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NEST-SITE BIOLOGY OF THE CALIFORNIA CONDOR[1]

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Abstract. A study of 72 historical and recent nests of the California Condor (*Gymnogyps californianus*) has revealed considerable variability in nest-site characteristics. This paper primarily summarizes the data on nest elevations and dimensions, entrance orientations, nest longevity and re-use, vulnerability of sites to natural enemies, and use of sites by other species. Although all known nests have been natural cavities, some have been little more than overhung ledges on cliffs, while others have been deep, dark caves with nest chambers completely concealed from the outside. Two sites have been cavities in giant sequoias (*Sequoiadendron giganteum*). Contrary to previous assumptions, condors do modify the characteristics of their nest sites significantly and commonly construct substrates of coarse gravel on which to rest their eggs. Many nests have been completely accessible to terrestrial predators, many have been poorly protected from avian predators, and some have had structural flaws leading directly to nesting failure. The use of suboptimal sites has not been clearly related to a scarcity of better quality sites.

Key words: California Condor: Gymnogyps californianus; *nest sites; nest longevity; treehole nests; cavity nests.*

INTRODUCTION

During intensive studies between 1939 and 1950 Carl Koford (1953) examined 15 nest sites of the California Condor (*Gymnogyps californianus*) in southern California. In addition, he received incidental nest-site information from several egg collectors who had been active earlier in the century. From these sources Koford provided a very useful summary of the general characteristics of condor nest sites.

However, Koford's sample size of nests was too small to illuminate the full range of condor nest-site preferences and tolerances. Because of the critically endangered status of the condor, the threats to a number of condor nests represented by the Sespe Creek Project proposed in the mid-1960s, and the fact that several recent nest failures were attributable in part to nest-site deficiencies, we began a more thorough analysis of the relationship of condors to their nest sites. From 1966 through 1969 nest-site studies were conducted by FCS. Studies from 1980 through 1985 were carried out by NFRS, RRR, and other staff members of the Condor Research Center in Ventura, California. During these efforts we analyzed the characteristics of 72 condor nests within the present range of the species, including 12 of Koford's 15 sites, 11 other historically known sites, and 49 newly discovered sites. In this paper we summarize the results of these analyses and discuss their implications for conservation of the species.

KOFORD'S NEST SITES

All of the nests Koford documented were natural cavities. Most were potholes or other kinds of caves in cliffs, but some were crevices among boulders, and one was a hole 29 m from the ground in a giant sequoia (*Sequoiadendron giganteum*). As far as Koford could determine, the sites were not significantly modified by the condors, and eggs were simply laid on available substrates within the cavities. With only one exception, the sites were between 460 and 1,370 m in elevation and were located in the Upper Sonoran Life Zone. The exception was the nest found in a giant sequoia, which Koford reported to be at 1,900 m elevation in the Transition Zone (it is actually located at about 1,800 m). Koford noted that all nests were situated either at some distance above the bottoms of cliffs or on steep slopes, presumably providing air space for the birds to approach and leave their nests. He emphasized, however, that many nests were not particularly high on cliffs and that most were lower in canyons than the most frequently used roosting snags or cliff roosts. He also remarked on an apparent requirement for nests to be near suitable roosting perches.

Nest-cave dimensions measured by Koford varied greatly. Entrance sizes ranged from as small as 38 × 43 cm to as large as 3.0 × 3.7 m. Cavity depths ranged from 0.8 to 9.1 m. Internal dimensions were also highly variable and seemed to be limited only by a need for the cavities to accommodate two adult-sized condors simultaneously. Eggs were placed on level substrates and were positioned between

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walls from 41 to 76 cm apart, which apparently provided the incubating adults with some tactile stimulation. Substrates consisted of silt or sand, often mixed with small rocks, and commonly included leaves, twigs, and acorns carried in by wood rats (*Neotoma fuscipes* and probably also *N. lepida*). Light levels at the egg position ranged from nearly complete darkness in some sites to direct sunlight during part of the day in others. Koford noted that condors appeared to avoid cavities facing south, perhaps to avoid exposure to storm-driven southerly winds.

METHODS

During the present study, condor nests were located primarily by observing the behavior of mated pairs and noting caves they investigated during the pre-laying period and sites they chose for actual egg laying. In addition, a number of sites were located by systematic investigation of cliffs in regions where condor activity had been reported either recently or historically. Sites were confirmed as condor nests either by direct observational evidence of egg laying (eggs or nestlings) or by presence of condor eggshell fragments in the litter of the sites.

Nests in which condors had reached the nestling stage of the reproductive cycle were characterized by "bathtub rings" of excrement on the internal walls near the egg position. In sites that were well protected from the weather, these excrement rings were still conspicuous many decades after the sites had last been used. In contrast, build-up of excrement external to nest sites was inconsistent and ephemeral, and was not usually obvious except during nesting and immediately thereafter. Shallow caves with conspicuous thick tongues of excrement dripping from their mouths generally proved to be condor roosts rather than nest sites. Although heavily used cliff roosts were a reliable indication of the presence of nearby condor nests, not all condor nests had nearby cliff roosts.

Nest sites were entered for study at times when they were not active. For each nest investigated we made entrance and floor-plan diagrams and noted the following characteristics: (1) elevation above sea level, (2) compass orientation of the entrance, (3) entrance height and width, (4) greatest depth from the center of the entrance, (5) distance from the entrance center to the egg position, (6) ceiling height at the egg position, (7) slope of the floor at the egg position, (8) substrate depth at the egg position, (9) substrate composition, (10) visibility of the egg from the entrance, (11) presence or absence of an entrance platform (porch) on which nestlings could exercise their wings, (12) accessibility of the site to large terrestrial predators, (13) evidence for multiple use of the site, as derived from eggshells, internal whitewash, etc., (14) evidence for use of the site by other species, such as wood rats, Turkey Vultures (*Cathartes aura*), and Common Ravens (*Corvus corax*), and (15) distances of the site from the nearest trail, nearest dirt road, and nearest paved road. Measurements were recorded first in feet, inches, and miles, then later converted to metric units. Nest bottoms in the vicinity of the egg position were thoroughly sifted with a fine-meshed (window) screen; and all bone, shell, and pellet material was collected. Detailed results of the analyses of bone, pellet, and shell materials will be presented elsewhere.

We did not make systematic attempts to characterize sizes or dimensions of nest cliffs or positions of nest caves on cliffs because many nests were located in jumbled, broken cliffs or in bouldered sites for which such characterizations would have been arbitrary and potentially misleading. Similarly, no systematic attempts were made to characterize the sites as to presence or absence of nearby sources of drinking water. Many water sources in the region are only seasonal, leading to considerable uncertainty and bias in assessing availability of water, especially since we visited many nests only once, and the seasonal timing of our visits varied greatly. Further problems in assessing water availability arose from difficulties in determining which sources were truly accessible to the birds, and from difficulties in even discovering the sources of water in the difficult terrain in which condors commonly nest. However, we emphasize that the presence of accessible nearby drinking water could be an important feature in nest-site selection, since we have frequently observed condors drinking from water sources near nests. Since there was no way for us to determine what roosting sites might have been used by the pairs nesting at a number of the historical sites and since certain active nests of recent years have had no nearby roost sites, the presence of nearby roosts was not considered to be an essential nest-site characteristic and was not examined in detail.

RESULTS

TYPES OF NEST SITES

The 72 nests studied can be conveniently classified into several major categories: potholes in cliffs (37 sites), crevices or cracks in cliffs (21 sites), crevices among boulder piles on cliffs or steep slopes (6 sites), overhung ledges on cliffs (6 sites), and cavities in giant sequoia trees (2 sites). Pothole nests were most char-

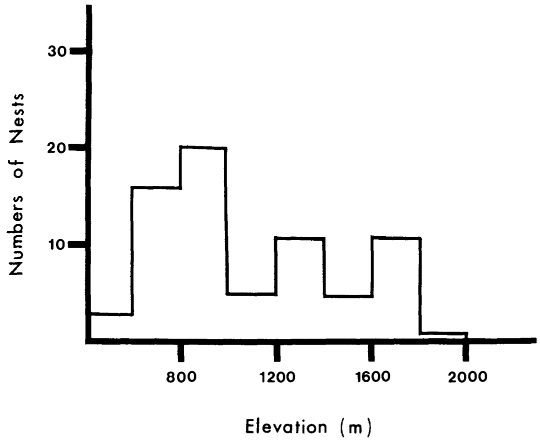

FIGURE 1. Distribution of nest elevations.

acteristically found in sandstone formations and were smoothly rounded, relatively shallow caves, often with approximately oval entrances and often in vertical or nearly vertical cliffs. Pothole sites were not generally associated with fractures in the cliffs and apparently owed their existence most commonly to accelerated internal weathering of depressions forming in the surfaces of cliff faces. Crevice or crack nest sites were found in many different kinds of cliffs, including sandstone. These sites were much more irregular in shape than pothole sites and followed fracture lines into the cliff faces often for many meters. Like crevice nests, ledge nest sites shielded by rock overhangs were found in a variety of cliff types and were highly variable in shape. Although certain of the above categories grade into each other (e.g., overhung ledges grade into crevices or potholes, and some overhung ledges were screened to a greater or lesser extent by boulder piles), the sites were nearly all assignable to the categories without ambiguity. Noteworthy was the high frequency of pothole sites (51% of the total), a prevalence that probably is due to the abundance of sandstone cliffs in the region.

NEST ELEVATIONS

The distribution of nest elevations (Fig. 1) indicates more nesting at moderately high elevations than was noted by Koford. While Koford found only a single site above 1,370 m, 17 of the 72 sites (24%) examined in the present study were at such elevations, and the highest recorded was at 1,830 m. Whether the relatively greater use of high elevation sites documented in the present study reflects an actual shift in nesting distribution or only a more thorough coverage of the nesting distribution than was possible at the time of Koford's study is unsure. We suspect that better coverage is the primary factor, as most of the high elevation sites we discovered have been

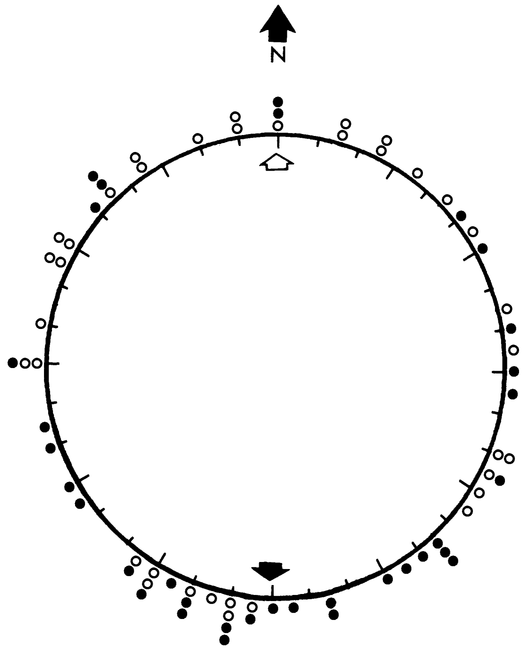

FIGURE 2. Compass orientations of California Condor nests. Open circles represent nests lower than 948 m; solid circles represent nests at higher elevations. Arrows give mean directions of low and high elevation nests.

in regions that Koford did not study intensively; yet there is evidence that these regions have been in continuous use for many decades.

Sites above about 1,500 m are subject to snows during the incubation period in late winter and spring, while lower elevation sites, depending on specific location, are subject to intense summer heat—regularly up to 43°C at some sites. However, no significant correlation was found between nesting elevation and laying date in the 29 cases for which accurate egg laying dates were available.

COMPASS ORIENTATIONS

The overall distribution of nest orientations (Fig. 2) indicates no significant bias toward any specific direction ($P > 0.10$, Rayleigh test; see Batschelet 1965). Many nests faced nearly south, contrary to Koford's conclusion. However, when the nests are classified into those at elevations above 948 m (the median elevation) and those below 948 m, an interesting apparent pattern emerges, with low nests showing some tendency to face north and high nests tending strongly to face south (mean directions of 359.4° and 180.8°, respectively). Although these tendencies do not reach statistical significance in the case of low-elevation nests ($P > 0.10$), they are highly significant in the case of high-elevation sites ($P < 0.001$). Moreover, the high and low elevation distributions are highly significantly different from each other ($P < 0.01$) by an F-test (Batschelet 1965).

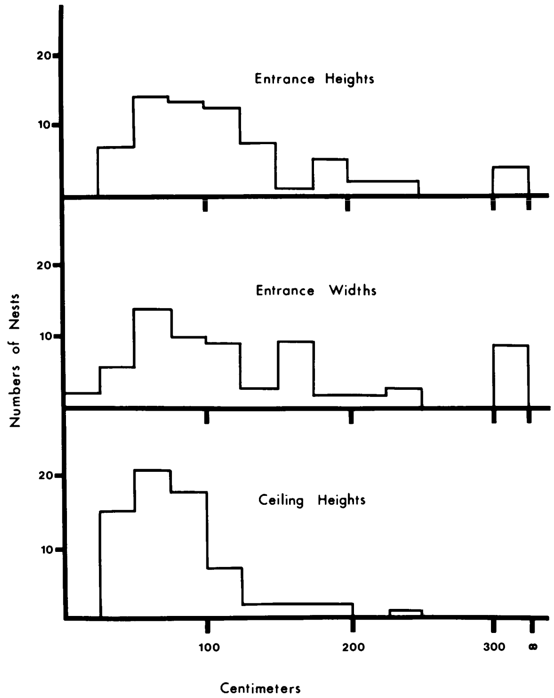

FIGURE 3. Distributions of (a) entrance heights, (b) entrance widths, and (c) ceiling heights at the egg position.

These results suggest that condors may tend to choose warmer sites at high elevations and cooler sites at low elevations, much as Mosher and White (1976) reported for Golden Eagles (*Aquila chrysaetos*). However, without knowing the exact availability distributions of potential nest caves at high and low elevations (prohibitively difficult distributions to determine rigorously), one could argue alternatively that the distributions of nest orientations might be more a reflection of cavity availability than of directional preferences of the condors. Casual observations do suggest a tendency for high-elevation cliffs to face south in the primary nesting region of the recent condor population, and it is plausible that this tendency could be the major cause of the biased distribution of high-elevation nest orientations. Whether low-elevation cliffs in the region tend to face in any particular direction is not obvious.

Koford's belief that south-facing sites might be especially susceptible to storms is questionable. In our experience, most storm fronts affecting the condor nesting regions have blown primarily from the southwest through northwest.

ENTRANCE SIZES

The distribution of entrance sizes found in the present study does not greatly expand the range indicated by Koford, although a few sites with larger or smaller entrances were located (Fig. 3). In a few cases it was even difficult and

FIGURE 4. Overhung ledge nest site used in 1984, a site only 3 m from an active raven nest. Egg was situated precariously close to cliff edge, and the ravens made several attempts to take it before it was removed for artificial incubation. The egg ultimately hatched into "Pismo," a female held currently at the Los Angeles Zoo.

somewhat arbitrary to define a cavity entrance, as the sites were best described as overhung ledges on cliffs almost completely exposed to the sky (Fig. 4). The lowest height observed for an entrance was 30 cm, and it is doubtful that condors could manage to enter anything with a much lower ceiling. The narrowest entrance was only 20 cm wide. At the other extreme, one nest entrance was a full 5.5 m high and 2.4 m wide. Because it was not practical to obtain an overall entrance size availability distribution, it is not clear whether condors have preferences with respect to cavity entrance sizes beyond the limitation of only using sites with entrances large enough for them to fit through.

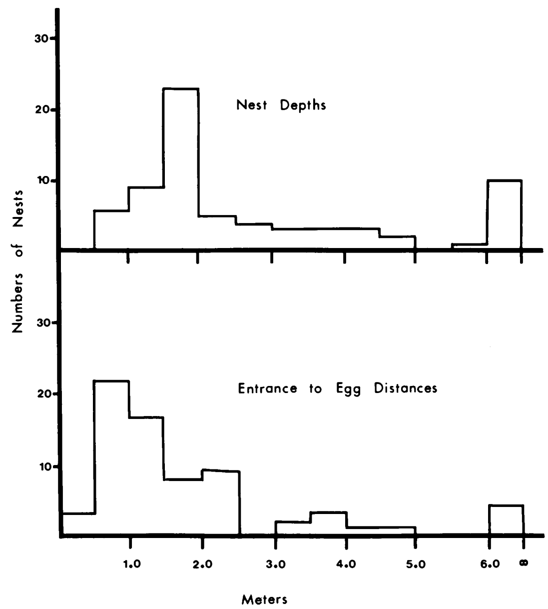

FIGURE 5. Distributions of (a) nest depths (entrance to farthest point in cave) and (b) entrance-to-egg distances.

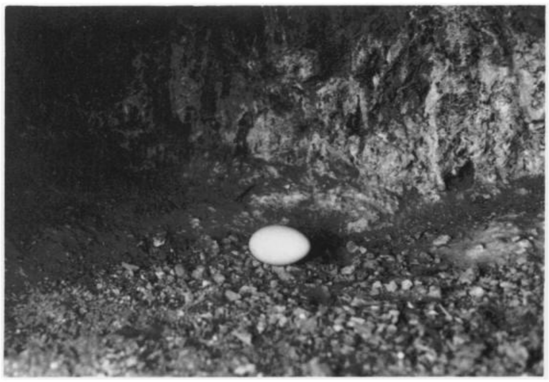

FIGURE 6. Nest site used in 1980, 1982, and 1983, illustrating gravel substrate deliberately fashioned by the adults. Egg was taken into artificial incubation and produced "Sisquoc," the first California Condor chick hatched in captivity.

FIGURE 7. Badly-sloped nest site from which an egg rolled to destruction over the cliff edge in 1982. Forty days later the pair laid a replacement egg in the site illustrated in Figure 6, the first conclusively documented case of replacement-clutching known for the species.

NEST DEPTHS

Maximum nest depths (Fig. 5) show a pronounced peak from 1.5 to 2.0 m, possibly reflecting the prevalent use of potholes (which do not commonly get deeper than about 2 m) as nest sites. The distribution of entrance to egg distances is not as tightly peaked, possibly because the precise floor structure of sites is relatively variable. In general, the birds apparently placed their eggs as far back in the caves as there was suitable level substrate and an adequately high ceiling.

In all actual nest sites, light levels were at least strong enough that we could discern basic internal structure of the sites without a flashlight. However, one site that a condor pair investigated and defended (but did not use for egg laying) in 1983 was effectively completely dark at the only possible nesting location at the end of a long, curving tunnel.

NEST CHAMBER CHARACTERISTICS

Unlike Koford, we did not find any consistent tendency for condors to lay their eggs between confining walls, although some pairs did so. In a number of sites the egg was simply placed close to the rear wall (Figs. 4 and 6). Nest floors were not always level. Six sites with bottoms sloping more than 5° at the egg position were located. From one of these (Fig. 7) an egg accidentally rolled out the entrance and over the cliff edge in 1982. From another, an Andean Condor (*Vultur gryphus*) nestling rolled out the entrance and over the cliff edge during an unsuccessful fostering experiment in 1983 (miraculously, the nestling survived). Evidently, the degree of slope at the egg position is an important nest characteristic not always fully appreciated by the condors.

Ceiling heights at the egg position (Fig. 3) varied from 38 to 229 cm, with a distribution peaking between 50 and 75 cm. One 1984 condor pair was observed investigating a site with a ceiling only 30 cm high, but the birds could not stand up in this cave, soon lost interest in it, and eventually laid elsewhere. Thirty-eight centimeters may represent an approximate lower limit for an acceptable ceiling height. The relatively low variance seen in ceiling heights at the egg position suggests strongly that condors are sensitive to this parameter in their choice of egg locations.

NEST SUBSTRATES

Nest substrates averaged about 8 cm in depth and ranged from about 1 to 20 cm deep. In several instances the levels of condor excrement on the cavity walls indicated that the substrate depth had changed significantly over the years. Excrement in active condor nests normally rises to a height of about 35–40 cm above floor level. Cases of bands of excrement high on walls and separated from the floor by bands of clean wall clearly indicated loss of substrate subsequent to nesting. Conversely, deeply buried eggshell fragments and partially buried bands of excrement indicated rises in substrate levels subsequent to nesting.

At least at the time of inspection, almost all nest substrates were dry, although one heavily used historical site showed signs of recent entry of water to the nest bottom, and watermarks on the cliff walls indicated susceptibility of another site to flooding. The classic nest site studied by Finley (1906) has no effective ceiling. Eggshell fragments found in this site in 1983, presumably dating from early in the century, were noticeably crumbly—presumably weathered by the action of water.

Nest substrates were often conspicuously surfaced with small chunks of rock, and it is clear from direct observations that adult condors deliberately gather these chunks in their bills from the vicinity of the nest chamber and place them close to the egg. Thus, condors do modify their nest sites to a limited extent and appear to prefer to rest their eggs on substrates of coarse gravel and other loose material (Fig. 6, see also plate 22 in Koford 1953). In some sites, however, little gravel or other loose material has been available within reach from the nest chambers, and eggs have rested on substrates of nearly pure sand or silt (Fig. 4).

Besides small chunks of rock, nest substrates commonly included abundant wood-rat droppings, twigs, leaves, acorns, and to a lesser extent, bone fragments, trampled pellet material, tiny eggshell fragments, and sometimes seashells. The fairly frequent presence of marine mollusk shells (both pelecypods and gastropods) was almost surely attributable to the condors, but does not necessarily indicate any recent beachcombing by the species. The shells may have been present in the caves for many years and some may have been collected by the birds as fossil or subfossil remains on inland hillsides. Condors have not been observed foraging along ocean shores for many decades.

The bones included small skeletal fragments of a variety of large mammalian species that probably had been fed upon by the adult condors. Many sites also contained abundant bones of wood rats that probably entered the sites with no assistance from the condors. Only two nests contained condor bones (a humerus, and a humerus and tibiotarsus, respectively, all from nestlings). By comparison, one late Pleistocene condor nest in the Grand Canyon of Arizona contained the skeletal remains of at least five different condor individuals (Steve Emslie, pers. comm.).

Occasionally man-made artifacts were found (Fig. 8), such as bottle caps (two recent sites), pull-tabs from aluminum can tops (two recent sites), fragments of a white comb (one recent site), jagged fragments from a brown glass bottle (one recent site), fragments of an aluminum can (one recent site), fragments of amber sheets of plastic (one recent and one historical site), archaic flashbulbs presumably left by photographers in a site active in 1941, and a spent lead bullet (one historical site). While it is not certain what agents brought in these artifacts, we suspect that most were brought in by the adult condors as a result of their swallowing bone- or shell-like objects in an effort to satisfy calcium needs of their nestlings, much as has been reported for Cape Vultures (*Gyps coprotheres*) by Mundy (1982). The sites where the artifacts were found were sufficiently remote from past human activities (with the exception of the site with the bullet and the site with the flashbulbs) that it is extremely unlikely that the objects were brought in by man or by wood rats. However, it is possible that some objects in some sites may have been brought in by ravens.

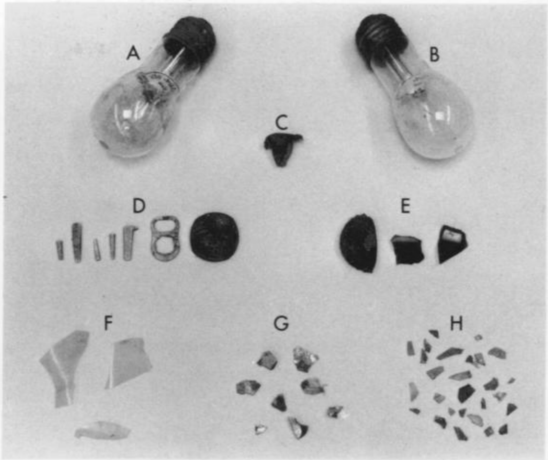

FIGURE 8. Man-made artifacts sifted from various condor nests: (A and B) flashbulbs from Koford site #9 active in 1941, (C) bullet from Koford site #4, (D) plastic comb fragments, aluminum can tab, and bottle cap from site active in 1983, (E) bottle cap and pieces of glass from sequoia site active in 1984, (F) pieces of plastic collected by Van Rossem from site in 1922, (G) fragments of aluminum can from sequoia site in 1984, and (H) pieces of plastic from sequoia site in 1984.

Examination of the spent bullet by the Ventura County Sheriff's Crime Laboratory indicated that it probably had been fired into the nest site, as red sandstone grains embedded in the head of the slug matched those of the nest walls (Vincent Vitale, pers. comm.). Hair packed into the center hollow of the slug suggested the bullet had later been ingested by a condor. As objects on the nest chamber floor are repeatedly ingested and regurgitated by nestling condors, this slug could conceivably have been responsible for the poisoning of generations of condor nestlings, though we hasten to observe that no condor bones were found in the site. The nest from which this bullet was recovered was a site discovered by Koford in 1940 (Koford #4) and was located within 0.5 km of an oil-drilling operation, making it one of the more vulnerable sites to human depredations.

USE OF CONDOR NESTS BY OTHER SPECIES

Virtually all condor nests contained abundant wood-rat fecal castings. Actual wood-rat nests were found deep in the inner recesses of five sites. One condor nest active in 1981, 1982, and 1983 had not only a large active wood-rat nest but also a large mound of solidified wood-rat urine immediately adjacent to the egg position, similar to the wood-rat urine mounds described by Betancourt and Van Devender (1981) for caves in New Mexico. Radio-carbon dating of such mounds has indicated that they are often built up over thousands of years.

Whether the usual presence of wood-rat activity in condor nests represents any threat to the condors in unknown. No losses of eggs or young have been clearly attributable to this species. However, wood rats may be partially responsible for the dearth of bone and eggshell material in some condor nest caves. In an experiment conducted in 1982 we deliberately placed fragmented domestic chicken (*Gallus gallus*) eggshells in two pothole caves containing wood-rat castings. When we sifted these sites six months later, most of the eggshell material was gone. A likely cause was ingestion by the wood rats, although this was not directly observed.

Six condor nests, including the primary site studied by Koford (1953), contained eggshell material from Turkey Vultures, indicating probable former use of the cavities by this species and considerable overlap in the two species in nest-site preferences. The sites used by the Turkey Vultures ranged from one of the shallowest condor nests (1.5 m in depth) to one of the deepest (10.0 m long). Very likely, Turkey Vulture eggshells were not found in more sites because this species nests only in certain local portions of the nesting range presently used by condors.

Ravens in southern California characteristically nest in very small-entranced holes, generally far too small for use by condors. However, one former condor nest cave, a relatively shallow (1.1 m deep) and narrow-entranced (64 × 71 cm) hole, contained a raven nest in 1982 and again a new raven nest in 1984. The basic attractiveness of this site to ravens provides a possible explanation for a case of condor egg breakage documented for the site in 1946 by Koford.

One other condor nest had remains of a stick nest, but in this case the nest was clearly that of a Red-tailed Hawk (*Buteo jamaicensis*), judging from red-tail eggshells and feathers and the remains of snakes, small mammals, and small birds found in the nest litter. Like the site used by ravens, this site was a small pothole, only 0.8 m deep. Numerous other condor nest sites contained fragments of thin white eggshell believed to be that of owls, most likely Great Horned Owls (*Bubo virginianus*), Barn Owls (*Tyto alba*), or Spotted Owls (*Strix occidentalis*).

Clouds of thousands of gnats (*Dasyhelea* spp.) were found in four of the deepest, darkest sites (all deeper than 4.9 m). In one of these we were able to observe interactions of the condors and gnats from a distant blind. The gnats caused nearly constant irritation and head-shaking in the birds, and were the apparent reason why late in the incubation period the male adult moved the egg from its original position to a position 3 m closer to the entrance.

Koford noted three condor nests with Mexican chicken bug (*Haematosiphon inodora*) infestations. In two of the sites there were hundreds of these bugs at the time the young condors fledged. We found no *Haematosiphon* infestations in any of the nests investigated during the present study. However, it should be emphasized that we entered only nine sites at times when they contained nestlings and did not closely inspect the sites during these visits. Koford also reported many ticks of the species *Argas reflexus* in one nest cave. We found no tick infestations during the present study.

At one small active site of 1985, several dozen bumblebees (*Bombus* spp.) were found on the cavity ceiling shortly after the start of incubation. Furthermore, honeybee (*Apis mellifera*) hives were found in or immediately adjacent to six nests, including one of the sites studied by Koford (1953). For three of these sites it is unknown if condors and honeybees were ever present at the same time, but in two recent nests and one historical site both species were definitely present simultaneously. In one of these, an active site of 1984, the entrance to the honeybee hive was only 56 cm from the condor egg. Nevertheless, there was no evidence that the close proximity of this hive caused the birds any difficulty. Whether there might by any preferential tendency for condors to nest near hymenopteran colonies for the protection this might provide against terrestrial predators is unknown. In fact, whether occupancy by bees preceded or followed occupancy by condors is not known for any of the above sites.

ACCESSIBILITY OF NESTS TO PREDATORS

All nest sites were rated as to their accessibility to large terrestrial predators, such as black bears (*Ursus americanus*) and coyotes (*Canis latrans*). Sites were classified as walk-in sites (accessible), scramble-in sites (questionably accessible), and rope-in sites (completely inaccessible). Of the 72 sites, 16 (22%) were walk-ins, 8 (11%) were scramble-ins, and 48 (67%) were rope-ins. In spite of the relatively frequent use of walk-in sites, no clear cases have as yet been documented of predation on eggs or young by terrestrial predators (Koford 1953, Snyder 1983). However, an instance was directly observed in 1983 of a black bear obviously attempting to climb to a condor nest—a rope-in site containing a nestling. The bear failed to reach the nest. In another instance in 1982, a pair of condors was observed harassing a black bear that came within 100 m of an active walk-in site. The bear did not discover the site. The relatively frequent use of walk-in sites is noteworthy, as there appears to be no necessity for the birds to occupy such sites. All recent nesting territories have had numerous rope-in sites of apparently good quality available to the birds.

With recent data indicating a considerable threat of raven predation to condor eggs, we assessed most of the sites for their vulnerability to this species. For 55 (87%) of the sites assessed, untended eggs could have been seen by ravens flying past the entrance. Eggs would not have been visible in only eight sites, primarily very deep and dark sites. Thus, the vulnerability of most condor nests to raven predation has been quite high in the sense of the ease with which ravens might be able to discover the existence of condor eggs within the caves. Direct observations have indicated that once ravens see a condor egg, they often make persistent attempts to steal it, with a high potential for success, considering the length of the condor incubation period (54 to 58 days) and the fact that condors commonly leave their eggs untended during nest exchanges. Ravens are sometimes remarkably brazen in their attempts to take eggs. In one instance we observed an individual entering a nest cave and jabbing under the abdomen of an incubating condor. The condor made only clumsy efforts to fend off its assailant. In other cases we have seen ravens following condor pairs in and out of caves as the latter have been prospecting for nest sites prior to egg laying.

FIGURE 9. Condor nest site active in 1984 in a giant sequoia. Site was a burn-out hole 30 m from the ground and had been used for numerous previous nestings, judging from layers of internal whitewash.

PRESENCE OF PORCHES

Forty of the 72 nests had well-developed external porches allowing enough space for nestlings to stretch and flap their wings comfortably and safely. Another 11 sites lacked substantial porches, but at least had enough space internally to allow full wing exercise inside. However, 21 sites lacked both the internal or external space for unimpeded wing-flapping, and chicks were faced with fledging from these sites without the benefit of full wing exercise during development. At one such site observed closely in 1983, the nestling was seen repeatedly attempting to perch on the steeply sloping entrance, repeatedly losing its balance, and nearly falling out of the site. At another such site discovered in 1968, the nestling was first found on a slope about 30 m under the site, apparently having survived a fall from the entrance. At still another such site found in 1966, a late-stage nestling was discovered dead at the base of the cliff, apparently having fallen some weeks earlier. Evidently the use of small potholes lacking external porches poses considerable risks to chick survival, especially if the sites are located high above the bases of nest cliffs. The frequent use of relatively low cliffs by condors may in part be a reflection of such dangers.

THE TREE NEST SITES

On 19 March 1984 an active condor nest was discovered 30 m from the ground in a giant sequoia by Forest Service personnel supervising a timbering operation on the Sequoia National Forest (Fig. 9). The site, only the second condor nest ever discovered in a sequoia, showed evidence of numerous previous usages, and the male of the pair using the site proved to be an individual that had previously been documented by photographic means to be associated with a cliff nesting site (Snyder and Johnson 1985). Thus it appears that there may not be any rigid association of individual condors with tree vs. cliff nest sites.

TABLE 1. Nest-site use by four recent pairs of California Condors.

Pair	Year	Nest site	Distance (km) from previous site	Outcome of nesting attempt
1	1980	A	–	Successful fledging
	1982	B	0.1	Failure (egg rolled out of site)
		A	0.1	Failure (ravens destroyed egg)
	1983	A	0.0	Egg taken for artificial incubation
		C	2.9	Egg taken for artificial incubation
	1984	D	2.4	Egg taken for artificial incubation
		E	0.8	Egg taken for artificial incubation
		F	0.4	Egg taken for artificial incubation
2	1980	A	–	Failure (unknown cause)
	1981	B	0.9	Successful fledging
	1982	B	0.0	Chick taken captive
	1983	C	1.0	Egg taken for artificial incubation
		A	1.1	Failure (apparent raven predation on egg)
		B	0.9	Chick taken captive
	1984	D	1.5	Egg taken for artificial incubation
		E	3.7	Egg taken for artificial incubation
3	1980	A	–	Failure (chick died in handling accident)
	1981	B	10.2	Failure (egg lost to unknown cause)
		C	11.5	Failure (chick died at hatching)
	1982	B	11.5	Successful fledging
	1983	D	11.0	Egg taken for artificial incubation
	1984	E	6.9	Egg taken for artificial incubation
		F	8.1	Egg taken for artificial incubation
	1985	G	0.4	Egg taken for artificial incubation
		C	7.6	Egg taken for artificial incubation
		H	3.7	Egg taken for artificial incubation
4	1983	A	–	Chick taken captive
	1984	B	4.0	Egg taken for artificial incubation

Both the 1984 sequoia nest and the sequoia nest discovered during Koford's study in 1950 were cavities produced by burn-outs of limbs into the main trunks of the trees, and both nest trees showed extensive fire scars at their bases. Of 96 large (>6.8 m circumference) sequoia trees we checked in the vicinity of the known nests, 20% had burn-out cavities, 83% had fire scars at their bases, and all trees with cavities had extensively fire-scarred bases. No cavities other than burn-out cavities were located. Apparently, standing sequoias are virtually invulnerable to the common decay processes that produce natural cavities in other tree species, and the existence of potential nest sites in giant sequoias appears to be a strict function of fires in the groves, especially fires severe enough to penetrate the bark of the larger trees and ignite dead limbs high above the ground.

The substrates within the sequoia nests were composed mainly of sequoia bark, twigs, cones, and needles. Surprisingly, the substrate of one of the two sites included some gravel, conceivably brought into the nest as crop contents of adults.

CAVITY RE-USE

In two recent cases, pairs that had successfully fledged young moved to different nest sites for their next nesting attempts, while there has been only one recent case of a pair immediately renesting in the same site after a successful fledging (Table 1). Similarly, most pairs have switched nest sites after nesting failures, although one recent pair failed twice in succession in the same site. Thus the usual pattern, at least in recent years, has been for pairs to change nest sites in successive reproductive attempts, regardless of the outcome of the attempts. The adaptive significance of frequent nest switches is unknown, but could relate to reduction of parasite buildups or to reduction of the threats represented by predators such as ravens or bears.

Nevertheless, the strong tendency for pairs to change nest sites does not commonly result in their adopting previously unused sites. A large majority of the nests examined had been used for multiple condor nestings, judging from eggshell evidence, excrement layers on cave walls, and other data. Of the 72 nests examined, 42 had clearly been used more than once, only four had apparently been used a single time, and multiple use of the remaining 26 could not be safely refuted or established.

Judging from observations at nests since 1980, most birds in the population may know of the location of a large fraction of the recently active nest sites, as visiting individuals, especially juveniles, have been seen with some frequency in the vicinity of most active nests.

The distances between successive nest sites of given pairs have varied greatly, with an average move of 3.8 km between nesting attempts (Table 1). The greatest distance documented between alternate nests actually used for egg laying by a single pair has been 12.6 km, although we have observed pairs investigating sites that are even farther apart. It is possible, with the presently reduced size of the condor population and the relatively large number of potential nest sites to choose from, that the remaining pairs have expanded the sizes of their nesting ranges and reduced the frequency of re-use of given nest sites compared to the historical situation. Unfortunately, no comprehensive information is available on sizes of nesting ranges of historical pairs or on historical frequencies of nest re-use, although it is known that historical pairs often nested much closer together than has been seen in recent years. Koford documented one case of two pairs nesting only 1.3 km from each other and another case in which active nests were only 1.5 km apart. Since 1980 the closest simultaneous condor nestings have been 19 km apart, although two pairs that did not lay eggs were associated with sites only 2.6 km apart in 1982.

NEST LONGEVITY

By virtue of their locations in rock outcrops and ancient sequoia trees, condor nests tend to be quite durable. Nevertheless, a number of sites have disintegrated or become otherwise unusable by condors in recent years. Of the 72 nests four have become unusable during 1,364 nest-years of observation (range of uncertainty = 1,315 to 1,415 nest-years) for an average loss rate of 0.3% per year and an average nest longevity of 341 years. Two of the four lost nests were destroyed as a result of partial collapse of nest cliffs (Fig. 10). The other two were lost from potential use because of a buildup of impenetrable brush around the sites. In addition to the four sites totally lost from use, another site has been sufficiently degraded that it remains only marginally usable—a site suffering from brush buildup. Also, one heavily used site lost half its length in a rock fall in 1983, but still retains an intact and usable nest chamber.

However, one may question the classification of brush-obscured sites as truly "lost," because at some point in the future, fire may clear out the brush and make the sites usable again. If we consider the brush-obscured sites as only temporarily lost, the average "structural" longevity of sites could be recalculated

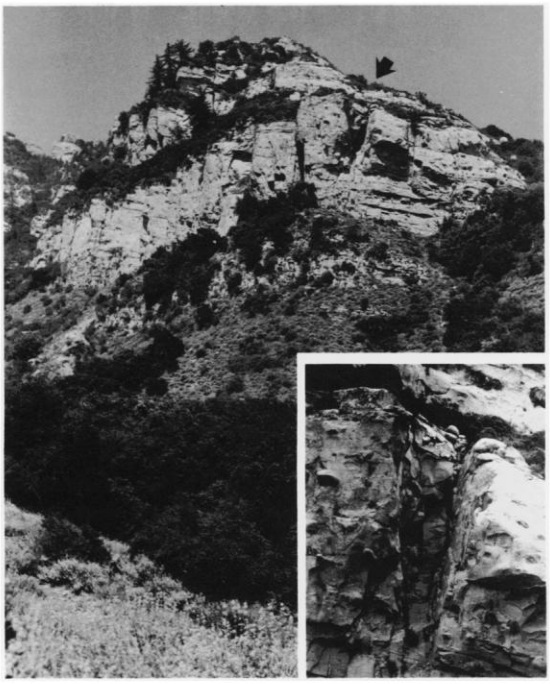

FIGURE 10. Before and after (insert) photographs of Koford's nest site #13 that collapsed between late 1973 and early 1975. Nest was in a crevice among boulders wedged in a cleft (arrow) and disappeared when the boulders broke free.

at 682 years and the annual loss rate at 0.15%. Whatever figures one prefers, other cavity-nesting birds cope with loss rates that are an order of magnitude greater. Erskine (1961) found an annual loss rate of 5.7% for tree-cavity nests of Buffleheads (*Bucephala albeola*) in British Columbia; Kemp (1974) found an annual loss rate of 6% for tree-cavity nests of *Tockus* hornbills in South Africa; and Saunders (1979) found annual loss rates varying from 2.0 to 4.8% for tree-cavity nests of White-tailed Black Cockatoos (*Calyptorhynchus baudinii*) in Western Australia.

Since condor nest sites in giant sequoias are formed by burning rather than by decay and are probably little changed after formation until the trees finally fall, the longevities of such sites are probably far greater than those of cavities in most tree species. Although data are presently insufficient to prove the point, the lifetimes of sequoia nests of condors may be comparable to or even exceed those of cliff sites. The sequoia nest found in 1950 looks identical today to the photographs taken by Harrison when it was first discovered (see Koford 1953).

DISTANCES FROM TRAILS AND ROADS

Despite the ruggedness of the region in which the remnant condor population nests, few nesting areas are truly inaccessible by trails or roads, at least dirt roads, although most of these trails and roads are now overgrown with brush and are very seldom traveled. Sibley (1969), reporting on a study of 26 condor nests, noted that active sites were located a minimum of 1.3 km from lightly used dirt roads, a minimum of 1.9 km from generally used dirt roads, and a minimum of 3.5 km from paved roads. There did not appear to be any minimum distance from active sites to trails.

Sibley's generalizations have held up quite well for the 36 nest sites found in more recent years, although there have been a few exceptions. Six of the 36 recently found sites were closer to paved roads than 3.5 km at the times they were active (range 1.6 to 3.4 km), but topographic features shielded five of the six from view from the roads, giving them effective buffering from the disturbance of traffic. Similarly, only two of the sites were closer to generally used dirt roads than 1.9 km (0.6 and 1.1 km, respectively), and in both cases the sites were effectively shielded from view from the roads. However, a total of 13 sites were found to be visible from and fairly close to occasionally or intermittently used dirt roads. All 13 were within 2.9 km of such roads and seven were closer than 1.3 km. These data suggest that proximity to roads in itself may not be the most significant factor controlling nest-site use, but the extent of motor vehicle traffic on roads and the extent of shielding of sites from roads may be of some importance. As in Sibley's earlier study, many of the sites were quite close to trails (30 were within 1 km and 18 were within 0.5 km), but none of these trails was used on more than an occasional basis.

Among recent nests, the site subjected to the highest degree of disturbance was the one found in 1984 in a giant sequoia tree. This nest tree, which was discovered by Forest Service personnel within a day or so of egg laying, was located right on the edge of a clearcut operation, only about 0.2 km distant and in direct view from an intermittently active dirt road, and only 1.6 km distant and in direct view from a frequently travelled paved road. Considering the noise and tumult inherent in timbering operations (which were being conducted during the period prior to egg laying at several locations along the dirt road within 1.6 km of the site) it seems remarkable that the condors might have accepted the site.

However, a number of considerations could have mitigated disturbance levels in the weeks preceding egg laying, although no direct observations were made at the nest site during this period. First, active timbering at the clearcut immediately adjacent to the nest tree had ceased about three weeks prior to egg laying; second, egg laying apparently took place over a weekend when cutting operations were not in progress anywhere in the area; and third, the nest hole faced away from the paved road and away from other clearcut operations along the dirt road, considerably reducing the disturbance values of these features to birds inside the nest.

Judging from the many layers of whitewash inside the nest cavity and judging from the fact that a number of condors (not members of the pair) visited the site during the next few months, this nest site was a traditionally used site well known to the condor population. It is possible that the pair adopting it in 1984 may have made only brief nest investigations prior to egg laying and by chance may have made their investigations at times when disturbance levels were limited. Three days before the calculated time of egg laying, the pair was photographed around a former nest cliff of the male 160 km distant.

Immediately after the sequoia site was discovered, the U.S. Forest Service closed down all lumbering operations in the area and closed off the dirt road passing by the nest site. Disturbances for the pair through the rest of the nesting cycle were limited to those emanating from the paved road 1.6 km distant from the nest, and these appeared to be relatively minor.

The extent to which condors may avoid nest sites because of disturbance levels is extremely difficult to determine rigorously, and it is likely that there is considerable individual variation in tolerances of disturbance. The male of the 1984 sequoia pair was known from previous observations to be an individual exceptionally tolerant of close approach by man. While it is clear that a number of historical sites that have not been active for many years are sites that are very close to areas of high human disturbance, it is possible that the reasons for disuse of the sites may lie as much in direct predation effects of man as in avoidance of the sites by condors.

DISCUSSION

The California Condor nests examined during this study all conformed to the basic cathartid pattern. All were natural cavities or "almost cavities," and most fit within the range of nest-site characteristics advanced by Koford (1953). However, the overall tolerances of the species appear to be sufficiently broad that it is difficult to specify the essence of what constitutes a condor nest beyond stating that nests are protected locations in cliffs, trees, or steep slopes that have (1) entrances large enough for the birds to fit through, (2) at least 38 cm head room at the egg position, (3) floors that are at least fairly close to level and are comprised of at least some loose substrate, (4) enough space at the egg position to accommodate an incubating adult without undue constriction, and (5) are accessible enough to the birds that they can approach them with no more than a short walk from a nearby landing point.

While the above requirements are fulfilled by all known nest sites, they are also fulfilled by many other sites within the condor range that give no evidence of ever having been used by the species. For reasons that are not obvious, the sites that have actually been used for nesting have been relatively limited in number and have received repeated, though intermittent, use through the years. As was emphasized by Koford (1953), the fact that condors do not use the same nests every year and have been observed returning to historically known nests after many years absence argues strongly for long-term protection of known nest sites, regardless of whether or not they have been used in recent times. If the present conservation program is ultimately successful in rebuilding the size of the wild population, re-occupancy of historically active sites can be anticipated. Fortunately, almost all known condor nests are within National Forest boundaries, and the U.S. Forest Service has implemented long-term regulations for protection of condor nest sites, involving restrictions on human activities within 2.4 km distances of all sites. We consider such protection to be an essential requirement for recovery and maintenance of the species.

SIGNIFICANCE OF ROCKY EGG SUBSTRATES

When we first began inspections of active condor nests we were alarmed by the frequent presence of rocky substrates in the egg position, and indeed some recent eggs have clearly been scored by contact with such substrates (including the egg in Fig. 6). At one time we were inclined to attribute much of the frequent egg breakage known for the species to the rough quality of egg substrates (Snyder 1983). However, we now suspect that rather than increasing the risks of egg damage, rough substrates may actually reduce such risks by damping uncontrolled egg movements. Condors frequently kick their eggs clumsily with their feet in attempting to settle on them, and we have seen eggs launched into long, meandering rolls across nest floors as adults have grappled with the task of attempting incubation. As condors have been observed egg laying from a standing position, loose gravel substrates may also be advantageous in absorbing some of the shock that eggs experience in hitting the substrate during the laying process. Other possible advantages of such substrates include reduction of contact of eggs with soil pathogens, partial protection of eggs from flooding of nest bottoms, and enhanced gas exchange for embryos.

USE OF SUB-OPTIMAL NEST SITES

One of the most inexplicable features of recent condor reproductive biology has been the more than occasional use of poor quality nest sites, despite the availability of better sites. Because of the strongly negative effect that use of poor sites has on condor nesting success, it is remarkable that natural selection has not long ago eliminated such tendencies. Specifically, it is surprising that condors might ever choose sites with dangerously sloping bottoms, sites vulnerable to terrestrial predators, or shallow sites adjacent to active pairs of ravens. Yet such choices have occurred with frequency. For example, a 1982 pair nested in a slope-bottomed site from which their egg rolled over the cliff edge only 12 days after the start of incubation. The pair chose this site despite the existence of a much better level-bottomed site within 100 m (a site the pair had used successfully in 1980). Several other good quality sites previously used for condor nesting were also available within a kilometer. Thus, it is difficult to argue that the condors were forced to use a poor site for lack of better alternatives.

Perhaps the greatest threat to condor nesting success today is that represented by ravens. In addition to directly observing ravens destroying the egg at one recent condor nest, we have seen numerous cases of attempted predation on condor eggs by ravens and have found condor eggshell in three old raven nests close to condor nests that are known to have suffered egg breakage in recent and historic times (including one of Koford's nests). While the presence of condor eggshell in raven nests does not prove that ravens were the cause of egg destruction, it certainly is powerfully consistent with this possibility. Thus, it now seems likely that ravens, rather than other factors, have been the primary cause of the historically high rate of egg breakage in the species. Yet several condor pairs of the past few years have chosen to nest in exposed sites within 100 m of active raven nests. An extreme example was a pair of 1984 that nested on an overhung ledge just 3 m from a pair of nestbuilding ravens (Fig. 4). As in the situation described above, a number of alternative sites were available to this pair which apparently would have been much safer from ravens.

From the perspective of reducing raven threats it is puzzling that condors have not evolved strong and consistent preferences for

FIGURE 11. Adult condor pursuing Common Raven near nest site. Bird pursuing the raven later nested with a different mate in the sequoia illustrated in Figure 9.

deep, dark nest caves with internal structures protecting the birds and their eggs from view from the entrances. While they do use such sites on occasion, the usual sites occupied have been quite shallow and have offered little concealment. Granted, it is possible to argue that the deeper caves carry an intrinsic penalty with respect to gnat swarms that can make them objectionable as nest sites. But gnat swarms occur only in the deepest sites, and it is surprising that we have not seen more occupancy by condors of at least moderately deep sites that are free from this problem.

Condors have coexisted with ravens for millenia (Howard 1930), and presumably have had ample time to evolve effective defenses against this species. They clearly recognize ravens as threats and expend large amounts of energy attempting to chase them from the vicinity of their nests (Fig. 11). Yet for unknown reasons they do not regularly choose nest sites with good intrinsic protection against this species. Conceivably, the tolerances of condors for nest sites vulnerable to ravens are a historical carry-over from times when condor populations were much denser, nest sites were more limiting, and ravens may have been less abundant. While quantitative evidence for long-term increases in raven populations is lacking, such increases are at least plausible, judging from the present-day dependence of ravens on man-generated food supplies, such as road-killed vertebrates.

IMPROVEMENT OF NEST SITES

One of the more important goals of the present condor conservation program is enhancement of nesting success, and one route to this goal is through improvement of defective nest sites. Specific remedial actions taken to date include deepening and leveling of the site from which an egg rolled out in 1982 and provision of a new entrance and porch for an awkwardly entranced site used by a pair in 1983. In addition, internal baffles have been provided for certain other sites to obscure their nest chambers from view from the outside.

Unfortunately, it is generally impractical to attempt transformation of walk-in sites into rope-in sites, and many of the improvements one might envision would be risky to implement at times when the condor nests are active because of the possibility of causing nest abandonment. Since condors often do not give much advance indication of which sites they are going to use for egg laying, there has been little potential for improving sites prior to egg laying, and we have usually had no option but to wait until condor nesting is through before attempting nest-site modifications. As there is only a moderate expectation of re-use of a given site for at least a number of years, the chances are limited for having a significantly beneficial effect on nesting success by nest-site improvements implemented after the breeding season. Only one improved site has yet been re-used by condors, a site for which we leveled the floor and added substrate.

At least in the case of raven predation, it is likely that more significant improvements in condor nesting success can be achieved by dealing directly with the threats than by nest-site improvements. For example, very promising results have been achieved in reducing egg predation of corvids by taste-aversion conditioning (Nicolaus et al. 1982; Nicolaus, unpub.), and it is possible that this technique may prove applicable to the condor situation. Direct control of ravens by shooting, on the other hand, has not proved very effective in the instances where we have tried it, as replacement ravens have filled in vacancies in territories almost instantaneously. In recent years, the most effective way to deal with the raven threat has been quick removal of condor eggs for artificial incubation, a practice that has had the considerable advantages of promoting not only survival of eggs but also the production of eggs through multiple-clutching (Snyder and Hamber 1985).

SUMMARY

Analyses of the characteristics of 72 recent and historical nests of the California Condor have expanded knowledge of the relationship of condors to their nest sites. With respect to earlier conclusions of Koford (1953), the main improvements in understanding are: (1) nesting substrates are not always level at the egg position, (2) nesting substrates are commonly modified by the birds to result in eggs resting on coarse beds of gravel and other loose material, (3) eggs are not always laid between confining walls, (4) compass orientations of nest sites are random overall, but there is an apparent tendency for low elevation sites to face north and high elevation sites to face south, possibly aiding in temperature regulation but possibly only an artifact of cave availability, (6) some recent sites have been little more than overhung ledges almost completely exposed to the outside environment, and (7) not all sites are located close to roosting snags or cliffs. In general, these modifications to Koford's conclusions indicate greater flexibility in nest choices than was recognized by Koford.

At least in recent years, pairs have generally changed nest sites with each nesting attempt, regardless of whether they have failed or succeeded in the sites. Nevertheless, the majority of sites used give clear evidence of repeated use in the past, and condors rarely appear to pioneer use of new sites.

Many nests have been accessible to terrestrial predators and most have been vulnerable to raven predation. Other sites have had structural flaws, for example sloping bottoms, that have led to nesting failure. Yet no nesting territories have appeared to be deficient in sites of good quality. The frequent use of poor quality sites by the species is presently enigmatic.

Recent efforts to improve poor quality sites have included leveling of the bottoms of slope-bottomed sites, and provision of baffles to conceal incubating birds from the view of ravens flying past the nest entrances.

Most nests active in recent years have been in locations remote from human disturbance. Although the extent to which condors may avoid highly disturbed sites is difficult to determine rigorously, the current Forest Service regulations protecting nest sites appear to be fully justified, so long as there are reasonable hopes for ultimate recovery of the wild population. The long traditions of use of known nest sites strongly suggest that the same sites will continue to be attractive to the species into the indefinite future.

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LITERATURE CITED

BATSCHELET, E. 1965. Statistical methods for the analysis of problems in animal orientation and certain biological rhythms. American Institute of Biological Sciences, Washington, DC.

BETANCOURT, J. L., AND T. R. VAN DEVENDER. 1981. Holocene vegetation in Chaco Canyon, New Mexico. Science 214:656–658.

ERSKINE, A. J. 1961. Nest-site tenacity and homing in the Bufflehead. Auk 78:389–396.

FINLEY, W. L. 1906. Life history of the California Condor. Part 1. Condor 8:135–142.

HOWARD, H. 1930. A census of the Pleistocene birds of Rancho La Brea from the collections of the Los Angeles Museum. Condor 32:81–88.

KEMP, A. C. 1974. The duration of natural treehole nests. Ostrich 46:118.

KOFORD, C. B. 1953. The California Condor. National Audubon Society Research Report 4.

MOSHER, J. A., AND C. M. WHITE. 1976. Directional exposure of Golden Eagle nests. Can. Field-Nat. 90: 356–359.

MUNDY, P. J. 1982. The comparative biology of southern African vultures. Vulture Study Group, Johannesburg, South Africa.

NICOLAUS, L. K., CASSEL, J. F., CARLSON, R. B., AND C. R. GUSTAVSON. 1982. Taste-aversion conditioning of crows to control predation on eggs. Science 220: 212–214.

SAUNDERS, D. A. 1979. The availability of tree hollows for use as nest sites by White-tailed Black Cockatoos. Aust. Wildl. Res. 6:205–216.

SIBLEY, F. C. 1969. Effects of the Sespe Creek Project on the California Condor. U.S. Fish and Wildlife Service, Laurel, MD.

SNYDER, N. F. R. 1983. California Condor reproduction, past and present. Bird Conservation 1:67–86.

SNYDER, N. F. R., AND J. A. HAMBER. Replacement-clutching and annual nesting of California Condors. Condor 87:374–378.

SNYDER, N. F. R., AND E. V. JOHNSON. 1985. Photographic censusing of the 1982–1983 California Condor population. Condor 87:1–13.