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Survival and Reproduction of California Condors Released in Arizona

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ABSTRACT.—A drastic decline in California Condors (Cymnogyps californianus) resulted in their complete removal from the wild in the 1980s and subsequent establishment of captive populations to propagate offspring for reintroductions. In 1996 The Peregrine Fund began releasing captive-raised condors in the Grand Canyon region of northern Arizona. By July 2005, 77 juvenile or immature condors had been released, 26 (34%) of which had died. Eight condors perished in their first 90 days following release and 14 in total during their first year in the wild (survival rate of 79.6% as determined by days of exposure). Survivorship increased to 89.5% for condors in the second through fourth years following release, and to 97.8% from the fifth year onward. Lead poisoning from ingested shotgun pellets and bullet fragments was the greatest cause of fatalities for birds after their first 90 days free-flying, with six birds known and two suspected to have died from lead toxicity. Many surviving condors were also treated with chelation therapy at least once to reduce high blood lead levels. Under a program of intensive management, survival rates were in the range expected for wild condors, and as of December 2005 the released population had aged to include 14 adults which had laid 11 eggs and fledged 5 young. Self-sustainability, however, will require that lead in the condors' food supply be greatly reduced or eliminated.

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The ranges of the two largest extant cathartids, the Andean Condor (*Vultur gryphus*) and the slightly smaller California Condor (*Gymnogyps californianus*), have contracted greatly in historical times, and the California Condor is critically endangered (BirdLife International 2000). Few California Condors remained by the time Koford (1953) undertook the first concerted effort to study them and little is known conclusively regarding their natural mortality, whether they ever occurred at high densities, or what factors limited their numbers in the past. It is certain, however, that human-related factors, including shooting, poisoning, and encroachment into breeding and foraging areas were associated with a precipitous population decline in the last two centuries (Koford 1953; Wilbur 1973, 1978; Kiff 2000; Snyder and Snyder 2000; Fry and Maurer 2003; Snyder this volume).

In the 1980s all remaining condors were brought into captivity, and captive breeding populations were established, with the ultimate goal of restoring wild populations (see Kiff 2000, Snyder and Snyder 2000). Reintroductions began in 1992, when two condors were released at the Sespe Condor Sanctuary in southern California. Since then the magnitude of the release program has grown, and more than 100 condors now fly freely in southern and central California, northern Arizona and southern Utah, and Baja California, Mexico.

Condors seem always to have occurred in landscapes that included rugged or otherwise inaccessible terrain for nesting, open areas that allowed for extended soaring flight, and an adequate supply of medium and large mammalian carcasses. California Condors ranged across North America in prehistoric times, and formerly bred in northern Arizona along the Colorado River in what is now Grand Canyon National Park (Miller 1960, Emslie 1987). Big birds require big country, and habitat in the canyonlands of northern Arizona and southern Utah appears suitable for condor recovery because it contains extensive rugged terrain with abundant potential nesting cliffs, open areas, strong updrafts, large ungulate populations, and relatively limited human disturbance (Rea 1981).

Since 1996, condors have been released in northern Arizona along escarpments 85 to 150 km north of Grand Canyon National Park as a "nonessential experimental" population under provisions of Section 10(j) of the Endangered Species Act. As of July 2005, 50 juvenile (less than one year of age) and 27 immature (one to six years of age) condors have been released, 26 of which have died. Now, as birds from the earliest-released cohorts have begun to breed and eventual population sustainability can be contemplated, a review of mortality factors for the released birds is timely. Meretsky et al. (2000) summarized early, unpublished reports on mortality for condors in both Arizona and California; here we update and examine the factors that have led to condor deaths specifically in Arizona and Utah, and provide estimates of survival for different age groups.

Methods

California Condors were released in groups of two to eight individuals (three birds were also released singly) at two sites in northern Arizona: a primary site at Vermilion Cliffs, Coconino Co., (release years: 1996, 1997, 2000 onward; Fig. 1) and an alternate one at Hurricane Cliffs, Mohave Co., (release years: 1998, 1999; see Harting et al. [1995] and Johnson and Garrison [1996] for site description and release protocol). Condors to be released were always first maintained together at the site. Prior to 2000, condors were generally held for four to six weeks in a release pen at the cliff edge before release (Plate 7). From 2000 onward, pre-release birds were usually held in a large flight pen set back from the cliff for weeks to months before being moved to the release pen, from which they were released after a week or so. After the first release, free-flying condors had access to the exterior of the pen(s) and sometimes interacted with the pre-release birds. Interactions with humans were kept to a minimum. Nearly half (49%) of all condors were released in November or December, and 65% were less than one year old when released, having hatched the previous March, April, or May (Table 1). Four captive-reared adult condors were released experimentally in December 2000, but two quickly perished and the remaining two were consequently retrapped (see Results for further details). Owing to the unique nature and short duration of those releases, data from those birds were not included in any analyses in this paper except where stated explicitly. The earliest releases typically consisted of cohorts of six or more condors released together, although this protocol was replaced in 2002 by successive releases of birds in smaller cohorts. Condors released in Arizona were captive-reared at three facilities: 53 birds were reared at The Peregrine Fund's World Center for Birds of Prey in Boise, Idaho; 12 at the Los Angeles Zoo; and 12 at the San Diego Wild Animal Park. Five wild-reared young



Fig. 1. Condor release site at the Vermilion Cliffs, Arizona, as seen from the southwest. (Photo by C. N. Parish.)

Release date	Condors released (n)	Mean age at release (days ± SD)	No. free-flying in July 2005	
12 Dec 1996	6	205 ± 9	3	
14 May 1997	4	771 ± 13	$\overset{\circ}{2}$	
26 May 1997	5	760 ± 19	4	
20 Nov 1997	4	211 ± 16	2	
18 Nov 1998	9 ^a	215 ± 22	23	
6 Dec 1999	7 ^b	246 ± 26	3	
29 Dec 2000	8 c	$243 \pm 10^{\rm d}$	5 6 e	
16 Feb 2002	6	289 ± 14	3	
25 Sep 2002	3	500 ± 4	2	
9 Dec 2002	2	592 ± 13	2	
3 Mar 2003	3	315 ± 9	3	
4 Oct 2003	2	532 ± 2	$\frac{3}{2}$	
29 Nov 2003	2	580 ± 5	$\frac{2}{2}$	
9 Jan 2004	1	614	1	
20 Mar 2004	4	338 ± 5	3	
16 Oct 2004	3	559 ± 10	3	
í Feb 2005	3	651 ± 15	3	
1 Mar 2005	5	298 ± 20	4	
Overall	77	394 ± 205	50	

Table 1. Release dates and numbers of California Condors released in northern Arizona between December 1996 and July 2005. All releases except those in 1998 and 1999 were at the Vermilion Cliff release site in Coconino County.

^aOne bird was released singly on 23 Nov 1998. That bird was 965 days old, and is not included in average age calculation for this release.

^bOne bird was released singly on 23 Dec 1999.

^cFour adults were also released about this time: one pair on 7 Dec 2000 and the second pair on 19 Dec 2000. These were not included in average age calculation for this release (see text for details).

^dNot included in average age calculation for this release is one 586-day-old condor.

^eOne bird from this cohort was permanently removed from the free-flying population.

also fledged in Arizona; data from those condors, one of which later died, were not included in analyses in this paper.

All released condors were fitted with a redundant system of two radio transmitters, usually consisting of paired patagial transmitters although for a few the second transmitter was tail-mounted (Wallace et al. 1980, Meretsky and Snyder 1992). All transmitters are presently equipped with a fatality sensor, although this was not the case for birds from the earliest releases, for which death was initially inferred from lack of variation in signal strength or direction. More recently some condors have also carried GPS satellite transmitters. All birds were given large numbered patagial tags for visual identification. Condors have been monitored continually since the initial release in 1996 using radio telemetry and visual

confirmation of individual identity. Whenever possible, birds have been located daily and, consequently, field data have confirmed to within a day or so the date of most deaths. For four birds that disappeared and were presumed to have perished, however, the last day of radio contact was used as the day of death, although those birds could conceivably have lived for weeks or months thereafter.

Carcasses of dead condors were removed from the field and chilled as quickly as conditions permitted, and then shipped to the San Diego Zoo, in California, where necropsies were performed. Two exceptions occurred in which law enforcement agencies were involved and took possession of the carcasses. Diagnosis of lead poisoning was based on toxicological analyses routinely performed for each fatality at the San Diego Zoo and by the presence of lead bullet fragments or shotgun pellets in some poisoned birds (determined by radiograph and/or necropsy). One condor whose carcass was unrecoverable but whose death coincided with a widespread lead-poisoning event was assumed to have succumbed to lead toxicity (see Results). Fatalities ascribed to Golden Eagles (Aquila chrysaetos), whether resulting from aggressive interactions or predation, were characterized by partially plucked carcasses, puncture wounds about the head consistent with large talons, and field observations of eagles in the vicinity. Deaths attributed to covote (Canis latrans) predation were characterized by partially consumed carcasses, chewed feathers, fresh coyote tracks, and scat in the immediate area. Signs of struggle distinguished predation by covotes from scavenging.

Because the daily fates of all members of the population were almost always known, survivorship of released birds could be determined precisely using days of exposure. For each bird, the day of first release was considered exposure day 1, and each subsequent day during which the bird was free-flying for any part of the day was considered an exposure day. All birds were periodically captured and re-released owing to concerns about transmitters, health, behavior, or to test for lead exposure. Complete days during which an individual was in captivity were not counted as exposure, although days of exposure were otherwise cumulative in regard to the time a condor was free-flying following its initial release. Nearly two-thirds (64%) of the birds were captive for less than 100 days in total following their release. Twenty-eight individuals, however, were held for longer than 100 days, and seven of those were held for one to three years and are thus substantially older than the number of days free-flying suggests.

To evaluate survivorship, we partitioned the number of exposure days into five stages based on annual benchmarks and our observations of apparent differences in survival rates. The stages were: initial release (the first 90 exposure days following release); remainder of the first year (91 to 365 exposure days post-release); second year (366 to 730 exposure days post-release); third through fourth years (731 to 1,460 exposure days

post-release); and the fifth year onward $(1,461 + \exp osure days post$ release). We determined daily, exposure stage, and annual survivorship $based on Trent and Rongstad (1974), where daily survival rate (<math>\hat{S}$) was calculated as the total number of exposure days within any stage, minus the number of days in the stage during which a death occurred, divided by the total number of exposure days in the stage. Survivorship throughout specific stages was \hat{S}^n , where *n* was the number of calendar days in each particular stage.

To gain an indication of what survival in the released population might have been without intensive management and chelation treatments to reduce acute blood lead levels (see Parish et al. this volume for methods), we also recalculated survival under two hypothetical scenarios: (1) all birds that were found to have blood levels of lead greater than 250 µg dL⁻¹ died on the date of detection, and (2) all those with lead levels above 100 µg dL⁻¹ died. For each situation, we used a standard growth rate calculation developed by Hunt (2002) to determine lambda (λ) values, which depict the direction and strength of population trajectories. For growth rate calculations, we used our calculated survival in the first year following release as a substitute for juvenile (first year) survival, our calculated survival in the second through fourth years free-flying as a substitute for immature survival, and our calculated survival from the fifth year free-flying onward to represent adult survival. We used hypothetical reproductive parameters determined by Meretsky et al. (2000).

We used chi-square analyses to evaluate differences in the number of condors that survived based on sex, rearing method (parent- vs. puppetreared), and age when released (more or less than one year old at release). Because many condors died in the first year following their release (see Results), we also repeated those analyses but tested specifically for differences in the number of condors that survived their first year free-flying. Data for all chi-square analyses included only condors released before July 2004 (65 in total), as the more recently released birds had not yet spent a full year free-flying. Also excluded was a single bird permanently removed from the free-flying population, since it was removed less than one year after its release.

For condors that bred, the date at which egg-laying occurred was determined by changes in behavior of the adult birds, including periodic incubation exchanges at nest sites. Behavioral changes that characterized hatching, including the sudden onset of daily nest exchanges by the adults, were also used to determine laying dates, assuming an average incubation period of 57 days (Snyder and Snyder 2000). Nest sites with young were monitored carefully as the date of fledging approached, and the date and time of fledging were determined by direct observation. Where possible, nest sites were entered for close examination after the breeding effort ended.

Unless otherwise noted, all statistics are in the form of mean \pm SD. The levels of lead in condors are frequently expressed in µg dL⁻¹ when measured in blood and ppm when measured in the liver, and we follow those conventions here. The two measurements are easily converted, however, since 1 ppm equals 100 µg dL⁻¹.

RESULTS

Survivorship overview.—As of July 2005, 77 young condors (43 males and 34 females) had been released in northern Arizona: 61 at the Vermilion Cliffs site and 16 at the Hurricane Cliffs site (Table 1). Of the released birds, 50 (65%) were released when less than one year of age (average age = 255 ± 46 days; range = 172-345) and 27 (35%) were released at ages ranging from 494 to 965 days (average age = 651 ± 116 days). The average age at release for all 77 birds was 394 ± 205 days. Twenty-six of the released birds died, one was removed from the free-flying population, and 50 remained in the wild in July 2005. Not included in the number of released birds or deaths are four adult birds (two breeding pairs eight to nine years old) that were released as an experimental effort to include breeders with other released birds. Coyotes killed two of the adults shortly after release (19 and 22 days), probably as a result of unsafe roosting behavior, and the other two were recaptured and permanently removed

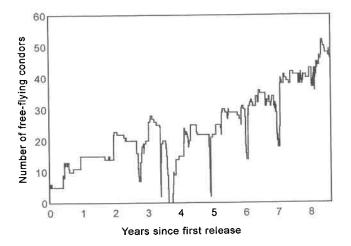


Fig. 2. Number of free-flying California Condors in northern Arizona since the first cohort was released in December 1996. Reductions in the population occurred when birds were captured and held temporarily for behavioral or health reasons. The population went to zero from mid-July through mid-August 2000 when all birds were held during a lead poisoning incident (see text).

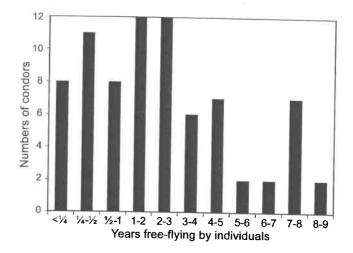


Fig. 3. Years free-flying by 77 California Condors released in northern Arizona between December 1996 and July 2005.

from the free-flying population. Since the first release in 1996, the number of birds in the wild generally increased over time, to a temporary maximum of 52 in March 2005 (Fig. 2). As of July 2005, 42 (55%) of the released birds were free-flying for 1.5 years or longer (Fig. 3), and individuals averaged 2.7 ± 2.5 years (n = 77; range = 4 days-8.2 years) in the wild.

The likelihood of survival did not differ significantly based on sex of the released birds, whether considering survival through the first year free-flying or overall ($\chi^2 = 0.84$, df = 1, P = 0.526; $\chi^2 = 0.06$, df = 1, P = 0.802, respectively). Survival also did not differ significantly based on rearing method (first year free-flying: $\chi^2 = 0.08$, df = 1, P = 0.772; overall: $\chi^2 = 0.15$, df = 1, P = 0.694). In contrast, individuals that were greater than one year of age when released were significantly more likely to survive than individuals that were released when less than one year old. Of 21 birds released when more than one year old, one (5%) perished in its first year free-flying, compared to 12 of 44 birds (27%) released when younger than one year of age ($\chi^2 = 4.94$, df = 1, P = 0.026). Overall, four of 21 birds (19%) released when greater than one year old ($\chi^2 = 4.50$, df = 1, P = 0.034).

We documented 75,053 exposure days in total, including 22,391 (77 birds) in the first year and 16,640 (20 birds) from the fifth year onward (Table 2). Annual survival through the first year, 79.6%, was heavily influenced by relatively high mortality of recently released birds; of the 14 that perished during their first year, eight died within the first three months. The likelihood of survival increased to 89.3% in the second year and 89.6% in the third and fourth years combined (89.5% for the second through fourth

Stage ^a	Condors (n)	Exposure days	No. of deaths	Survivorship (%)		
				Daily	Stage	Annual
Initial release*	77	6,519	8	99.877	89.5	
Remain. 1st year ^b	69	15,872	6	99.962	90.1	
Combined 1st year	77	22,391	14	99.937		79.6
2nd year	50	16,069	5	99.969		89.3
3rd and 4th year	38	19,953	6	99.970	22	89.6
5th year onwards	$\frac{30}{20}$	16,640	1	99.994		97.8
Overall	77	75,053	26	99.965	2	88.1

Table 2. Survivorship based on exposure days for 77 California Condors released in northern Arizona, December 1996 through July 2005.

^aInitial release is the first 90 days following release.

^bRemain. 1st year is the remainder of first year following release (see text for further details).

years). Survival from the fifth year onward was 97.8%. Fatalities occurred sporadically throughout the release program, with the exception of four deaths in June 2000, but condor deaths were rare following four years in the wild, and by July 2005 only one bird that had been free-flying for longer than four years had perished.

Given the rates of survival found in our study, and assuming a population with a stable age distribution and a conservative reproductive rate of 0.25 for breeding age females (e.g., 50% of females breed per year with 50% breeding success), the Arizona population would be expected to grow at the rate of 2.6% per year (i.e., $\lambda = 1.026$). If the reproductive rate increased to 0.33 per year, the annual growth rate would rise to 3.7%. If, on the other hand, there were no management for lead exposure, and one assumed that all condors with acute blood levels of lead above $250~\mu g~dL^{-1}$ died, resulting in an additional nine deaths, immature and adult survival would have been 81.7% and 90.9% respectively (juvenile survival would have been unaffected), and the population would have declined at 2.8% per year. With the more stringent assumption that lead levels in blood greater than 100 µg dL⁻¹ were always lethal, resulting in seven deaths in addition to the nine previously mentioned, immature and adult survival would have been 72.4% and 76.9% respectively (again, there would have been no affect on juvenile survival), and the population would have declined at the greater rate of 18.6% per year.

Sources of mortality.—Fourteen condors perished in the first year following their release, mainly from predation or other experience-related factors (Table 3). Amongst those 14 deaths, predators (coyotes and Golden Eagles) killed four and possibly five condors, three birds disappeared and are

Source of mortality	Sex free-flying	Days	Age at death (days)	Month/year of death
Deaths during first	year free-flyi	ing		
Coyote	M	4	284	02/2002
Eagle	Μ	24	225	01/1997
Coyote	М	37	271	12/1998
Poor Condition ^a	Μ	39	326	04/2005
Septicemia ^b	Μ	40	256	01/2000
Poor Condition ^a	\mathbf{F}	43	287	02/2001
Eagle	F	60	317	02/2000
Unknown-lost	F	62	817	07/1997
Unknown–lost	F	120	333	04/2000
Powerline	F	158	350	05/1997
Unknown–lost	F	173	509	09/2004
Lead	Μ	177	487	08/2002
Shot	Μ	242	508	10/2002
Coyote suspected		318	501	10/1998
Deaths after first ye	ar free-flying	5		
Lead	F	522	768	06/2000
Lead suspected	Μ	524	810	06/2000
Eagle	\mathbf{F}	537	880	09/2000
Shot	Μ	542	1,599	08/2002
Shot	\mathbf{F}	609	1,436	03/1999
Lead	Μ	816	1,355	01/2005
Lead	Μ	932	1,149	06/2000
Unknown ^c	Μ	1,021	1,634	09/2003
Lead	Μ	1,024	1,785	03/2000
Lead suspected	F	1,263	1,491	06/2000
Lead	\mathbf{F}	1,345	1,700	01/2005
Unknown-lost	F	1,696	2,155	02/2004

Table 3. Causes of death for 26 California condors released in northern Arizona between December 1996 and July 2005. Birds are ranked by the number of days free-flying prior to death.

^a Poor body condition of unknown cause led to starvation-like deaths in these birds (see text for further details).

^b Septicemia resulted from airsacculitis owing to aspiration.

^c Cause of death undetermined by necropsy.

presumed to have perished, and two succumbed to starvation-like poor body condition resulting from an unknown cause or causes. In each case where coyotes appeared to kill a condor, the bird had roosted in a location that was accessible to coyotes. It is unknown whether poor body condition or other factors increased the susceptibility to predation of birds whose deaths were attributed to coyotes, but one bird appeared healthy and vigorous when captured by field personnel eight days prior to its death and another was killed

after only four days in the wild. Necropsy could not determine or explain what led to the poor body condition apparent in the birds that died with starvation-like symptoms, especially considering that each had been in the wild for only a few weeks and had been seen feeding at the release site during that time (lead poisoning was not implicated in either death).

Twelve condors that had been free-flying for more than one year died, and the single greatest contributor to mortality was lead toxicity, to which seven of those birds were known (5) or suspected (2) to have succumbed. Two of the other five condors that died were shot, one by a hiker who killed the condor with a small caliber handgun in Grand Canyon National Park, and another that was shot with an arrow in the Kaibab National Forest.

At least four confirmed or suspected lead toxicity deaths and many chelations were associated with episodes characterized by multiple poisonings, but two or three birds that died of lead poisoning did so in what appeared to be isolated events. The source of lead was identified in four deaths: three involved shotgun pellets and the fourth followed the ingestion of bullet fragments. Additionally, 10 non-lethal exposures occurred in which the source of lead was identified: six involved bullet fragments and four involved shotgun pellets.

The first lead poisoning death occurred in March 2000, and the first known multiple poisoning occurred in June of that year. Within a four week period beginning in June 2000, at least two and as many as four birds perished from lead toxicity, and nine others with high lead levels received chelation therapy. The first of those fatalities occurred early in June, but the carcass had deteriorated by the time of recovery and necropsy was inconclusive. The second death occurred on 12 June and followed the ingestion of at least 17 lead shotgun pellets of two or more different sizes (as determined by radiograph). A third condor died on 16 June and had a lead level in the liver after death (17 ppm) that strongly suggested the bird succumbed to lead poisoning. In contrast to the other poisoned birds, however, it was also severely emaciated when captured on the day prior to its death and had a high copper level in the liver after death (181 ppm); these factors, as well as a lack of lead shot visible on radiographs, suggest that it may have been poisoned in an unrelated incident. The cause of the fourth fatality on 25 June was unknown because the carcass was unrecoverable, but the timing of this bird's death suggested lead poisoning. Evidence indicates that most if not all of the lethal and non-lethal poisonings were associated with shotgun pellets, owing to both the temporal proximity of the poisonings and the fact that shot of three different sizes was found in five of the poisoned birds. It is unlikely that groups of condors would encounter and consume enough carcasses of the smaller animals usually hunted with shotguns to explain the number of poisoned birds. Consequently, we suspect that the exposure occurred

at a single large carcass or many closely-spaced smaller ones, which were loaded with shot of varying sizes.

Large-scale lead exposure episodes also occurred during and just after the local November hunting seasons in 2002 and 2004 (Parish et al. this volume). During November many mule deer (*Odocoileus hemionus*) are killed by hunters on the Kaibab Plateau, which is heavily used by condors for foraging during fall (Hunt et al. this volume; Plate 7). No birds died, and bullet fragments appeared on radiographs of only two poisoned birds during the two episodes combined, but in each episode approximately 35 to 40% of the free-flying population (2002: 11 birds; 2004: 17 birds) received chelation therapy in response to blood lead levels that ranged from 50 to 900 μ g dL⁻¹.

The episodic pattern of wide-scale poisonings, as well as the seemingly sudden onset of lead exposures within the population, was highlighted by the fact that no bird perished or required chelation in the first 18,000 exposure days of the release program, and only a single chelation treatment was necessary in over 15,500 exposure days between August 2000 and August 2002. In the years following the first poisoning episode, however, blood lead levels determined during semi-annual and opportunistic testing frequently were above the expected background levels of 20 μ g dL⁻¹. Furthermore, nearly all the older birds in the population have been exposed to high lead levels since 2002, and most have received chelation therapy at least once (Parish et al. this volume).

Reproduction.—The first breeding attempt in the new Arizona population occurred in 2001, when a six-year-old male courted two six-year-old females, one of which laid an egg that was broken shortly afterward. In the years since, at least nine adults (five females, four males) attempted to breed (including courtship, nest selection, and egg laying), and all six tenyear-olds—the oldest cohort in the population—had produced one or more fledglings by the end of 2005. The average age at which the nine confirmed breeders first attempted to breed (i.e., the first time an egg was laid by the female in a pair) was 7.6 ± 1.3 years, but two birds attempted to breed at six years of age and another did not breed until its tenth year.

The population in July 2005 included 14 condors seven years of age or older, five of which were not confirmed breeders. Four of those five were males, however, and thus three lacked available mates (Fig. 4). Breeding pairs nested at seven different sites: four in Grand Canyon National Park (e.g., Fig. 5), two in Vermilion Cliffs National Monument, and one in the Kaibab National Forest. One site was used three times, two sites twice, and four sites were used only once. Early pair formation was sometimes equivocal—three or more birds were associated with two nesting attempts, and one male bred with at least two females in successive years. Two established pairs, however, have not switched mates in three breeding attempts each over four years and as of December 2005 remain paired.

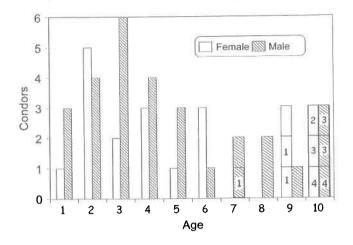


Fig. 4. Age structure of free-flying released condors in northern Arizona as of July 2005. Numerals within bars indicate the number of times an individual bred or attempted to breed between 2001 and 2005.



Frg. 5. Nest cave on the west face of The Battleship, Grand Canyon National Park, Arizona. An established condor pair bred at the site in 2002, 2003, and 2004, successfully producing one fledgling condor in 2004. (Photo by C. N. Parish.)

Overall, at least 11 eggs were laid, five of which were known to hatch, and five condors fledged successfully. Success for nesting attempts from 2001 through 2005 was thus 45% (5 fledglings produced from 11 eggs laid), but pairs typically failed in their first breeding attempts, and consequently success generally improved over time. Nesting success in

2001 through 2003 was 17% (one of six nests), but was 80% (four of five nests) for 2004 and 2005. The dates at which eggs were laid varied widely, the earliest being 21–22 February and the latest 7–10 April, but at least six and as many as eight eggs were laid in March. All eggs that hatched did so between 3–5 May and 4–5 June. The earliest bird to leave the nest site fledged on 5 November (at 184–186 days of age) and the latest on 23 December (at 202–203 days of age); the others fledged on 23 November (at 195–196 days of age), 25 November (at 186–187 days of age), and 30 November (at 185–187 days of age).

DISCUSSION

Impact of natural predators.—The natural predation rate on wild condors is unknown, but as for most vultures it was probably always very low, especially for adults (for example, see Mundy et al. 1992). Few predators have been identified that prey on free-flying condors, and although harassment and/or predation by Golden Eagles and Common Ravens (*Corvus corax*) may impact egg and nestling survival, condor mortality has been mostly attributed to human-induced causes (Koford 1953, Snyder and Snyder 2000). Our data support the notion that immature and adult condors are rarely killed by predators other than humans, since only a single fatality was attributed to predation in more than 52,000 exposure days for birds that have been in the wild longer than 1 year, and moreover that death was of a two-year-old condor.

The same was not true for newly-released birds, however, as predation by coyotes or Golden Eagles accounted for the deaths of four or more birds in their first year free-flying. Black-backed jackals (Canis mesomelas), which compete for food with vultures, are known to kill juvenile African Whitebacked Vultures (Gyps africanus), and red foxes (Vulpes vulpes) sometimes kill recently fledged Egyptian Vultures (Neophron percnopterus; Mundy et al. 1992). Coyotes specifically appeared responsible for half or more of the eight actual predator-caused deaths (including the two adults released and killed in 2000), suggesting that in Arizona coyote predation could become a significant contributor to mortality of newly-released condors that do not roost in appropriate locations. There is no historical evidence to indicate that coyotes were a cause of condor fatalities in the past, but young condors in historical populations presumably benefited by observing the behavior of adult birds, an opportunity that was lacking early in the Arizona release program. Moreover, the coyote population may be artificially increased in the vicinity of the release site as a result of readily available carcasses placed for the condors, thus exacerbating the potential for predation. No newlyreleased condors have been preyed upon, however, since March 2002 when a program of hazing new birds to safe roost spots was instituted.

Human causes of condor deaths.—In modern times, condors and vultures must contend with hazards for which they are perhaps ill-equipped through their evolution (Mendelssohn and Leshem 1983). Collision with power transmission lines and electrocution, for example, have emerged as global threats to vultures (e.g., Mundy et al. 1992, Sarrazin et al. 1994, van Rooyen 2000), and at least nine condors have perished in California as a result of power line collisions. Only one condor died in a similar collision in Arizona during our study, and the lower frequency is probably related to the scarcity of power lines in the vicinity of the release sites (Harting et al. 1995). Releases in Arizona, however, also followed the onset of aversion training to utility poles in 1995. Shooting was also a prominent source of mortality for condors in the past (Wilbur 1978, Snyder and Snyder 2000, Snyder this volume), and the fact that at least three condors were shot in Arizona during our study reflects the continuation of this unfortunate human habit.

Factors influencing survival of newly-released condors.—The success of any species reintroduction is dependent in part on survival of the young animals that are produced or released. In Arizona, the increased vulnerability of some newly-released condors could be due to differences between birds captive-reared by different methods and released at different ages. Puppet-rearing, for example, is an efficient technique used in the captive breeding of many rare birds slated for future release, because excess young can be produced in the absence of adults to rear them (Cade and Fyfe 1978, Wallace 1994). The technique can be counter-productive, however, if puppet-reared birds die at a substantially higher rate than parent-reared or wild-reared offspring. Superficially, puppet-reared birds may be assumed to be less behaviorally adept than those reared by parents, especially for social birds that are slow to mature, but our data do not support that assumption, at least for condors reared in captivity, since there was no apparent difference in mortality between those that were puppet-reared and those that were parent-reared.

The advantages and disadvantages of releasing birds at an early age are also equivocal for long-lived birds that require an extended period of maturation. Increased maturity during additional time spent in captivity prior to release could result, for example, in acclimation to captivity and a reduction in age-appropriate behavior on release. On the other hand, young birds released prematurely might lack wariness or other behavioral attributes necessary for survival, some of which may be innate and slow to develop. In Arizona, 95% first-year survival of birds released when greater than one year of age, compared to 73% for birds released at less than one year old, strongly indicates that older birds benefited from increased maturity prior to release, even in the absence of free-ranging experience in the wild. This finding has important implications for managing the release of

young condors and perhaps other species with life histories that include long periods of juvenile dependence and maturation.

Adult survival.—For long-lived animals with low reproductive rates and few natural predators, breeding success or the survival of young birds are not as critical to the stability of populations as adult survival, since even in the best of times slow breeding rates place a higher premium on longevity than fecundity (cf. Mertz 1971). Thus, populations of long-lived birds are generally characterized by both low adult mortality and a relatively small proportion of immatures (e.g., Houston 1974, Weimerskirch et al. 1987). although not necessarily in newly reestablished populations (Blanco and Martínez 1996, Blanco et al. 1997). Verner (1978) and Meretsky et al. (2000) modeled hypothetical cases of condor mortality, and both generally concluded that annual survival for adults and immatures must exceed 90% to maintain population stability (Verner: 91% adult and 89% immature; Meretsky et al.: 90.1% for both adult and immature), and that adult survival should approach 95% annually to compensate for immature survival of about 85%. In Arizona, where immature condors currently outnumber adults, survival of 89.5% for birds in their second through fourth years free-flying has thus met those immature survival requirements. Because there are still relatively few adults in the population, the long-term adult survival rate remains speculative, but it is promising that none of the 14 condors to reach adulthood has perished, and that survival has approached 98% for all birds free-flying for more than four years.

Reproduction and population growth.-Given the current rates of survival and reproduction, can this population become self-sustaining or grow without supplementation as long as management of the lead exposure problem continues? A near-term increase in the number of breeding pairs is complicated by the shortage of unpaired adult females (Fig. 4). Two or three additional females should, however, become potential breeders in 2006 or 2007, and barring unanticipated catastrophes there could be at least 15 adult females and 20 or more adult males in the population within five years due to natural aging of individuals. Not all adults in the Arizona population will necessarily breed, but so far most with the opportunity to breed have done so. Moreover, nesting success improved as pairs became established, and success for established pairs presently lies in the range proposed for wild condors historically (estimates range from 22 to 56% prior to 1980, and 41 to 47% in the 1980s; Snyder and Snyder 2000). It remains speculative whether these rates are adequate for population stability or growth, but they appear to be when compared to hypothetical models of California Condor demography (Meretsky et al. 2000), as well as data on colonial Griffon Vultures (Gyps fulvus) in France (Sarrazin et al. 1994), and several solitary-breeding Old World vultures (Mundy 1982).

Lead poisoning and its consequences .- Poisoning by various means is a ubiquitous contemporary threat to adult vultures and condors (e.g., Mendelssohn and Leshem 1983, Janssen et al. 1986, Mundy et al. 1992, Mundy 2000), and lead contamination is the primary concern for longterm viability of modern California Condor populations (Wiemeyer et al. 1988. Pattee et al. 1990. Kiff 2000, Meretsky et al. 2000, Snyder and Snyder 2000, Fry and Maurer 2003, Cade et al. 2004). Because condors are gregarious and efficient scavengers that feed principally, although not exclusively, on medium and large mammalian carcasses, they are particularly vulnerable to lead poisoning when animals are shot and carcasses are not recovered or viscera are left. Lack of recovery may arise from unintended hunter loss or shooting activities that place little emphasis on carcass recovery, including poaching big game for trophy mounts, shooting covotes and other predators, and killing jackrabbits (Lepus spp.), ground squirrels (Spermophilus spp.), and other small animals. Consequently, as long as lead ammunition is used by hunters and shooters in regions where condors and other scavenging animals live, wildlife will continue to be inadvertently killed by lead poisoning.

Meretsky et al. (2000) suggested that lead in general, and lead bullets in particular, are a pervasive component of the contemporary environment, with patterns of contamination and rates of exposure that make the reintroduction of condors untenable at present. We agree that lead contamination has hindered and will continue to hinder condor restoration, especially considering that lead poisoning was the only verified cause of mortality for adult or immature birds after their first two years in the wild. Moreover, although annual survival was nearly 98% for condors that had been freeflying for more than four years, that value does not represent expected survival of those condors in the absence of management for lead poisoning, as all of them received chelation therapy one or more times, and some might have perished otherwise. How many might have died? Acute lead levels greater than 100 μ g dL⁻¹ in blood indicate that a condor's physiology has been compromised, but they are not necessarily lethal. Crop stasis and other complications resulting in death can, however, occur at blood lead levels in the range of 250 µg dL⁻¹ or more (Fry and Maurer 2003). Without intervention, adult survival might therefore have been 90% or less during our study, and perhaps one third or more of the current adult population could have been lost. Thus, although our data suggest that lead poisoning should not prevent the establishment of a condor population in Arizona that is stable or able to grow in numbers, the population will require continued monitoring of lead levels in blood and chelation therapy when lead poisonings occur.

Conclusions.—For long-term survival and self-sufficiency of condors in Arizona, the lead that they encounter must be reduced or eliminated, because as the population grows and expands its range, intensive

management of individual birds will become increasingly difficult and costly. To that end, several factors critical in understanding the risks of lead require further study. The pattern of lead encounters that has so far emerged in Arizona includes intermittent but widespread episodes that have resulted in the poisoning of multiple birds, superimposed on a persistent background of individual poisonings. Identifying the sources of lead that have caused those poisonings is essential to safeguard Arizona's condors. The shotgun pellet-related poisonings in June 2000 were enigmatic, and it is possible that an inadvertent or unique shooting event led to the exposure. Lead shot is, however, an environmental hazard that killed many North American water birds until its use for waterfowl hunting in the United States was banned in 1991, and two additional condor deaths attributed to shotgun pellets in 2005 suggest that ingestion of lead shot may be more onerous to condors than had been presumed. Poisoning of birds during autumn is more troubling still, since exposures in our study during 2002 and 2004 were likely associated with the annual hunting season on the Kaibab Plateau, where condors fed on the carcasses of deer and covotes that had been shot (Hunt et al. this volume). The magnitude of future poisonings associated with lead-based bullets is uncertain, but lead fragments extensively contaminate the wound channel and offal of hunter-killed deer (Hunt et al. 2006) and lead bullet-induced poisonings may threaten populations of Steller's and White-tailed Sea Eagles (Haliaeetus pelagicus and H. albicilla, respectively) in Japan (Iwata et al. 2000, Kurosawa 2000, Ueta and Masterov 2000). Finally, subclinical lead levels in condors throughout the year often exceed anticipated background levels, and although the cumulative effects of chronic sublethal exposure on reproduction and survival are unknown, there are likely dysgenic effects on condors of continued, long-term exposure to lead (Cade et al. 2004).

Successful breeding by released birds in the wild nevertheless portends the coming of a new period in condor reestablishment. Given the production of wild-reared condors, as well as the high survival of birds after their first year free-flying, we are optimistic about the long-term prospects of establishing a self-sustaining condor population in Arizona, even considering significant problems associated with lead exposure. The fact that an experimental population of this, or any, endangered species is not yet adequately protected from humans and their environmental contaminants does not in itself argue for the suspension of restoration efforts, as some have maintained (e.g., Meretsky et al. 2000, Snyder and Snyder 2000). Small populations will always be vulnerable to stochastic and catastrophic events (Pimm 1991), and removal of condors from Arizona would substantially hinder our ability to identify sources of lead contamination and other biological hazards. We must instead maintain the effort to build a condor population in Arizona large enough to sustain losses while continuing to

identify the sources of lead in the environment, inform the public of the threat of lead to condors and other wildlife, and promote the adoption of environmentally safe alternatives to lead ammunition.

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