materials found give an accurate representation of overall condor diet or that they represent any particular eras.

Nevertheless, it is important to note the substantial frequency of remains of cattle, as was also noted by Koford (1953), and we have little doubt that cattle have represented a very important part of condor diet in recent times. Despite the many remains of cattle, however, we emphasize that like Miller et al. (1965), we commonly observed foraging condors failing to descend to carcasses of full grown steers. Although they sometimes fed on such carcasses, in the balance it appeared that they strongly preferred calves, and many of the cattle remains in nests were indeed of immature individuals.

Direct observations indicated that condors focus mainly on soft tissues of vertebrate carcasses in their feeding behavior, and they normally avoid tough materials such as hair, hide, and gristle. This avoidance is the probable cause of a relatively low frequency of pellet-casting seen in the species and may in part be a consequence of the difficulty of dismembering such hard materials. However, a diet of soft tissues is a relatively poor diet with respect to its calcium content. Calcium is especially important for skeletal development of chicks, and, as noted by Koford (1953), adults evidently make special efforts to provide supplementary bone materials in the foods they bring in their crops to feed nestlings. In large vertebrate carcasses, most bones are too large for ingestion by the condors, and the hard materials collected were often teeth, parts of vertebrae, and other small fragments. In smaller carcasses, a much larger fraction of the bone material is small enough for ingestion, and this could be one of the most important factors leading to an apparent preference for smaller carcasses.

Condors were sometimes seen making specific efforts to collect bones and other bone-like materials independent of feeding on carcasses. One pair we watched in the early 1980s frequently foraged along the edge of a lake, using their bills to test light-colored objects they encountered, including pieces of plastic and styrifoam (Fig. 1). Although we did not actually document them ingesting such objects, the presence of plastic, metallic, and glass objects in nests (Table 1) was probably a result of such ingestion. The birds seemed attracted to white and shiny objects, and this could also be observed in nestlings, who often ingested light-colored objects in their nest substrates, including hardened chunks of excrement.

Similar behavior has been studied extensively in Cape and White-backed Vultures in South Africa, where artifacts such as bottle caps, pieces of glass, and pieces of china have often been found in and around nests, apparently as a result of the birds mistaking them for bone fragments (Mundy and Ledger 1976, Richardson et al. 1986, Mundy et al. 1992). In the 1970s and 1980s, certain colonies of Cape Vultures in rangeland habitats were under major stress from calcium deficiencies and such artifacts were especially common in these colonies. Evidently this species of vulture has been traditionally dependent on bone fragments left around carcasses by hyenas. With the extirpation of hyenas in rangeland habitats throughout much of South Africa, the vultures were having great difficulty finding enough bone material to allow successful nesting. Many chicks in nests had wing bones so weak that they broke frequently and healed improperly, leading ultimately to an inability to fledge and nestling death. In recent years this problem has been corrected by deliberately offering the birds bone fragments at carcass "restaurants" established in the vicinity of the affected colonies.

The frequency of artifacts among hard materials collected from Cape Vulture nests in the 1970s reached about 45% in colonies located in rangeland habitats, but was only about 8% in colonies in more natural habitats (Plug 1978). By comparison, we recorded an artifact frequency of 12% for contemporary and historical condor nests, a value that could be interpreted to suggest relatively low calcium stress for condors, if the values for Cape Vultures are considered applicable.

Also correlated with artifact collection, Plug (1978) and Mundy and Ledger (1976) found that Cape Vulture colonies under extreme calcium stress tended to collect relatively long bone fragments, apparently because of a dearth of shorter ones. Thus, they found bones as long as almost 30 cm in nests of such colonies and directly observed that bones this large gave the birds obvious difficulties in swallowing, getting stuck in their throats. Approximately 20% of the faunal materials collected from Cape Vulture nests in rangeland habitat exceeded 10 cm in length, whereas only about 10% exceeded 10 cm in length in nests from relatively natural habitats.

By comparison, only 0.2% of the bones and shells considered likely brought in by condors in contemporary and historical nests exceeded 10 cm in length. If the bone-length relationships seen in Cape Vultures have some applicability to condors, the small size of faunal elements found in condor nests, like the low–moderate frequency of artifacts, could be interpreted to suggest a low level of calcium stress.

However, we caution that part of the apparent differences in bone lengths and artifact frequencies for the two species may trace to methods of collection. Whereas the condor materials were collected by thorough sifting of substrates, the Cape Vulture materials were collected by visual inspection only, which may well have led to a bias toward larger objects and artifacts.

Bone lengths found by Emslie (1988) in Pleistocene condor nests in the Grand Canyon also tended to be fairly small, with only approximately 7% exceeding 10 cm in length. However, the frequency of relatively long bones recorded in the Emslie study may have been unrealistically high, as bones of small mammals were deliberately excluded from analysis. It should also be noted that the Pleistocene form of the condor, *Gymnogyps californianus amplus,* was somewhat larger than the contemporary form. Emslie's Pleistocene condor nests were free of human artifacts.

Still another aspect suggesting relatively low calcium stress for recent condors was the fact that there was no evidence for broken wings in condor nestlings in the 1980s. Although one condor nestling died of a broken wing in 1939, the precise cause of this event was unknown, and it could have been a result of mishandling (C. Koford field notes, Museum of Vertebrate Zoology, Berkeley, California).

Taken together, the data available from faunal and artifact remains in nests and from other sources do not provide strong support for the hypothesis of Cowles (1967), that condors might be suffering major difficulties in obtaining adequate calcium supplies in their diet. Condor reproductive effort and success remained reasonably strong through the 1980s and the major sources of population decline were evidently mortality factors unrelated to calcium supplies (Snyder and Snyder 1989).

The extremely remote locations of most condor nests made it unlikely that the artifacts found in nest substrates might have been brought in as trash by woodrats. However, the flashbulbs found in one nest that was heavily photographed in the 1940s and the bullet found in another site active in the 1940s very likely owed their presence to human activities, as discussed in Snyder et al. (1986). To our knowledge, the great majority of sites, including all but two of the sites containing man-made artifacts of potential condor deposition, had not been entered earlier by humans. The above two sites accounted for only 4 of the 64 artifacts found.

The presence of shell fragments of marine molluscs and barnacles in the substrates of a number of sites also seems best explained as an effort on the part of the birds to satisfy calcium needs of their nestlings. None of these shells came from nest caves in shell-bearing rock formations, so the shell materials must have been brought in from the outside. They could have been collected along beaches of the nearby Pacific Ocean, although condors have not been seen foraging along these beaches for many decades (Koford 1953). Alternatively, they could have been picked up as fossil or subfossil remains on inland hillsides. In the judgement of P. Scott (pers. comm.), a specialist in molluscs, the marine shell materials were likely of fossil origin, and were probably no older than late Pleistocene. The species of molluscs and barnacles represented all occur in the fossil record in California starting in the Miocene and continuing into the present (Grant and Gale 1931). Pleistocene-aged marine deposits are scattered throughout interior portions of central and southern California that were inhabited by the recent condor population.

Overall, the faunal remains found continue to support a generalization that condors feed nearly exclusively on mammalian carrion. The only reptilian remains found were bones of a coachwhip snake in one site, and the only avian remains that were identifiable and seem reasonably likely as of condor origin were feathers of an unknown grebe (Podicipedidae) in one site. However, we acknowledge with these remains, as with all others, that other methods of deposition cannot be ruled out.

Species that represent additions to the list of nest remains given by Koford (1953) include coyote (*Canis latrans*), gray fox (*Urocyon cinereoargenteus*), long-tailed weasel (*Mustela frenata*), cottontail rabbits (*Sylvilagus*), Botta's pocket gophers (*Thomomys bottae*), kangaroo rats (*Dipodomys*), and coachwhip (*Masticophis flagellum*). These are all small to medium-sized species, and suggest that condor diet may not be as concentrated on large species as was suggested by Koford. Koford believed that cattle, sheep, horses, deer, and ground squirrels together comprised at least 95% of the food of the species. Yet assuming our classification of food remains might have been reasonably accurate, these five food types comprised only 64% of the individual food remains likely taken by condors (excluding molluscs, barnacles, and man-made artifacts). Nevertheless, we acknowledge that the food remains data may be sufficiently biased that they may give no better quantitative estimates of condor diet than the estimates of Koford. As yet, no truly unbiased quantitative documentation of California Condor diet has been achieved.

It is noteworthy that bones of condors themselves were quite infrequent in the contemporary condor nests. Only two sites contained condor bones—a humerus and a humerus and tibiotarsus, respectively, all from nestlings. In contrast, Emslie (1988) found bones from as many as five condor individuals in a single Pleistocene nest cave. Reasons for this difference are obscure, but could reflect the relatively deep substrates and potentially long histories of use of the condor nest caves in the Grand Canyon.

Finally, we call attention to the many similarities in bone and artifact collection tendencies between condors and the species of Old World vultures studied by Plug (1978), Mundy and Ledger (1976), and Richardson et al. (1986). As New and Old World vultures are only very distantly related, these similarities presumably represent additional examples of convergence in characteristics of the two groups.

The results reported in this paper are derived from the cooperative efforts, within the framework of the condor conservation program, of organizations like the U.S. Fish and Wildlife Service, National Audubon Society, U.S. Forest Service, California Department of Fish and Game, and Santa Barbara Museum of Natural History. We are especially grateful for the assistance rendered in nest-site studies by L. Andaloro, V. Apanius, D. Clendenen, D. Ledig, R. Ramey, B. Roberts, and F. Sibley. We are grateful to G. Sibley, J. Schmitt, and P. Scott for the assistance they rendered with identification of faunal remains found in nest caves. E. Johnson, W. D. Koenig, and an anonymous reviewer provided constructive comments on an earlier draft of the manuscript.

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