Demography of the California Condor: Implications for Reestablishment

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Abstract: *The remnant wild population of California Condors (*Gymnogyps californianus*) of the 1980s exhibited a rapid population decline caused by high mortality rates among adult and immature birds. The most prominent mortality factor was lead poisoning resulting from ingestion of bullet fragments in carcasses. Successful captive breeding has allowed many birds to be released to the wild since 1992, based originally on an assumption that exposure to lead could be prevented by food subsidy. The mortality of released birds, however, has generally exceeded levels needed for population stability calculated from simple population models. Collision with overhead wires was the most frequent cause of death in releases before 1994. Lead poisoning again surfaced as a problem starting in 1997 as older birds began feeding on carcasses outside the subsidy program. Although poisonings have been treated successfully by chelation therapy in recaptured birds, food subsidy is proving an ineffective solution to lead exposure. The best long-term solution appears to be either the creation of large reserves where hunting is prohibited or the restriction of hunting to nontoxic ammunition in release areas. Until sources of lead contamination are effectively countered, releases cannot be expected to result in viable populations. In addition, problems involving human-oriented behavior have resulted in the permanent removal of many released birds from the wild. The most promising reduction in human-oriented behavior has been achieved in one release of aversively conditioned, parent-reared birds. Rigorous evaluation of the factors reducing attraction to humans and human structures has been hampered by confounding of techniques in releases. Behavioral problems could be more quickly overcome by adoption of a comprehensive experimental approach.*

Demografía del Cóndor de California: Implicaciones para su Restablecimiento

Resumen: *Las poblaciones silvestres remanentes del cóndor de California (*Gymnogyps californianus*) de los anõs 80 exhibieron una disminución poblacional rápida debido a altas tasas de mortalidad de individuos adultos e inmaduros. El factor de mortalidad más prominente fue el envenenamiento por plomo ocasionado por la ingestión de fragmentos de municiones en cadáveres. La reproducción exitosa en cautiverio ha permitido muchas liberaciones en ambientes silvestres desde 1992, bajo el argumento de que la exposición al plomo puede ser prevenida mediante el subsidio de alimento. Sin embargo, la mortalidad de aves liberadas ha excedido generalmente los niveles necesarios para alcanzar una estabilidad poblacional calculada a partir de modelos poblacionales simples. Las colisiones con alambres en lo alto fueron la causa más frecuente de las muertes en liberaciones anteriores a 1994. A partir de 1997, el envenenamiento con plomo surgió una vez más como un problema, puesto que las aves de edad avanzada comenzaron a alimentarse de cadáveres fuera del programa de subsidio. A pesar de que el envenenamiento ha sido tratado exitosamente mediante terapia de quelación de las aves recapturadas, el subsidio de alimento ha probado ser una solución ineficaz contra la exposición al plomo. Las mejores soluciones de largo plazo aparentan ser la creación*

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de reservas grandes donde la caza sea prohibida o se restrinja la caza a municiones no tóxicas en las áreas de liberación. Solo una vez que la contaminación por plomo sea contrarrestada efectivamente, no se podrá esperar que las liberaciones resulten en poblaciones viables. Además, los problemas de conductas orientadas hacia humanos ha resultado en la remoción permanente de muchas aves liberadas de zonas silvestres. La reducción más prometedora de conductas orientadas hacia humanos ha sido obtenida en una liberación de aves criadas por sus padres y condicionadas adversamente. La evaluación rigurosa de los factores que reducen la atracción hacia humanos y estructuras de humanos ha sido obstaculizada por la confusión de técnicas en las liberaciones. Los problemas de conducta podrían ser superados más rápidamente mediante la adopción de una estrategia experimental comprensiva.

Introduction

The decline of the wild California Condor (*Gymnogyps californianus*) population was documented by Koford (1953), Miller et al. (1965), and Wilbur (1978). In the early 1800s, the species ranged along the Pacific Coast from British Columbia to Baja California. By the late 1970s, this range had shrunk to a limited region surrounding the southern San Joaquin Valley of California, and the population had dropped to about 30 birds (Wilbur 1980).

In 1980, concern over the decline led to a new conservation program involving intensive field research and captive breeding (Ricklefs 1978; Verner 1978; Snyder 1986). Establishment of a captive flock began in 1982, at first largely through multiple clutching of wild pairs and artificial incubation of their eggs (Snyder & Hamber 1985) but later through capture of free-flying birds when it became clear that the wild population was beyond rescue (Snyder & Snyder 1989). By 1987, when the last wild condor was captured, the captive population consisted of 27 individuals (14 females and 13 males). First reproduction in captivity occurred in 1988 and was followed by near-exponential growth of the captive population (Kuehler 1996). By mid-1998 total numbers of condors exceeded 150. Reintroductions started in 1992; by early 1999, 88 birds had been released in 16 attempts.

To evaluate the potential for condor reestablishment, we present (1) a simple demographic model of the historic wild population to derive benchmark mortality rates that may allow populations to persist in the wild and (2) an analysis of releases based mainly on demographic and behavioral considerations.

Demographic Characteristics of the Historic Wild Condor Population

Reproductive Parameters

Although few data exist on the age of first breeding among wild California Condors, adult coloration is normally achieved at 6 years, and no subadults have been documented breeding (Koford 1953; Snyder & Snyder 1989). In captivity, both males and females have usually begun breeding at 6–8 years of age (Kuehler 1996). For modeling purposes, we assumed that this range also applies to the wild population.

A 32-year-old male is the oldest California Condor of known age breeding in captivity, but other captive breeders of unknown age may be much older. One female of unknown age, who has ceased egg laying in the past 4 years despite consistent earlier production, appears from surgical examination to be post-reproductive (P. Ensley, personal communication). A male Andean Condor (*Vultur gryphus*) at the National Zoo (Washington, D.C.) successfully fertilized an egg at age 55 (S. Derrickson, personal communication). In modeling efforts, we explored ages of reproductive senescence ranging from 50 to 100 years and found that senescence had little effect on model outcomes, mainly because few individuals lived beyond 50 years in most scenarios.

All data on wild and captive birds indicate a clutch size of one egg (Koford 1953; Snyder & Hamber 1985; Kuehler 1996). Snyder and Hamber (1985) documented that breeding pairs normally lay each year they do not continue to care for juveniles produced in the previous breeding season. Pairs that fledge young in September, however, often breed again late in the following laying season, whereas pairs that fledge young in October and November generally forego breeding the following year if their fledglings survive. Thus, successful pairs are likely to breed in 2 out of 3 years, and unsuccessful pairs can be expected to lay every year.

In addition, pairs failing early in breeding often lay replacement eggs in the same laying season (Snyder & Hamber 1985). Four of seven natural nesting failures (57%) in the 1980s occurred early enough to allow replacement eggs. Because this sample size is too small to give an accurate frequency of natural replacement clutching, we assume a wide range of values (25–75%) for chances of a second egg after loss of a first (i.e., double clutching). No natural cases of triple clutching have been observed in the wild, although induced triple clutches occurred occasionally, usually when both first and second eggs were taken rapidly for artificial incubation. Because natural triple-clutching appears to be rare, we assume double clutching only.

Records of sexed birds from the wild (Wilbur 1978) and from captivity (Kuehler 1996; M. Mace, personal communication) total 136 males and 131 females, a ratio close to unity. All our calculations assumed a 1:1 sex ratio.

Data from the early 1980s (Snyder & Snyder 1989) indicate that roughly 50–80% of all adults, or an average of 80% of paired adults, bred in any year. Mundy (1982) documented nearly identical proportions of paired adults breeding in four species of African vultures, so breeding effort was apparently normal in condors. In our model, we assume that 50–80% of adults breed.

The historic wild condor population fledged young from about 40–50% of eggs laid (Snyder 1983; Snyder & Snyder 1989). This rate is similar to the nesting success of other solitary-nesting New World and Old World vultures (Jackson 1983; Mundy et al. 1992), although colonial-nesting Old World vultures generally have somewhat higher success rates. Thus, both the breeding effort and the nesting success of California Condors appear to have been reasonably strong. Our calculations assumed 40–50% nesting success.

Mortality Rates

Data on mortality rates are available for only the final few years of the historic wild population, when accurate censusing and identification of individual condors became feasible through photodocumentation (Snyder & Johnson 1985; Snyder & Snyder 1989). Between early 1982 and early 1986, when the population dropped from 23 to 5 birds, the average annual mortality rate for the population was 26.6%, as calculated on the basis of deaths per bird year, or 18.9%, 16.7%, 43.2%, and 27.5% for the 4 years, respectively. Surprisingly, the average mortality rate for immature birds (22.2%) was slightly lower than that for adults (26.8%), suggesting that the factors responsible for mortality were not markedly age-dependent. Although the deaths-per-bird-year method of calculating mortality rates differs from the method used by Snyder and Snyder (1989) for the same period, the results are virtually the same, both with respect to the overall mortality rate (26.6 vs. 23.9%, respectively) and the rates for immature birds (22.2 vs. 23.1%, respectively) and adults (26.8% vs. 24.0%, respectively). Because only two wild fledglings were documented through this period, a meaningful mortality rate for first-year birds alone cannot be calculated.

Modeling Mortality Rates for Stable Condor Populations

Using the reproductive characteristics of the remnant wild population, we calculated mortality rates that would permit population stability and then compared these rates with those experienced by condors in the 1980s and by birds currently being reintroduced to the wild. We constructed a female-based, age-based, deterministic, single-population model with a prebreeding census and a 1-year time step (Caswell 1989; Noon & Sauer 1992; Beissinger & Westphal 1998). We used Excel and MATLAB (1992) programs to estimate annual mortality rates that would result in stable populations ($\lambda = 1$) under varying levels of reproductive success. Although this simple model does not incorporate stochasticity or catastrophes, it provides a method to compare survival and reproductive rates to assess causes of decline (Hitchcock & Gratto Trevor 1997) and allows estimation of minimum levels of survivorship required for recovery of California Condors as a guide for reestablishment efforts.

To encompass uncertainties in some demographic rates, we investigated a variety of values for age of first breeding, percentage of adults breeding, percent breeding success, probability of renesting within a breeding season, and age at senescence. Because no substantial differences were documented in the mortality rates of adult and immature condors in the 1980s, we first developed models with equal mortality rates for all ages. We also explored models in which mortality for immature birds (1 to 5-year-olds) was twice the adult rate, a situation more typical for large carnivorous birds. Maximum age was set at 100 years.

We calculated the number of juveniles produced annually per adult female (J) from $J = bcf + bc(1 - f)rf$, where b is the proportion of females that breed and accounts for pairs that are not nesting because they are caring for juveniles produced during the prior breeding season, c is clutch size (always 1 for condors), f is the probability of a nesting attempt producing a chick that survives to the start of the next breeding season, and r is the probability of renesting after a failed attempt in the same breeding season. The first term of the equation (bcf) estimates productivity from initial nesting attempts each year, and the second term ($bc(1 - f)rf$) accounts for productivity from renests. We converted J to the number of female juveniles produced per adult female by assuming an equal sex ratio at fledging.

We developed four scenarios to represent potential levels of reproductive success that condors might attain in the wild (Table 1). The "most likely" scenario was based on average values from field studies of California Condors in the 1980s. For the "optimistic" scenario we used more favorable values for variables which were indicative of the upper limits observed or projected from the field, and for the "pessimistic" scenario we used values indicative of lower limits observed or projected. In a "maximum conceivable" scenario we assumed perfect (100%) nesting success of females, that all females produced two young every 3 years, and that all bred at age 6. This latter scenario is surely unattainable in the wild but provides a useful benchmark for calculating the maximum value for mortality rates that condors could sustain.

Rates of mortality required to sustain a stable condor population were derived for all possible rates of reproduction (Fig. 1). Modeling results showed that age of first breeding had relatively little effect on levels of permissible mortality but, not surprisingly, that permissible adult rates were considerably higher when adult rates equaled immature rates than when immature rates were double adult rates. Adult mortality rates allowing population stability for the pessimistic (5.3–6.7%), most likely (7.5–9.9%), and optimistic (9.5–13.4%) scenarios were only about 25–50% of the mean mortality rates documented for wild condors in the 1980s (26.6%) (Table 1). Even the highly unrealistic maximum conceivable (10.4–14.9%) scenario required mortality rates no greater than 56% of the average wild rates. These comparisons strongly suggest that the wild population was suffering from excessive mortality in the 1980s and that there was limited potential for resuscitating the population by improving its reproductive performance.

The Reestablishment Program

It is a primary axiom of reestablishment efforts that the main causes of population extirpation be identified and corrected before releases are attempted. Research indicated that extirpation of the condor was due mainly to excessive mortality rather than deficiencies in reproduction, but evidence as to which mortality factors were most crucial was less conclusive. Only 4 of 15 free-flying condors that perished in the early 1980s were recovered for necropsy. Three of the recovered birds were victims of separate lead poisoning incidents, however, leaving little doubt that lead poisoning was a major threat (Janssen et al. 1986; Snyder & Snyder 1989). The fourth dead condor was a victim of cyanide poisoning, evidently a result of contact with a coyote trap or a cyanide-poisoned coyote (*Canis latrans*) (Anderson 1984). Other mortality factors of potential importance in recent times were collisions with overhead wires and illegal shooting.

Evidence suggests that the lead poisoning resulted from bullet fragments ingested from carcasses of animals killed by hunters or other shooters. Lead bullets remain the standard ammunition used in hunting many mammalian game species in the western United States. The switch to steel shot in the 1980s (primarily for waterfowl hunting) offered little benefit to condors, which do not commonly eat waterfowl or other animals killed with shotguns.

Because much of the risk to condors apparently was associated with contaminated food, first releases to the wild were defensible only on the assumption that birds would be maintained on a subsidy of clean carcasses until better ways of countering the lead threat could be implemented. The results of releases of large vultures in Peru (Wallace & Temple 1987, 1988) and France (Terrasse 1985) suggested that captive-reared birds might be close to fully controllable with food subsidy, even though feeding programs with the original wild California Condor population did not result in strong dependency of experienced wild birds on subsidy (Wilbur 1977; Snyder & Snyder 1989).

Releases of captive-reared California Condors were initiated by the U.S. Fish and Wildlife Service (USFWS) in 1992 in the Sespe Condor Sanctuary of Ventura County, following temporary experimental releases of Andean Condors in the same region in 1988–1990 (Wallace 1989). Subsequent releases of California Condors were conducted by the USFWS and the Ventana Wilderness Society in other locations in California and by the Peregrine Fund in the Grand Canyon region of Arizona. By early 1999, 88 California Condors had been released, all as juveniles (Table 2).

Early releases involved puppet-reared birds and did not involve aversive conditioning of birds to humans and human structures. Releases since 1995 in California have involved aversive conditioning by exposing birds to electrified dummy utility poles and repeated aggres-

Table 1. Estimates of mortality rates of stable California Condor populations from deterministic modeling of four reproductive scenarios.

	Model parameters				*Calculated mortality*				
Reproductive scenario	*adults breeding (%)*	*breeding success (%)*[a]	*probablility of renesting*[b]	*fledglings/ female/ year*	*age of first breeding*	*age of last breeding*	*mortality by age*[c]	*annual adult mortality*	*annual immature mortality*
Pessimistic	50	40	0.25	0.2300	8	50	I = A	0.067	0.067
	50	40	0.25	0.2300	8	50	I = 2A	0.053	0.106
Most likely	65	45	0.50	0.3729	7	75	I = A	0.099	0.099
	65	45	0.50	0.3729	7	75	I = 2A	0.075	0.150
Optimistic	80	50	0.75	0.5500	6	100	I = A	0.134	0.134
	80	50	0.75	0.5500	6	100	I = 2A	0.095	0.190
Maximum conceivable	67	100	0.0	0.6700	6	100	I = 2A	0.149	0.149
	67	100	0.0	0.6700	6	100	I = 2A	0.104	0.208

[a] *Breeding success accounts for mortality in the first year of life.*
[b] *Probability of renesting indicates chance that a pair will lay a second egg after a failed first egg in a single breeding season.*
[c] *Mortality by age shows the relationship between immature (I) and adult (A) mortality.*

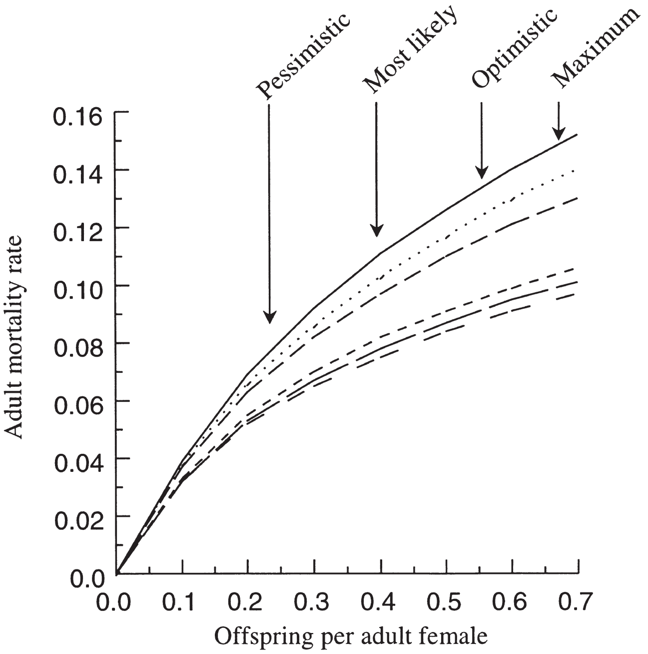

Figure 1. Stable population mortality isobars (i.e., populations with $\lambda = 1$) for combinations of adult mortality and reproductive success in California Condors. The upper three curves are for ages of first breeding, ranging from 6 to 8 years with immature mortality equal to adult mortality. The lower three curves are for first breeding at 6-8 years, and immature mortality was twice the rate of adult mortality. For both sets of curves, the highest represents first breeding at age 6 and the curves require lower mortality as age of first breeding increases. Populations increase at points below the isobar (higher reproduction and/or lower mortality than needed for stability) and decline at points above the isobar (lower reproduction and/or higher mortality than needed for stability). The effects of different ages of senescence are not included because they had negligible impact on λ. Positions marked by arrows show reproductive and mortality rates that match the scenarios discussed in the text.

sive capture with a net in flight pens prior to release (Table 2). Since 1998, researchers in California and Arizona have also often employed post-release aversive conditioning in the form of "hazing" procedures, such as chasing birds away from developed areas. Beginning in 1996, some releases also involved parent-reared birds.

Releases have not yet yielded self-sustaining populations. This is not surprising from a reproductive standpoint because no released birds are old enough to breed. In addition, however, annual mortality rates have exceeded permissible levels of approximately 10% in nearly all releases, despite provision of clean food (Table 2). Of ongoing releases, only the November 1997 release of parent-reared birds in the Ventana Wilderness (with no mortalities as of late 1999) has achieved acceptable mortality rates for any appreciable length of time (when interventions to prevent imminent mortality are considered mortalities).

Specific causes of mortality and near mortality have been diverse (Table 3), but two factors dominate: collisions with overhead wires (including electrocutions) and lead poisoning. Released birds have not remained strictly dependent on food subsidy (contrary to early assumptions), and there has been a major resurgence in cases of lead poisoning beginning in 1997 (six cases requiring capture and chelation therapy, and seven other cases of low-level lead exposure). Moreover, because the frequency of released birds feeding at naturally occurring carcasses has been increasing in all releases, the frequency of lead poisoning may increase. In contrast, collisions with overhead wires were especially frequent in the earliest releases and have declined more recently.

Other sources of mortality and near mortality apparently were less pervasive than collisions and lead poisoning (Table 3). Only one (perhaps two) birds were killed by shooting, although another unsuccessful shooting attempt was witnessed and prosecuted. In addition, drownings, starvation, an anti-freeze poisoning, and one apparent death from a Golden Eagle (*Aquila chrysaetos*) and one from a coyote (or scavenging) have occurred.

Mortality and near-mortality (Tables 2 & 3) do not account for losses prevented by permanent retrapping of 19 birds showing excessive human-oriented behavior. Mortality rates might have been higher if these interventions had not occurred.

Discussion

Verner (1978) concluded that condor populations could not remain stable if annual adult mortality exceeded 5% and juvenile mortality exceeded 13–15%. These figures are similar to our most likely scenario figures (Table 1), which assume juvenile mortality to be twice as great as adult mortality. The close correspondence of results, however, stems from some different (but fortuitously compensating) assumptions. Verner assumed no replacement clutching and no annual breeding, but he used nest success levels that were considerably higher (up to 75%) than those indicated by recent field data (Snyder 1983; Snyder & Snyder 1989).

Our results (Fig. 1) agree with those of Verner (1978) and Mertz (1971) in confirming that slow maturation and low reproductive rates in condors demand high survival rates. Under the most likely scenario (Table 1), condor mortality must average <10% annually to achieve stable or increasing populations. Condors in the early 1980s, however, had a much higher mortality rate (26.6%). Similarly high mortality may also have characterized earlier decades. A mortality rate of 26.6% implies an average life

Table 2. **Chronology of condor releases showing release information, rearing and aversive conditioning regimes, and fate of released birds.**[a]

Release date	*Release location*[b]	*Number and species released*	*Aversive conditioning*	*Parent-reared*	*Deaths*	*Interventions*	*Annual mortality rate*	*Adjusted mortality rate*[c]	*Recaptures due to behavior*	*Status of the release*
California releases										
December 1988–February 1989[d]	Sespe	7 Andean	no	no	1	0	0.20		6	remaining birds retrapped for behavioral problems
January–February 1990[e]	Sespe	6 Andean	no	no	0	1	0.00	0.15	6	remaining birds retrapped for behavioral problems
January 1992	Sespe	2 Andean, 2 California	no	no	1	0	0.23		3	Andeans retrapped, remaining California Condor relocated to Lion Canyon (November 1993) and then retrapped for unsuitable behavior (March 1994)
December 1992	Sespe	6 California	no	no	3	0	0.53		3	remaining birds relocated to Lion Canyon (November 1993) and then retrapped for unsuitable behavior (March 1994)
December 1993	Lion	5 California	no	no	2	0	0.42		3	remaining birds retrapped for unsuitable behavior (March 1995)
March 1995	Lion	6 California	yes	no	1	2 (3)[f]	0.05	0.18	1	ongoing
August 1995	Lion	8 California	yes	no	1	3	0.04	0.17	0	ongoing
March 1996	Castle Crags	4 California	yes	yes	2	1	0.23	0.35	0	ongoing
November 1996	Lion	4 California	yes	no	2	0	0.49		1	three birds still alive retrapped by January 1997 and released at Castle Crags; two still in the wild
January 1997	Ventana	4 California	yes	no	0	0	0.00		4	three birds retrapped for unsuitable behavior (Spring 1997); remaining bird retrapped and released at Hurricane Cliffs
November 1997	Lion	4 California	yes	no	2	0	0.45		0	ongoing
November 1997	Ventana	5 California	yes	yes	0	0	0.00		0	ongoing
January 1999	Ventana	7 California	yes	yes & no	0	0	0.00		3	ongoing
March 1999	Lion	6 California	yes	no	1	0	1.00		1	ongoing
Arizona Releases										
December 1996	Vermilion	6 California	yes	yes	2	0	0.19		0	ongoing
May 1997[g]	Vermilion	9 California	yes	no	2	1	0.14	0.15	1	ongoing
November 1997	Vermilion	4 California	yes	no	1	0	0.18		0	ongoing
November 1998	Hurricane[h]	9 California	yes	yes & no	1	0	0.20		1	ongoing

[a] *Information is in order by state and covers the period from the beginning of condor releases through the end of June 1999. Data for Sespe, Lion Canyon, and Castle Crags sites provided by U.S. Fish and Wildlife Service; data for Ventana Wilderness provided by Ventana Wilderness Society; data for Arizona sites provided by the Peregrine Fund. Lion Canyon and Castle Crags flocks comingle, Hurricane and Vermilion Cliffs flocks comingle, and a single meeting of Lion Canyon and Ventana Canyon birds has occurred.*

[b] *Sespe Condor Sanctuary, Lion Canyon, Castle Crags, Ventana Wilderness Area, Vermilion Cliffs, Hurricane Cliffs.*

[c] *Adjusted mortality rate shows rate if intervention had not occurred and death had resulted.*

[d] *Released in three groups on 17 December 1988, 21 January 1989, 14 February 1989.*

[e] *Released in two groups on 3 January 1990 and 20 February 1990.*

[f] *Two interventions on one bird.*

[g] *Released in two groups on 14 and 27 May 1997.*

[h] *An older bird, originally released at Ventana Canyon, was released at Vermilion Cliffs rather than with the younger birds at Hurricane Cliffs*

Table 3. Causes, numbers, and dates of actual and near mortalities of Andean and California Condors during releases to the wild in California and Arizona, December 1988–June 1999.

Cause	*Actual mortalities*	*Near mortalities*	*Location*	*Dates of actual and near (N) mortalities*
Collisions	7	0	California	February 1989,[a] May 1993, October 1993, June 1993, June 1994, August 1997
			Arizona	May 1997
Lead poisoning	0	5 birds, 6 incidents	California	September 1997 N (3), May 1998 N, September 1998 N (2)
Disappearances	4	1	California	April 1996 N, September 1996, November 1996, December 1996
			Arizona	July 1997
Drownings	2	0	California	July 1998 (2)
Starvation	2	2	California	April 1996 N, February 1997, June 1999
			Arizona	July 1997 N
Shooting	1 + (1)[b]	1	California	July 1992 N, June 1998
			Arizona	March 1999
Antifreeze	1	0	California	October 1992
Cancer	1	0	California	July 1994
Golden eagle	1	0	Arizona	January 1997
Coyote (?)[c]	1	0	Arizona	December 1998
Unknown injury	0	1	California	October 1990 N[c]
Found dead	1	0	Arizona	October 1998

[a] *Andean condor mortality or near mortality.*
[b] *Injured by shooting, taken to zoo to heal, cause of death unknown.*
[c] *Possibly scavenging, not predation.*

span of only about 4 years, less than the age of sexual maturity.

Primary Sources of Mortality

Identified sources of release mortality are consistent with lead poisoning and collisions with overhead wires as major causes of the recent historical decline of the California Condor (Table 3), as argued by Snyder and Snyder (1989). Shooting has been a less important source of release mortality, despite earlier fears that it might be the most important mortality threat (Dawson 1923; Koford 1953; Miller et al. 1965; Wilbur 1978).

We consider lead poisoning a more important cause of mortality than collisions, both historically and for the future, for several reasons. First, the nearly equal mortality rates of immature and adult condors in the original wild population seem better explained by lead poisoning than by collisions. Ingestion of lead in carcasses may be equally likely in adults and immature birds, whereas collisions are often more frequent in immature birds than adults in large avian species (e.g., Leshem 1985; Hunt 1997). Second, the frequency of lead poisoning in releases presumably would have been much higher in the absence of food subsidy, even though food subsidy has been less than fully effective in reducing lead poisoning. Third, frequent collisions by released birds may have resulted largely from excessive attraction of birds to humans and human structures caused by flaws in training procedures. With improvements in release techniques, collision frequencies have declined.

None of the six cases of acute and near-acute lead poisoning documented in released birds has led to mortality because the poisonings were detected early and affected birds were captured and treated with chelation therapy. Emergency chelation, however, is not a cost-effective or feasible means for sustaining wild populations in the long term. For long-term projections, therefore, birds saved by such therapy are best considered mortalities. If they are, the mortality rates of the releases involved (March and August 1995, March 1996) rise to 18%, 17%, and 35%, respectively, substantially exceeding the 10% needed for sustainability.

Mortality typically is high at the start of any release program and then progressively stabilizes at a lower level as problem individuals are eliminated and survivors adapt to the wild. For the condor, however, mortality rates may show progressive increases as birds abandon food subsidies and become more susceptible to lead poisoning. If lead contamination persists in the environment and increased feeding on natural carcasses continues, the ultimate mortality rates of released birds seem likely to converge on the unsustainably high rates of the historic wild population.

Achieving Adequately Low Mortality Rates

To achieve viable wild populations of condors, primary mortality threats must be reduced greatly. All releases to date have used multiple-subsidy sites rather than single-subsidy sites. This practice teaches food-searching behavior to the birds and is the procedure normally employed to get birds to abandon subsidy. Thus, in spite of early program justifications, all release efforts have in effect pursued a goal of wild populations that forage naturally, and no real attempt has been made to maintain populations dependent on clean food subsidy in the long term.

Long-term, single-site subsidy offers one potential solution to the resurgence of lead poisoning, although it has not yet been demonstrated that birds can be restricted indefinitely to single foraging sites. Pursuit of this approach would require retrapping all birds currently feeding at natural carcasses and starting over with naive birds. At best, this solution poses perpetual food subsidy obligations and expense, and it represents a permanent distortion of the natural foraging behavior of the species.

In our view, two other solutions are preferable: (1) creation of large reserves free of hunting and/or (2) replacement of lead ammunition with nontoxic alternatives in regions of condor releases. Because of the large size of individual condor ranges, both historically (Meretsky & Snyder 1992) and in the release program, creation of reserves large enough to sustain wild populations would entail major expense. Although some acquisitions of foraging habitat have been made (e.g., the Hopper National Wildlife Refuge, the Bitter Creek National Wildlife Refuge, and the Wind Wolves Preserve), these holdings are still much too limited to effectively counter the lead poisoning threat.

More promising is the development of nontoxic ammunitions. A newly developed TTB ammunition material (a composite of tungsten, tin, and bismuth), with ballistic characteristics equal to and in some respects better than those of lead, has proved nontoxic in ingestion tests with Mallards (*Anas platyrhynchos*) and Turkey Vultures (*Cathartes aura*) (Ringleman et al. 1993; R. Risebrough & V. Oltrogge, personal communications). The TTB ammunitions may soon be commercially available, and a regional switch to their use may be possible without the political difficulties that occurred with substitution of steel shot for lead shot. Although TTB ammunitions can be expected to cost more than lead ammunitions, initial field tests of TTB performance by hunters have proved highly encouraging (B. Brown, personal communication), and the U.S. military is anticipating conversion to this ammunition type. The TTB ammunitions are not the only nontoxic ammunitions currently under development, but they represent a type that can compete well with lead in accuracy, range, and killing power, and, like lead, they pose little threat of damage to gun barrels.

If nontoxic ammunition can replace lead ammunition in condor release areas, the need for reserves free of hunting diminishes. In fact, if limited to nontoxic ammunitions, hunting could benefit condors by providing enhanced safe food supplies via unrecovered carcasses and discarded viscera piles. Such benefits may at least partially compensate the risks of condor mortality from shooting that are inherent in any strategy that allows hunting in condor range.

Excessive tameness and curiosity shown by released birds toward humans and urbanized areas have also contributed to high mortality rates, mainly via collisions. Despite efforts to minimize the direct exposure of prerelease birds to humans by rearing with condor puppets, all birds in early releases were exposed to rectangular human structures and to the sounds of civilization in zoo environments. Further, all had occasional opportunities to view humans directly in nonthreatening contexts. Birds reared under these conditions have on release readily approached humans and settled areas.

Aversive conditioning of puppet-reared birds in later releases may have reduced initial tendencies to approach humans and human structures, but it has not yet produced birds with behavior typical of wild fledglings. For example, all birds in the first Ventana release were recaptured because three of the four repeatedly approached humans despite aversive conditioning. Human-oriented behaviors have been especially problematic among released condors in southern California during the summer of 1999 (Whitaker 1999). Although historic wild condors, especially fledglings, were known to be quite approachable near their nests, condor visits to settled areas and voluntary interactions with humans were virtually nonexistent.

Despite continuing problems with tameness among puppet-reared birds, one potential beneficial effect of the aversive conditioning has been a drop in the frequency of collisions. We suspect that this decline may be primarily a result of training with electrified dummy utility poles, but this conclusion is not certain because other changes, such as new release locations and aversive training with nets, were implemented simultaneously, confounding interpretations.

The condors that have shown the best behavior in releases have been parent-reared birds, especially those in the November 1997 release in the Ventana area. The Ventana birds, which were also aversively conditioned with dummy utility poles, were released in the same location as an earlier failed release of aversively conditioned, puppet-reared birds, but as of this writing they have have suffered no mortalities and have shown virtually no inclination to interact with humans or human structures. In January 1999, four more parent-reared birds were released into this group, along with three puppet-reared birds. Despite aversive conditioning of all birds, the puppet-reared individuals immediately began approaching and interacting with humans and were soon retrapped, whereas the parent-reared birds have behaved in a manner similar to parent-reared birds released earlier.

Other releases of parent-reared birds (Table 2) are more difficult to interpret than the 1997 Ventana release because they involved early mixing of parent-reared birds with puppet-reared birds, which could have resulted in detrimental influences of one group on the other. Nevertheless, 76% of 21 parent-reared birds released overall are still alive in the wild, compared with only 49% of 67 puppet-reared birds.

Achieving Adequate Reproduction

Reducing mortality rates is not the only hurdle to be overcome in the reestablishment of the California Condor. Birds must also develop successful breeding traditions. The historic wild population nested preferentially in areas of low Golden Eagle abundance, potentially removing most eagle threats to nestlings (Snyder & Snyder 1989). Released condors, however, may tend to nest close to release areas, as was found by Sarrazin et al. (1996) for Eurasian Griffons (*Gyps fulvus*) in France. Some condor release sites have had Golden Eagles residing nearby, so problems with eagle predation could compromise the reproductive success of these releases. To achieve adequate breeding success, future releases may have to be limited to regions of low eagle density.

Another significant threat to nesting success which may require control is egg predation by Common Ravens (*Corvus corax*). Historic wild condors lacked fully effective defenses against ravens, possibly because of recent substantial increases in raven numbers (Knight et al. 1993); ravens were the most important cause of nesting failure documented in the historic wild condor population (Snyder & Snyder 1989). Released condors, lacking experience with ravens, may suffer even worse losses. With the exception of the Ventana Wilderness, all current release regions have abundant raven populations. Effective means for controlling raven depredations have not been devised or tested, although taste-aversion conditioning might reduce such threats (Nicolaus et al. 1983).

Lessons from Other Release Programs

Compared with California Condor releases, releases of Eurasian Griffons in France and Andean Condors in Peru and Colombia have been relatively trouble-free (Wallace & Temple 1987, 1988; Lieberman et al. 1993; Sarrazin et al. 1994, 1996). Adult mortality of released Eurasian Griffons (mainly from power-line electrocutions) is <2% annually, and the wild population has expanded rapidly through natural reproduction. The released population has fed mainly on domestic animals, supplied largely as subsidy, and no cases of lead poisoning have occurred. The relative success achieved in Peru and Colombia may have resulted from the opportunity to integrate released birds into existing wild populations.

Releases in France have mainly used breeding pairs rather than immature birds, and the relatively sedentary nature of birds after release may have resulted from this practice. Unfortunately, testing whether California Condor releases might benefit from using older birds poses conflicts. Release of any captive, wild-trapped adults would likely pose threats of lead contamination, regardless of food subsidy, because such birds may return quickly to foraging habits they practiced before capture. Although older birds might serve as beneficial behavioral role models for captive-reared birds in some respects, they could lead them into a similar susceptibility to lead poisoning. Release of wild-trapped adults should be considered only after sources of lead contamination have been removed from the range.

Release of both captive-born and wild-caught adults poses tradeoffs between captive productivity and potentials for improved release results. Further, none of the presently available captive-reared adults have been held in strict behavioral isolation from humans. Nevertheless, releases of adults may be worth some careful future experimentation if adequate success proves elusive with releases of fledglings.

Future Directions for Condor Releases

Given the discouraging degree of human orientation universally exhibited by released puppet-reared birds and by some parent-reared birds released with puppet-reared birds, we see no value in continued releases of puppet-reared birds. There is no evidence that their human-oriented behaviors are declining with age: the oldest birds in the wild are still showing such behaviors 5 years after release. Unlike the condors in the purely parent-reared Ventana population, puppet-reared condors and their parent-reared flock mates have repeatedly visited settled areas, have frequently approached and sometimes accepted food from bystanders, and have repeatedly vandalized human property. They are sufficiently tame that they may also pose a threat of injury to bystanders. All released birds presently showing human-oriented behaviors should be returned to captivity because they pose a significant risk of permanently contaminating future wild populations with such detrimental behaviors.

Instead, we favor restricting future releases to parent-reared birds and testing additional variants of parent rearing, such as moving parental stocks out of zoo environments into naturalistic field enclosures, as recommended by Verner (1978) and by participants in the California Condor Workshop of September 1994 (Anonymous 1994).

Unfortunately, most releases have lacked experimental controls, so they have not provided unambiguous evaluation of the importance of various release variables. Thus, the importance of aversive techniques remains uncertain, although continued use of electrified dummy power poles seems likely to be beneficial. Future releases should be conceived as true experiments so that results can be interpreted conclusively and the program can proceed as rapidly and surely as possible to optimum release methodologies.

Current captive-breeding strategies aimed largely at maximizing production of progeny are in partial conflict with the goal we favor of maximizing numbers of parent-reared birds. Only 7 of 18 nestlings from 15 fertile pairs are being parent-reared in the 1999 breeding season, largely because opportunities for parent rearing are reduced under strategies that emphasize multiple clutching, but also because not all pairs have yet proved competent in rearing young.

Maximizing production has been justified both by genetic arguments and by a premature proliferation of release sites. We believe that genetic concerns are of rapidly declining priority and that there is little to be gained by proliferating release sites prior to achieving self-sustaining populations at any site, especially when this proliferation entails penalties in the production of parent-reared birds. Production of parent-reared birds could be significantly increased if human-oriented birds now in the wild were retrapped and made part of the captive-breeding population. Such birds need not strain the space limitations of existing zoo facilities if a policy of moving some breeding pairs to field enclosures in release areas were also implemented.

Finally and most important, because lead poisoning has become frequent in the release program, current reestablishment efforts are inconsistent with the premise that reintroductions be conducted only when principal limiting factors are under control. With current trends toward feeding on natural carcasses, released condors will soon be exposed to essentially the same mortality risks that caused the rapid decline of the historic population. Although continued releases, if properly implemented, could resolve ongoing behavioral problems, they cannot be expected to result in self-sustaining wild populations unless solutions to lead contamination (and possibly other mortality factors) are implemented. Because alternative nontoxic ammunitions appear to offer a long-term solution to lead poisoning at low cost, their adoption should become the overriding near-term goal of condor conservation efforts.

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Note Added in Proof

Since final acceptance of this paper, a number of significant developments have occurred, all in 2000: (1) the three lead-poisoning deaths of California Condors in Arizona, (2) release of one adult from the historic wild population back into the wild in the Sespe region despite continuing lead contamination threats in this region, (3) range expansion by the Ventana population of parent-reared condors, leading to repeated contact with the Lion Canyon condors. Ventana condors have already followed Lion Canyon birds into a community where the latter have repeatedly vandalized property. With the end of isolation of the Ventana birds and the addition of two puppet-reared birds in a spring, 2000, Ventana release (one remains in the wild), no opportunities presently remain to study uncontaminated behavior of a parent-reared flock of released California Condors.

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