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REPLACEMENT-CLUTCHING AND ANNUAL NESTING OF CALIFORNIA CONDORS

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ABSTRACT.—Observations since 1981 have conclusively documented the capacity of California Condors (*Gymnogyps californianus*) to lay replacement clutches within breeding seasons and to nest successfully on an annual basis. Deliberate encouragement of these capacities led to a better than three-fold increase in reproduction of the remnant population in 1983 and 1984.

In summarizing a wealth of data on the California Condor (*Gymnogyps californianus*), Koford (1953) found no evidence that wild pairs might lay more than a single egg in a breeding season. No clutches of more than one egg and no cases of replacement laying following egg loss had ever been documented. Koford noted (p. 85) that "if second layings occur, egg collectors should have discovered this fact long ago." In addition, he concluded that a pair of condors cannot produce more than one young every two years because of the time required to raise the young. These assertions, coupled with Koford's conclusion that individuals take at least six years to reach sexual maturity, led to a widespread perception among ornithologists that one of the major causes of endangerment of the California Condor was a remarkably limited reproductive potential. In this paper, however, we summarize recent findings on replacement clutches and annual nesting which indicate that the reproductive capacities of the species have been significantly underestimated.

RESULTS

REPLACEMENT CLUTCHES

Strong evidence that wild California Condors lay replacement clutches was first obtained in 1974 when E. Harrison and L. Kiff of the Western Foundation of Vertebrate Zoology acquired a collection of eggs that had been assembled originally by M. C. Badger, a native of Santa Paula, California (Harrison and Kiff 1980). Among the eggs was one that Badger had taken from a condor nest on 16 March 1939. Because photographs of the nest accompanied the egg, Harrison and Kiff were able to establish immediately that the nest was the same site where Harrison, Peyton, and Koford had found and photographed a condor nestling in the fall of 1939. This nestling was surprisingly young at the time of discovery (30 September) and did not reach fledging age until late fall. Clearly, two nesting attempts had been made in the same nest cave in 1939, and the most reasonable conclusion was that the same pair was involved in both, although this cannot be proved.

More recently, biologists of the Condor Research Center in Ventura, California, have documented several additional cases of replacement-clutching during intensive observations of the breeding pairs that remain in the wild population. The first of the recent cases involved a pair that nested in Santa Barbara County in 1981. Attempts to study the reproduction of this pair were hampered by poor weather and the inaccessibility of the nesting area. From late February through late March, however, the pair was observed from a distance of several kilometers repeatedly performing what appeared to be typical incubation exchanges in the vicinity of a remote canyon. On 31 March, it finally became possible for observers to get to the canyon to see the nest directly. At this point, however, the birds were no longer exhibiting typical incubation behavior, but were entering and exiting from the nest cave in a manner similar to what we have seen in other pairs that have just lost eggs. The birds left the canyon within a few days, began investigating alternative nest caves in other canyons, and finally laid an egg on about 27 April in a site approximately 11.5 km from the site they had used for their apparent first egg. This very late laying date, coupled with our discovery of eggshell fragments in the first site later in the year, strongly suggested that the 27 April egg was a replacement egg. The eggshell fragments in the first site, although apparently fresh, could not be confirmed, however, as coming from a 1981 nesting.

In 1982, we obtained conclusive evidence of replacement-clutching with a different pair. Egg-laying by the female was witnessed on 14 February. Unfortunately, the adults were not well coordinated in sharing incubation duties

TABLE 1. Replacement eggs laid by California Condor pairs.

Pair and year	Egg #	Laying date	Date egg lost or taken	Days incubation when egg lost or taken	Days until replacement egg laid	Distance (km) between nest sites
Pair #1						
1982	1	14 Feb	26 Feb[a]	12	40	0.1
	2	7 Apr	29 Apr[a]	22	none laid	—
1983	1	2 Feb	23 Feb[b]	21	35	2.9
	2	30 Mar	—[c]	—	—	—
1984	1	12 Feb	13 Feb[b]	1	28	0.8
	2	12 Mar	13 Mar[b]	1	31	0.4
	3	13 Apr	16 Apr[b]	3	none laid	—
Pair #2						
1983	1	10 Feb	8 Mar[b]	28	(31)[d]	1.1
	2	(6 Apr)	(7 Apr)[a]	(1)	(30)	0.9
	3	7 May	—	—	—	—
1984	1	7 Mar	8 Mar[b]	1	31	3.5
	2	8 Apr	10 Apr[b]	2	none laid	—
Pair #3						
1981	1	late Feb	late Mar[a]	unknown	(~1 month)	11.5
	2	27 Apr	—	—	—	—
1983	1	31 Mar	26 Apr[b]	26	none laid	—
1984	1	15 Feb	20 Feb[b]	5	27	8.2
	2	18 Mar	20 Mar[b]	2	none laid	—
Pair #4						
1984	1	12 Mar	15 Mar[b]	3	none laid	—

[a] Natural egg loss.
[b] Egg taken intentionally for artificial incubation.
[c] Second egg taken for artificial incubation on 8 April, but replaced with artificial egg for rest of incubation period.
[d] Values in parentheses are approximate.

and, on 26 February, they lost their egg over the cliff edge during a dispute over access to the egg. Forty days later, the female (clearly the same bird, based on photographic evidence) laid a second egg in another cave about 100 m distant on the same cliff.

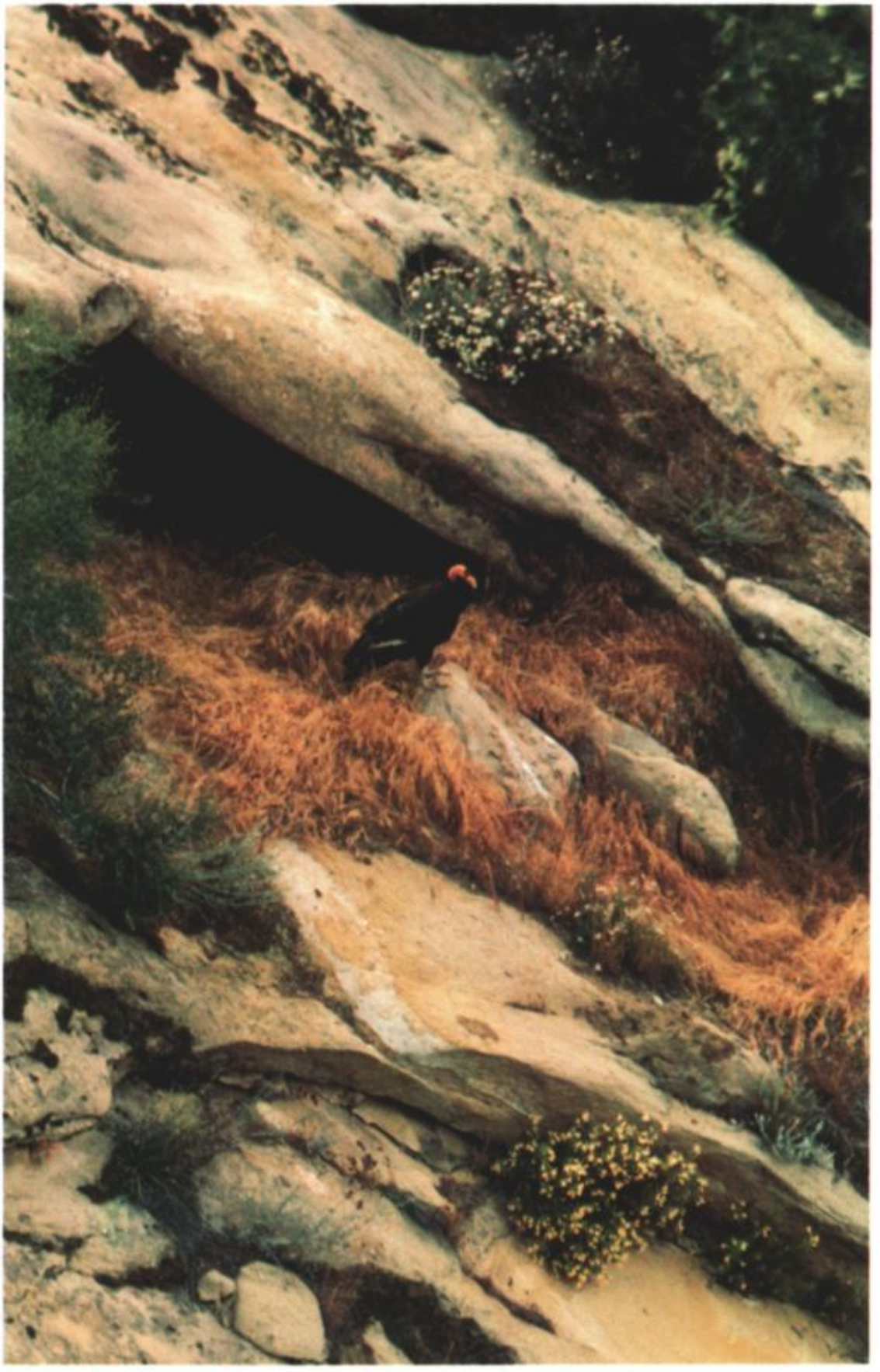
As a result of the unequivocal documentation of replacement-clutching in 1982, the California Fish and Game Commission and the U.S. Fish and Wildlife Service granted permission for the Condor Research Center biologists to attempt deliberate replacement-clutching of all condor pairs to aid in establishing a captive population. This effort resulted in three additional replacement clutches in 1983 and four more in 1984 (Table 1). Three of the four pairs from which eggs were taken laid replacements; two pairs even laid three eggs within single breeding seasons. Only one attempt to induce replacement-clutching was made with the pair that failed to lay replacements.

The interval between losing or taking of eggs and laying of replacements ranged from about 27 to 40 days, with a weak correlation between recycling time and the duration of incubation before eggs were taken ($r_s = 0.500$, $P = 0.10$, one-tailed Spearman rank correlation). In all recent cases, the birds changed nest sites to lay replacements. The distances between successive nests varied from about 100 m to about 11.5 km (mean of 3.3 km), and in only one case were successive nests in the same canyon.

The latest date for egg loss followed by a replacement egg was about 7 April, although several cases of earlier egg loss were not followed by replacements. Egg-laying in 1984 began later and ended earlier than in 1983, possibly because of unusually dry and warm weather in 1984.

ANNUAL NESTING

The first person to question Koford's conclusion that California Condors cannot nest successfully on a more frequent than biennial basis was F. Sibley, who led the U.S. Fish and Wildlife Service's condor program from 1966 through 1969. In a paper delivered at the 1970 meeting of the Cooper Ornithological Society, Sibley reported that a pair of condors in San Luis Obispo County (possibly always the same birds) nested four years in succession—1966, 1967, 1968, and 1969—and fledged a young each year. The nesting area was not checked early in the breeding seasons of 1967, 1968, and 1969, however, so it is unknown if annual nesting was concurrent with survival of fledglings from previous years. The only evidence bearing on this question was two reports of an immature condor seen within 10 km of the



nesting area in January and February of 1967. Possibly the young bird was the 1966 fledgling. In 1970, a four-day trip in mid-March by S. Wilbur and D. Carrier revealed the presence of a yearling bird with one adult in the vicinity of the nest sites, but no active nest was found. Thus, the history of the San Luis Obispo County nests provides only suggestive, not conclusive, evidence for annual nesting concurrent with survival of previous years' fledglings.

Additional suggestive evidence was obtained with a pair that was discovered with a recent fledgling in Santa Barbara County in January, 1976, by D. Smith. On 23 October 1976, a five-month-old chick was found in a nest cave in the same area and may well have been progeny of the same pair. Again, on 24 August 1977, a four-month-old chick was discovered in the same nest cave. Survival of the fledgling found in January, 1976, however, was not certain subsequent to that month, just as survival of the nestling produced in 1976 was not certain past 21 December 1976. Immature birds were sighted in the nesting region on 2 March, 8 April, 14 May, and 6 July 1977, but it is unknown if these sightings were of fledglings produced there in previous years. Moreover, it is uncertain, although it appears likely, that the same adults were involved in the successive nestings in the region.

In 1982, we observed the first well-documented case of annual nesting concurrent with survival of a fledgling from the previous year. This case involved a Ventura County pair that fledged a chick in late September, 1981. The fledgling was seen and photographed intermittently in the nesting area until as late as 19 June 1982 and in other more distant areas as late as 7 August 1982. Meanwhile, the pair (clearly including at least the same female, judging from her consistently thin eggshells over the years) laid another egg about 1 April 1982 in the same cave they had used in 1981.

A second well-documented case occurred in 1983 with a pair in Santa Barbara County. On 17 April 1982, we discovered a nest site of this pair containing a newly-hatched chick. The chick fledged on 22 September. The two adults (easily recognizable by plumage characteristics) were seen repeatedly within 5 km of the nest during the remainder of 1982. In mid-January, 1983, we began daily observations of the family. The fledgling remained closely associated with the pair into March, when the adults began treating it more and more aggressively, driving it away on many occasions. Finally, on about 31 March, the pair laid an egg in a nest cave about 11 km distant from their 1982 nest. The fledgling was last seen near the nest cave on 29 March, but was subsequently seen and photographed in a variety of localities, sometimes with its parents but usually alone or with other condors.

DISCUSSION

Recent observations suggest that replacement-clutching is normal for California Condor pairs that lose eggs early in the breeding season (February through mid-April). Because of the difficulty in traversing the terrain where condors nest, the long distances beween successive nests, and the intensive observations that are necessary to identify and follow pairs as they move from one nest site to another, it is not surprising that replacement clutches were unknown to the early egg collectors. Nevertheless, the process probably occurred regularly as a result of their activities. Since falconiform and cathartid birds in general commonly lay replacement clutches (Morrison and Walton 1980, Carpenter 1982), there is no reason to suspect that California Condors suddenly evolved the capacity to lay replacements in the last few years.

The regularity with which annual nesting occurs concurrent with survival of fledglings of previous years is still speculative. Both recent well-documented cases involved pairs that produced late eggs in years following early fledgings. Available data from pairs studied since 1980 suggest that fledglings are strongly dependent on adults until about six months beyond fledging. During this period, parent birds appear to be inhibited from laying eggs. We do not know whether annual nesting can occur in a year following a relatively late fledging. Annual nesting clearly is not an invariable occurrence, since one closely-studied pair in Ventura County attended a strongly dependent young during the spring months of 1980 and did not lay during that year. Judging from the clumsiness of this immature bird, it may well have fledged late in 1979. Similarly, we obtained no evidence of egg-laying in 1981 by a pair that fledged a young in November, 1980, although this pair was not followed as closely as the previous pair. No additional opportunities to study the incidence of annual nesting have been available in recent years.

We think it reasonable to postulate a max-

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FIGURE 1. Adult condor at nest cave used in 1981 and 1982 for first conclusively-documented case of annual nesting concurrent with survival of a previous year's fledgling. The same cave was used for the last of three eggs laid by the pair in 1983. Photograph by H. Snyder.

imum potential production of two naturally-fledged young in every three years for successful pairs: an early fledgling the first year, followed by a late fledgling the next year, and no fledgling the third year. Thus, to the extent that wild pairs are intentionally double- or triple-clutched to increase net reproduction, and to the extent that they are allowed to fledge young from their last-laid eggs, it appears unlikely that annual nesting will occur. Presumably, maximal productivity of the wild pairs, involving both multiple clutching and annual nesting, can be achieved only if natural fledgings of young are avoided. This can be achieved either by taking all eggs for artificial rearing or by taking into captivity all nestlings raised in the wild from last eggs.

In recent years, the total natural production of the wild condor population has averaged about two fledglings annually (Snyder 1983; Snyder et al., unpubl. data). Under a regime of multiple clutching and annual nesting, the 1983 and 1984 totals were six and seven fledglings, respectively. Thus, artificially-induced multiple clutching and annual nesting offer a demonstrated potential for increasing reproduction of the remnant population several-fold over what occurs naturally.

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