

Lead, trash, DDE, and young age of breeders linked to lower fertility in the first two decades of reintroduction for critically endangered California Condors in California

Victoria J. Bakker,^{1,*} Myra E. Finkelstein,² Daniel F. Doak,³ Rachel Wolstenholme,⁴ Alacia Welch,⁵ Joe Burnett,⁶ Arianna Punzalan,⁷ Joseph Brandt,⁷ Steve Kirkland,⁷ Nadya E. Seal Faith,⁸ Erin R. Lehnert,⁵ and Estelle A. Sandhaus⁸

¹Department of Ecology, Montana State University, Bozeman, Montana, USA

²Microbiology and Environmental Toxicology Department, University of California, Santa Cruz, California, USA

³Department of Environmental Studies, University of Colorado, Boulder, Colorado, USA

⁴National Park Service, San Francisco, California, USA

⁵National Park Service; Pinnacles National Park, Paicines, California, USA

⁶Ventana Wildlife Society, Monterey, California, USA

⁷U.S. Fish and Wildlife Service, Ventura, California, USA

⁸Department of Conservation and Science, Santa Barbara Zoo, Santa Barbara, California, USA

*Corresponding author: vjbakker@gmail.com

ABSTRACT

In the first comprehensive assessment of the reproductive rates of critically endangered California Condors (*Gymnogyps californianus*) recovering from complete extirpation in the wild, we analyzed 20 years (1999–2018) of data from condor flocks in southern and central California. We found that several anthropogenic threats affected reproductive rates: (1) coastal space use by female condors was associated with lower hatch probability, presumably due to foraging on marine mammals and associated DDE exposure; (2) trash ingestion by chicks decreased fledging probability prior to implementation of trash management in 2007; and (3) all parent deaths during rearing resulted in chick or early fledgling deaths, and most parental deaths were due to lead poisoning. We also detected several effects on reproductive rates from the complex individual-based management of condors, which involves ongoing releases of captive-bred individuals and health interventions including treatment of lead poisoning. Recruitment rates were lower for new release sites, which we attribute to a lack of individual- and flock-level experience. In addition, the number of free-flying days in the wild in the year before first breeding and in the 8 weeks before subsequent breeding was positively associated with female and male recruitment and with female rebreeding probabilities, respectively, indicating that removing individuals from the wild may reduce their breeding success. Finally, probabilities of recruitment, rebreeding, and fledging all increased with age, and given the age distribution skew of the recovering flocks toward younger individuals, overall reproductive success was lower than would be expected at the stable age distribution. Thus, reproductive rates should increase over time as the mean age of California Condors increases if current and emerging threats to reproduction, including the loss of breeders due to lead poisoning, can be addressed.

Keywords: California Condor, endangered species recovery, *Gymnogyps californianus*, reintroduction, reproductive rates

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LAY SUMMARY

- In the first comprehensive assessment of reproduction in California Condors (*Gymnogyps californianus*) recovering from complete extirpation in the wild, we analyzed 20 years (1999–2018) of data from flocks in southern and central California.
- At the inception of the recovery program, reintroduced flocks of this critically endangered species consisted of young captive-bred individuals without breeding experience.
- We found that California Condor reproductive rates generally increased with age and time spent in the wild. Condors also faced anthropogenic threats that reduced reproductive rates. Hatch success was lower for coastal females, presumably due to DDE exposure from feeding on marine mammals, and fledge success was lower before nests were managed for trash.
- Overall reproductive success should increase over time as the age of California Condors increases if current and emerging threats to reproduction, including the loss of breeders due to lead poisoning, can be addressed.

Plomo, basura, DDE y edad temprana de los reproductores están relacionados con una menor fertilidad en las dos primeras décadas de reintroducción de la especie en peligro crítico *Gymnogyps californianus* en California

RESUMEN

Como parte de la primera evaluación exhaustiva de las tasas de reproducción de la especie en peligro crítico *Gymnogyps californianus*, que se está recuperando de una extirpación completa en la naturaleza, analizamos 20 años (1999-2018) de datos de bandadas de cóndores en el sur y centro de California. Encontramos que varias amenazas antropogénicas afectaron las tasas de reproducción: (1) el uso del espacio costero por parte de las hembras estuvo asociado con una menor probabilidad de eclosión, presumiblemente debido a que se alimentan de mamíferos marinos y la exposición asociada a DDE; (2) la ingestión de basura por parte de los polluelos disminuyó la probabilidad de emplumamiento antes de que se implemente la gestión de la basura en 2007; y (3) todas las muertes de los progenitores durante la crianza resultaron en la muerte de los polluelos o de los volantones más jóvenes, y la mayoría de las muertes de los progenitores fue debido a envenenamiento por plomo. También detectamos varios efectos en las tasas de reproducción a partir del complejo manejo individual de los cóndores, que implica la liberación continua de individuos criados en cautiverio e intervenciones sanitarias que incluyen el tratamiento del envenenamiento por plomo. Las tasas de reclutamiento fueron más bajas en los nuevos sitios de liberación, lo que atribuimos a la falta de experiencia a nivel individual y de la bandada. Además, el número de días de vuelo libre en la naturaleza en el año previo a la primera reproducción y en las 8 semanas previas a la reproducción subsecuente se asoció positivamente con el reclutamiento de hembras y machos y con las probabilidades de volver a reproducirse de las hembras, respectivamente, lo que indica que la remoción de individuos de la naturaleza puede reducir su éxito reproductivo. Finalmente, las probabilidades de reclutamiento, de volver a reproducirse y de emplumamiento aumentaron con la edad, y dada la distribución sesgada por edad hacia individuos más jóvenes de las bandadas en recuperación, el éxito reproductivo general fue menor de lo esperado considerando una distribución estable por edad. Por lo tanto, las tasas de reproducción deberían aumentar con el tiempo a medida que la edad promedio de los individuos de *G. californianus* aumente, siempre y cuando se puedan abordar las amenazas actuales y emergentes para la reproducción, incluida la pérdida de reproductores debido al envenenamiento por plomo.

Palabras clave: Cóndor de California, *Gymnogyps californianus*, recuperación de especies en peligro, reintroducción, tasas de reproducción

INTRODUCTION

Critically endangered California Condors (*Gymnogyps californianus*) are recovering from their complete extirpation in the wild in 1987 (Snyder and Snyder 1989). Although reintroductions were initiated in 1992 (Walters *et al.* 2010) and at the end of 2022 over 180 birds were in the wild in California, population growth has been reliant on the release of captive-bred juveniles (Finkelstein *et al.* 2012). Lead toxicosis is the primary cause of death for free-flying juvenile and adult condors (Rideout *et al.* 2012, Viner *et al.* 2020), and their principal source of lead exposure is feeding on carcasses of animals shot with lead-based ammunition (Church *et al.* 2006, Cade 2007, Finkelstein *et al.* 2012).

The California Condor is a classic *K*-selected species, with a long lifespan and heavy investments in few offspring, typified by high adult survival coupled with low reproductive rates (Mertz 1971). Because the population growth of *K*-selected species is more sensitive to adult survival than to reproduction (Doak *et al.* 2009), reducing lead-related mortality is a priority for conservation, but robust reproduction can nonetheless help offset anthropogenic mortality of adults (Finkelstein *et al.* 2010). Maximizing reproduction is especially important when threats to survival prove difficult to modify, such as the case for scavengers poisoned from the use of lead-based ammunition (Friend *et al.* 2008, Cromie *et al.* 2019).

Reintroduced populations may struggle to initiate breeding and achieve their maximum reproductive potential, especially if they have complex breeding requirements or face anthropogenic threats affecting reproduction (Mee *et al.* 2007a, Berger-Tal *et al.* 2020). California Condors exhibit highly social behaviors coupled with delayed maturity and a monogamous breeding system (van Overveld *et al.* 2020). Both parents participate in selection of nest sites, located in cliff faces or cavities in large coastal redwood trees, and in incubation and rearing (Finkelstein *et al.* 2020). Laying to fledging typically requires ~8 months and adults provide parental care after fledging, especially for the first 6 months, resulting in a general pattern of biennial breeding (Finkelstein *et al.* 2020).

California Condors have faced two well-documented anthropogenic threats to reproduction: reduced hatching success due to egg-shell thinning, attributed to DDE exposure from feeding on marine mammals (Burnett *et al.*, 2013, Kurle *et al.*, 2016) and reduced fledgling success from chicks ingesting trash (e.g., bottle caps, washers, bolts, fabric, plastic; Mee *et al.* 2007b, Finkelstein *et al.* 2015). Seeking to maximize reproductive success, managers have closely monitored nests and instituted a variety of interventions, including swapping captive-laid eggs for wild eggs, removing trash in the vicinity of nests, and evacuating chicks with impacted crops or other life-threatening conditions for medical treatment.

Due to the comprehensive data collected on each wild individual, California Condors present a unique opportunity to investigate the drivers of reproduction for long-lived birds and for reintroduced populations. We analyzed 20 years (1999–2018) of reproductive data from 2 distinct condor flocks in California (southern and central, Figure 1) along with hypothesized correlates, including external factors such as threats, management, flock, and time, as well as intrinsic factors such as age, behavior, past reproductive history, and previous blood lead levels. To better distinguish the factors influencing overall success for breeding condors, we separated fertility into five individual component probabilities: recruiting, rebreeding, hatching an egg, fledging a chick, and the fledgling being female. This approach allowed us to account for management actions at specific reproductive stages (e.g., egg, chick) to estimate reproductive rates in the absence of management.

We hypothesized that factors correlated with experience, such as age and free-flying days, would be positively associated with all components of California Condor reproduction. We further hypothesized that factors correlated with anthropogenic threat exposure would be negatively associated with specific reproductive rate components. For example, we hypothesized that maternal coastal space use, which is linked to DDE exposure, would be negatively associated with the probability of hatching an egg, while factors associated with

contaminant exposure for chicks (i.e., absence of management of nest-associated trash, parental behaviors linked to high lead exposure) would be negatively associated with the probability of fledging a chick. Our analyses generated reproductive rate estimates to help guide recovery of the critically endangered California Condor while also informing potential drivers of reproduction for other imperiled large scavengers (Ogada *et al.* 2012, 2016) and reintroduced populations of avian species with similar life history strategies (Servanty *et al.* 2014, Morandini and Ferrer 2017).

METHODS

Study Species and Data

Between 1999 and 2018, the free-flying California Condor population consisted of a southern California (hereafter, southern) flock managed by the U.S. Fish and Wildlife Service and a central California (hereafter, central) flock managed by Pinnacles National Park and the Ventana Wildlife Society (Figure 1). The free-flying population size increased during the study period with the southern and central flocks consisting of 90 and 95 birds, respectively,

at the end of 2018. As opposed to the southern flock, the central flock has been observed foraging on beach-cast marine mammal carcasses (Kurle *et al.* 2016) and nesting in cavities in coastal redwoods trees (J. Burnett personal observation). Observational data on reproduction (e.g., recruitment, fledgling) and behavior (e.g., coastalness) were collected (Supplementary Material Table S1) as part of ongoing management efforts under the authority of the U.S. Fish and Wildlife Service.

Overview

Because we intended our analyses to be used to guide condor recovery, we estimated reproductive rates suitable for parameterizing quantitative models, typically summarized as the number of female fledglings produced per female per year, which is the product of these annual probability components: (*Recruit*|*Rebreed*) * *Hatch* * *Fledge* * *Female* (see Table 1, Supplementary Material Table S1 for definitions). To contribute a female offspring, a female must breed, which means a pre-breeding female must recruit into the breeding population by laying her first egg (*Recruit*), or a female that has bred in the past must rebreed by laying an egg (*Rebreed*). These probabilities are multiplied by the clutch size, which for condors is invariably a single egg (Finkelstein *et al.*

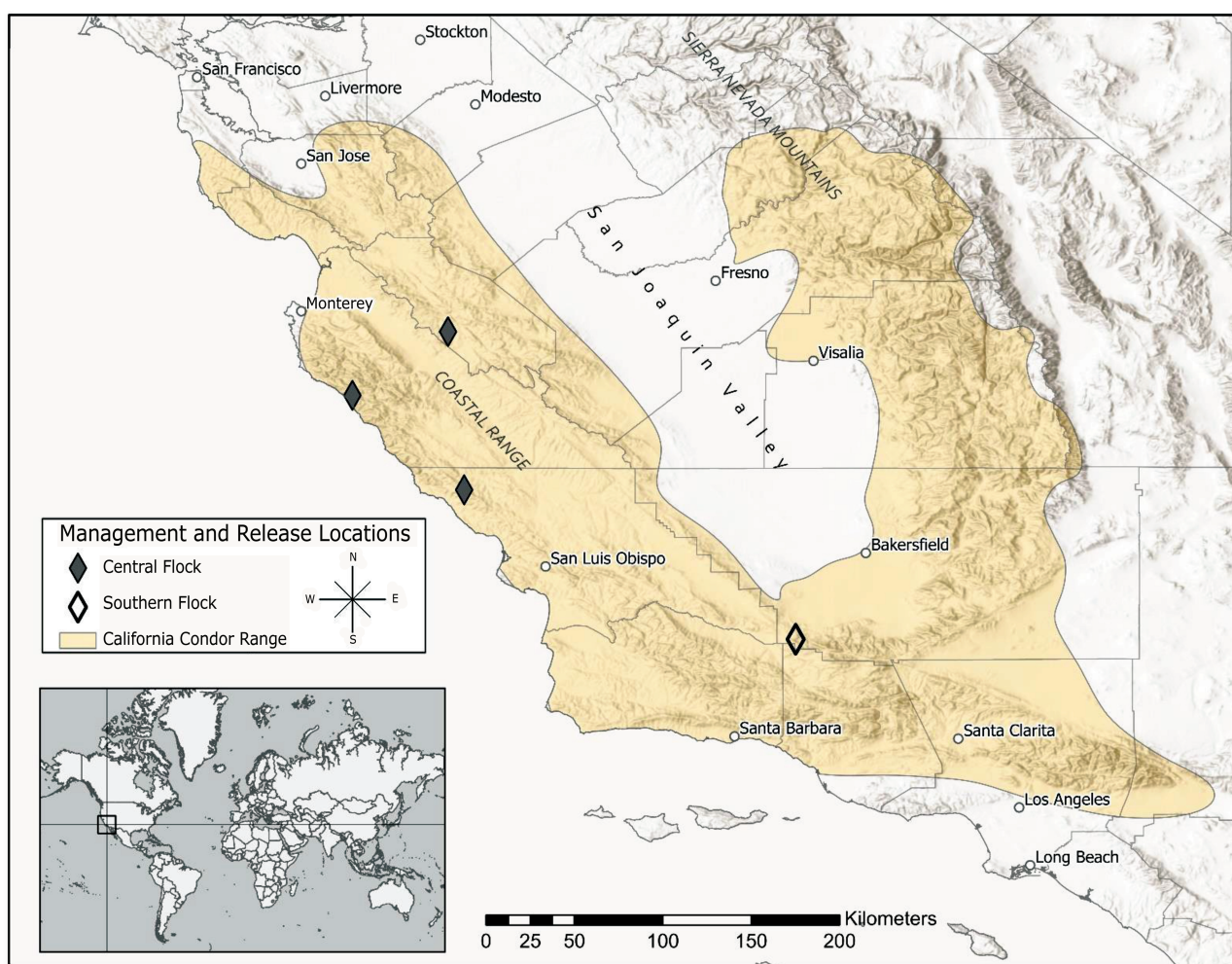


FIGURE 1. Map of California Condor range and the release sites in California for the central (filled diamonds) and southern (open diamonds) flocks. Although there is occasional inter-flock movement, currently the central flock generally occupies the area from San Luis Obispo County northward, while the southern flock generally occupies the areas from Santa Barbara County inland, including the Sierra Nevada, with limited use of the areas in between by both flocks. Figure courtesy of Evan McWreath, Ventana Wildlife Society.

Table 1. Variables considered in models to estimate the reproductive rates *Recruit*, *Rebreed*, *Hatch*, and *Fledge* for California Condors (*Gymnogyps californianus*) by variable type. See [Supplementary Material Table S1](#) for expanded methods and definitions.

	Analyses				
Variable	Recruit	Rebreed	Hatch	Fledge	Description
Temporal or locational attributes					
<i>FirstYYrs</i>	x				Binary variable indicating if reproductive event occurred in the first Y years that breeding-age birds were present at release site.
<i>Flock</i>	x	x	x	x	Categorical variable indicating flock (central or southern, Figure 1).
<i>Matepool</i>	x	x			The ratio of unpaired breeding-age individuals of the opposite sex per unpaired individuals of the target sex (i.e., $Matepool_{M:F}$ for females, $Matepool_{F:M}$ for males). Only considers individuals free-flying for $\geq 50\%$ of the previous six months.
<i>NBreedF</i>	x				Number of females observed breeding in previous year.
<i>PreTrashMgmt</i>				x	Binary variable indicating time period before 2007 after which trash management practices were implemented by southern flock managers. No fledging attempts were made in the central flock prior to 2007 so this temporal effect applies only to southern flock nests.
<i>Tree</i>			x	x	Binary variable indicating nest was located in a tree cavity (vs. a cliff).
<i>Year</i>	x	x	x	x	Calendar year used as factor variable as a random effect.
<i>Yr</i>	x	x	x	x	Sequentially numbered calendar year used as an integer variable to indicate annual trend. Also considered <i>YrtoYYYY</i> , which was annual trend plateauing in <i>Yr YYYY</i> .
Intrinsic					
<i>Age</i>	x	x	x	x	Age of condor in years. Model forms considered included: <i>Age</i> (age as integer variable), Age^2 (age as quadratic function), and binary variables to denote specific age groups. For example, <i>Age5</i> is a binary variable for 5-yr-olds and <i>Ages7to8</i> is a binary variable for 7- and 8-yr-olds. Finally, <i>Age7</i> indicates age as an integer variable plateauing at age 7.
<i>WildHatch</i>	x				Binary variable indicating an individual was hatched and reared in the wild (vs. released as a captive-bred juvenile).
Behavioral and physiological					
<i>Coastalness</i> ^a			x		Proportion of all observations in the previous year (<i>TotObs</i>) that were visual observations in the coastal region (<i>VisCoast</i>), corrected for the bird's proportion of tracked free-flying days in the previous year (<i>TFreeFly</i>). Specifically, $(VisCoast/TotObs) * TFreeFly$. Also considered <i>Coastalness</i> over 2, 4, and 6 years, denoted $Coastalness_{xyr}$.
<i>FreeFly_D</i> ^a	x	x	x	x	The proportion of the previous D days that the condor was free-flying. Time frames considered were 365, 180, and 56 days.
<i>Pb</i> ^a			x	x	An individual's maximum blood lead level in previous year, in $\mu\text{g/dL}$.
<i>Presence</i> ^a	x	x	x	x	Proportion of tracked free-flying days in the previous 180 days that condor was observed (signal or visual observation), excluding visual feeding observations (i.e., <i>Proffered</i>).
<i>Proffered</i> ^a	x	x	x	x	Proportion of tracked free-flying days in the previous 180 days that a condor was visually observed feeding on a proffered carcass.
Breeder class and experience					
<i>Failed</i>		x	x	x	Binary variable indicating condor laid an egg in the previous year but failed to fledge a chick.
<i>Skipped</i>		x	x	x	Binary variable indicating condor was a recruited breeder but did not lay an egg in the previous year.
<i>Succeeded</i>		x	x	x	Binary variable indicating condor successfully fledged a chick in the previous year.
<i>Widow</i>		x	x	x	Binary variable indicating condor was a recruited breeder but its mate died prior to the current breeding season. Widow status overrides all other classes.
<i>EverHatchedOwn</i>			x		Binary variable indicating condor previously hatched its own egg.
<i>EverHatched</i>			x		Binary variable indicating condor previously hatched an egg.
<i>EverFledged</i>				x	Binary variable indicating condor previously fledged a chick.
<i>HatchFail</i>				x	Binary variable indicating condor failed to hatch current year's egg but was provisioned with a replacement captive-reared egg.
<i>NHatched</i>				x	Number of previous eggs that a condor hatched.
<i>NFledged</i>				x	Number of previous chicks that a condor fledged.

^aFor variables that characterize previous 365 days, 180 days, or 56 days, we summarized the time period prior to laying for *Recruit*, *Rebreed*, *Hatch* and prior to hatching for *Fledge*.

2020). The female and her mate must then successfully incubate the egg to hatching (*Hatch*) and then rear the chick to fledging (*Fledge*, when the chick leaves the nest and is capable of flight). The calculation must also account for the probability that the fledged chick is female (*Female*).

We primarily focused on the drivers of female reproduction. Our female focus was justified because females produce eggs, female behavioral traits were strongly correlated with their mate's (Supplementary Material Figure S1), and most mated pairings were maintained long-term. We ran limited analyses to test for distinct correlates of male reproductive rates. We distinguished between four breeder classes—succeeded, failed, skipped (i.e., did not lay an egg in a given year), or widow—and tested whether breeder class in one breeding season predicted reproductive rates in the subsequent season. By definition, paired individuals became widows at the death of their mate, regardless of whether they succeeded, failed, or skipped breeding in the previous season, although for some components of reproduction we still tested whether their previous breeder experience influenced performance.

California Condors are assumed to require bi-parental care to fledge a chick (Finkelstein *et al.* 2020). To increase the flexibility of our analyses for use in population models, we censored nests from our analyses if a parent died before the chick fledged to avoid the potential for double counting the effects of parent deaths in population models, where a parent death can deterministically result in chick death. In the infrequent cases where nests ($n = 9$) were attended by trios (7 nesting attempts: 3 trios of 2 females and 1 male; 2 nesting attempts: 1 trio of 1 female and 2 males), we assigned the reproductive event to the biological parent if known or inferred or randomly if unknown. The second female or male in the trio was considered a nonbreeder.

Nest Management

Nest management consisted of egg swaps, chick treatment, or both, although management effort varied within the study period. Egg swaps entailed removing wild-laid eggs due to known or suspected inviability or for other considerations (e.g., genetics, research) and replacing them with artificial eggs for the parents to incubate. If the removed eggs were viable, they were incubated in captivity. Artificial eggs in wild nests were replaced with captive-incubated eggs—either the wild nests' original egg or a captive-laid foster egg, typically within ~2 weeks. Chick treatment entailed removing chicks with potentially lethal medical conditions from wild nests for treatment, and these chicks generally but not always remained in captivity. Of 185 wild nest attempts (2000–2018), 57 (31%) were manipulated, and the frequency of interventions decreased markedly through time, with 47% of nests manipulated in the first 9 years (2001–2009) and 26% in the second 9 years (2010–2018). Analyzing *Hatch* and *Fledge* separately increased our sample sizes for quantifying fertility rates, allowing us to estimate *Fledge* for failed nests that received foster eggs. We estimated *Hatch* only for nests with wild-laid parent-incubated eggs and *Fledge* for nests with any wild-hatched chicks, including captive-incubated and foster eggs.

Statistical Models

We estimated the annual probabilities of *Recruit* using general linear models (GLM, R Core Team 2021) and *Rebreed*, *Hatch*, and *Fledge* using general linear mixed effects models (GLMMs, *glmer* function in *lme4* package; Bates *et al.* 2015) with bi-

nomial response variables (i.e., logistic regression models). We used both individual *ID* of condors and *Year* as random effects to account for repeated measures of individuals through time for analyses of *Rebreed*, *Hatch*, and *Fledge*, but excluded these effects for *Recruit* because there was zero variance associated with these random effects. We visually inspected plots to determine that the models conformed the assumptions of logistic regression including outliers and linearity of the logit and tested for multicollinearity using variance inflation factors (VIF, *car* package). We report *P*-values from the *glmer* function, which were based on Wald *t* values and are widely reported for GLMMs: these values are somewhat anti-conservative for linear mixed effect models (Luke 2017), and thus should be interpreted with caution. We used information theoretic approaches to judge support for alternative models including different fixed effects by comparing model AIC_c (*MuMIn* package, Barton 2020; *AICcmodavg* package, Mazerolle 2020). We performed model selection in a sequential process, first screening hypothesized drivers and key interactions (see Table 1, Supplementary Material Tables S2–S18), then performing multivariate model selection with all supported variables and interactions. We present results from the best-supported models for each component of reproduction. We tested for effects of age, flock, and time, as well as measures of experience and behavior. We also explored hypothesized drivers tied to individual components of reproduction as identified below.

Recruit

Recruit is the probability of first breeding. We estimated the annual probability that individuals that had not yet recruited into the breeding population would breed for the first time. To avoid including individuals not available to form pair bonds prior to the start of the breeding season, we limited our sample to individuals in the wild in California that were free-flying (i.e., not held in field pens or zoos) for ≥50% of the 8 weeks preceding the start of the breeding season (February 1). Age is known to have a dominant influence on the recruitment schedule, and thus we first tested the fit of a variety of age structures for both females (Supplementary Material Table S2) and males (Supplementary Material Table S3). After identifying the best age structures, we tested for other predictors of female and male *Recruit* including an influence of available mates (*Matepool*), and time lags indicating lower recruitment during the early years of the reintroduction program (*FirstYYrs*, Supplementary Material Tables S4–S7).

Rebreed

Rebreed is the probability of rebreeding. We estimated the annual probability that recruited female breeders (individuals that have laid at least one egg in their lifetime) would rebreed. We again limited our sample to individuals in the wild that had been free-flying for ≥50% of the 8 weeks preceding the start of the breeding season. Breeder class is hypothesized to have a strong influence on rebreeding, and thus we first estimated the best structure for the influence of breeder class, testing for differences in *Rebreed* for individuals who in the previous year were successful breeders, failed breeders, widows, or skippers and whether age influenced any differences observed (see Table 1 for variable descriptions and Tables S8–S9 for models). Because one intent was to assess whether the experience of raising a chick to fledging affected *Rebreed*, for this analysis, we categorized females who had previously fledged chicks that received

emergency medical care including temporary evacuations as successful breeders ($n = 2$).

Hatch

Hatch is the probability of hatching an egg. We estimated the probability that a parent laying an egg in a wild nest would successfully incubate and hatch it. We censored manipulated nests in which eggs were removed for nonviability, other (e.g., genetics, research), or unknown reasons and hatched and fledged in captivity ($n = 7$) or were removed and incubated in captivity due to predation concerns from raven activity ($n = 1$) or undocumented reasons ($n = 1$) and later returned to and hatched in the nest. We considered manipulated nests as hatch failures if the egg was removed for any reason and failed in captivity ($n = 5$) or was removed for viability concerns and hatched in captivity ($n = 1$). California Condors are known to lay a replacement egg in the event of hatch failure, but such events appeared rare and may not have been observed; we considered *Hatch* as the probability of hatching an egg during the current breeding season, including replacement eggs.

We tested for temporal trends, age structure, and differences by behavior and other predictors (i.e., *Pb*, *Tree*), as well as by breeder class and experience (Supplemental Tables S10–S13). Based on previous work, we considered marine mammal feeding a potential driver of *Hatch* (Burnett *et al.* 2013, Kurl *et al.* 2016). Marine mammal feeding exposes condors to marine-associated contaminants, including DDE, which is known to cause egg-shell thinning in avian species (Lundholm 1997). To index marine mammal feeding, we used an individual's annual *Coastalness*, or the proportion of all its observations in the previous year that were visual observations in the coastal region, corrected for monitored free-flying days and also tested for an effect of *Coastalness* summarized over longer timeframes (e.g., 2, 4, and 6 years) (Table 1, Supplementary Material Tables S14–S15).

Fledge

Fledge is the probability of fledging a chick. We estimated the probability that a parent hatching a chick in a wild nest would successfully fledge that chick. We considered several types of manipulated nests as fledge failures: nests in which chicks were removed for medical treatment (due to elevated lead, broken wing, trash impaction, etc.) and died in captivity ($n = 4$), fledged in captivity ($n = 8$), or were returned to the nest and fledged ($n = 2$). Trash impaction was the leading cause of death for California Condor chicks in the southern flock early in the release program (Rideout *et al.* 2012) and management to reduce trash in nests in this flock was fully implemented in 2007. Thus, we considered the temporal variable indicating the era before this management was implemented (*PreTrashMgmt*) as a predictor of *Fledge* (see Supplementary Material Tables S16–S18 for models).

Female

Female is the probability that a fledgling is female. Offspring sex ratio is a necessary component of any fertility equation when using female-only models and is of particular importance for California Condors given the recent emergence of male skew in adult sex ratios. For wild California Condor nests in California from 2001 to 2018, sex determination was available for nearly all fledglings (Supplementary Material Table S1).

RESULTS

Recruit

Based on 250 observations of 81 females over 20 years, female recruitment was first observed at age 5 ($n = 4$ of 74), peaked at ages 7–8 ($n = 27$ of 69), and was constant for all other ages (i.e., age 6 and age 9+, $n = 24$ of 107) (Figure 2A, Supplementary Material Table S2 and Figure S2). The best model for recruitment into the breeder class using this age structure included a positive effect of the proportion of free-flying days in the previous year (*FreeFly*₃₆₅), which outperformed free-flying days over shorter time frames (*FreeFly*₁₈₀, *FreeFly*₅₆, Supplementary Material Table S4). The best model also included a flock effect, with recruitment probability higher in the southern flock, and a time lag effect such that recruitment was lower in the first 4 years that breeding-age birds were present in each flock (*First4Yrs*) (overall best model, $\text{Recruit} = \text{Age5} + \text{Age7to8} + \text{FreeFly}_{365} + \text{Flock} + \text{First4Yrs}$, Figure 2A, Table 2, Supplementary Material Table S6). The sex ratio of available breeders did not influence female recruitment, nor did behaviors (i.e., *Proffered*, *Presence*) (Supplementary Material Table S4).

Male recruitment was lower overall compared to females and the age-specific recruitment schedule differed, based on 351 observations of 97 males over 20 years. In contrast to female recruitment peaking at ages 7–8, male recruitment rates steadily increased across age categories age 5 ($n = 1$ of 93), age 6 (3 of 78), ages 7–8 ($n = 17$ of 109), before plateauing at ages greater than 8 ($n = 26$ of 71) (Supplementary Material Figure S2, Table S3). Like female recruitment, male recruitment was positively associated with the proportion of free-flying days in the previous year (*FreeFly*₃₆₅) (Table 2, Supplementary Material Tables S5, S7). However, in contrast to females, males were more likely to recruit when the sex ratio of available breeders (female:male) was higher (*Matepool*_{F:M}), and males were also more likely to recruit if they were wild hatched (*WildHatch*) or were present less often in the management area (*Presence*) (Table 2). Overall, male recruitment patterns were consistent with the observed male-skewed sex ratios, which limit breeding opportunities for males, with males more likely to recruit when more females were available and when they were in the wild longer, which may have enhanced their access to females.

Rebreed

We observed 229 rebreeding opportunities for 42 female breeders over 17 years. The best model for *Rebreed* (Table 3) included separate probabilities for failed and successful breeder classes and equal rebreeding probability for skippers and widows. Failed breeders were most likely to rebreed ($n = 56$ of 74), followed by skippers ($n = 40$ of 75), widows ($n = 6$ of 15), and successful breeders ($n = 16$ of 65) (Figure 2B, Supplementary Material Tables S8–S9). Rebreeding probability increased with age up through age 11 and then stabilized (*Age11*). There was a negative interaction between the age effect and the failed breeder class, such that rebreeding probability was essentially constant and high for failed breeders regardless of age. Finally, the proportion of free-flying days in the previous 8 weeks (*FreeFly*₅₆) was a positive predictor of female rebreeding, but measures of free-flying over longer time frames were not supported predictors (Supplementary Material Table S9). We found no

Table 2. Predictors of recruitment probability for female and male California Condors. Shown are estimated coefficients (*B*), standard errors (SE), and p-values (*P*) for the best-supported model to predict the probability that female (Supplementary Material Table S6) and male (Supplementary Material Table S7) condors will breed for the first time, based on logistic regression models (GLM, R Core Team 2021) using data collected from central and southern flocks in California (Figure 1) from 1999 to 2018. See Table 1 for variable definitions.

Variable	<i>B</i>	SE	<i>P</i>
Females			
Intercept	−3.984	1.939	0.040
<i>Age5</i>	−1.606	0.569	0.005
<i>Ages7to8</i>	0.834	0.350	0.017
<i>FreeFly</i> ₃₆₅	2.705	2.010	0.178
<i>Flock:southern</i>	0.506	0.334	0.130
<i>First4yrs</i>	−1.106	0.661	0.095
Males			
Intercept	−10.633	4.626	0.022
<i>Age5</i>	−4.756	1.083	0.000
<i>Age6</i>	−3.293	0.689	0.000
<i>Age7to8</i>	−1.592	0.411	0.000
<i>FreeFly</i> ₃₆₅	10.650	4.814	0.027
<i>Matepool</i> _{F:M}	0.798	0.412	0.053
<i>Presence</i>	−1.635	0.729	0.025
<i>WildHatch</i>	1.178	0.531	0.027

Table 3. Predictors of rebreeding probability for female California Condors. Shown are estimated coefficients (*B*), standard errors (SE), and p-values (*P*), for the best-supported model (Supplementary Material Table S9) to predict the probability that a female condor that has previously bred will rebreed, based on generalized linear mixed effects models with a binomial response (GLMER, R package *lme4*, Bates et al. 2015) using data collected from central and southern flocks in California (Figure 1) from 2002 to 2018. See Table 1 for variable definitions.

Random effects	Variance	N	
<i>ID</i>	0.907	42	
<i>Year</i>	0.182	17	
Variable	<i>B</i>	SE	<i>P</i>
Intercept	−9.340	3.559	0.009
<i>Succeeded</i>	−2.042	0.527	<0.001
<i>Failed</i>	6.850	2.968	0.021
<i>Ageto11</i>	0.542	0.226	0.017
<i>FreeFly</i> ₅₆	4.112	2.769	0.138
<i>Failed</i> * <i>Ageto11</i>	−0.568	0.291	0.051

evidence that breeders fledging chicks early in the year were more likely to rebreed in the following year (Supplementary Material Figure S3).

Hatch

We analyzed hatching data for 163 wild-laid eggs by 53 female breeders over 18 years. The best model for estimating hatch probability included a negative effect of the female's time spent on the coast (*Coastalness*) and a positive effect of tree nesting (*Tree*) (Figure 3, Table 4, Supplementary Material Tables S10–S15). There was an increasing trend in hatch success in the central flock that plateaued after 2014 (Supplementary Material Table S10), consistent with declining *Coastalness* of central flock birds over time. However, it was not supported in models that included *Coastalness*, illustrating the influence of coastal behavior on this trend. No difference was found in hatch success by age, behaviors other than *Coastalness*, or experience, and, after accounting for *Coastalness*, there was no

difference in *Hatch* between the southern and central flocks (Supplementary Material Tables S12–S15).

Fledge

We analyzed 125 wild-hatched chicks reared by 46 females over an 18-year timespan. The best model to predict *Fledge* (Table 5) was age of the female through age 11 (*Age11*) and time before 2007, when trash management was initiated (*PreTrashMgmt*) (Figure 2C, Supplementary Material Tables S16, S18), such that *Fledge* increased with age before plateauing at age 11 and older and *Fledge* was lower in the *PreTrashMgmt* era. No chicks hatched in the central flock prior to 2007 so this temporal effect applies only to southern flock nests. Because many parents that failed to hatch eggs received swapped eggs ($n = 31$), we were able to assess correlations between *Hatch* and *Fledge*, and hatch success did not predict fledge success ($P = 0.37$) under these circumstances. Presence of the female parent in the release area

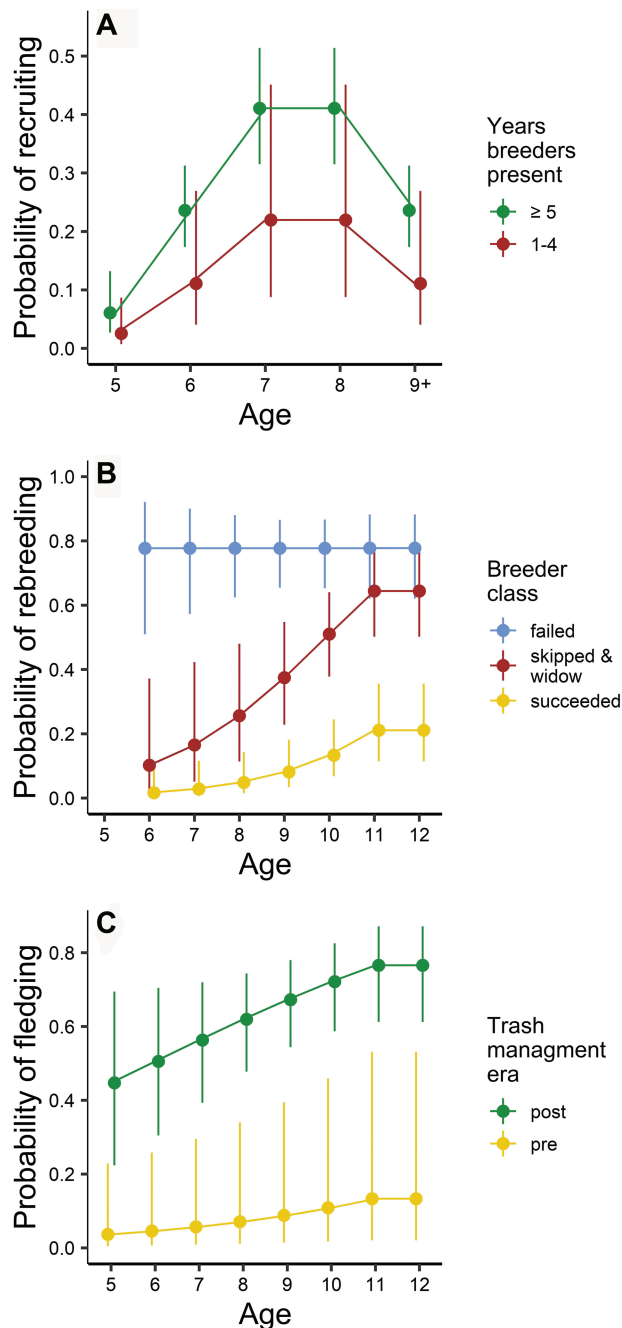


FIGURE 2. Effects of age and other factors on reproductive rates for female California Condors. **(A)** Probability of recruiting by age, initially and 5 or more years after breeding-age birds are present, based on the best-supported model without behavioral variables ($Recruit \sim Int + Age5 + Ages7to8 + First4Yrs$, [Supplementary Material Table S6](#)). $First4Yrs$ (depicted as 1–4 in legend in red) indicates the time period during the first 4 years breeders were present and represents a time lag in initial recruitment rates. **(B)** Probability of rebreeding by age and class, where class is the breeding outcome in the previous year. Plot is based on the best-supported model without behavioral variables ($Rebreed \sim Int + Succeeded + Failed * Ageto11$, [Supplementary Material Table S9](#)). **(C)** Probability of fledging a chick by age and trash management era. Plot is based on the best-supported model ($Fledge \sim Int + Ageto11 + PreTrashMgmt$, [Supplementary Material Table S18](#)). Plotted probabilities are population-level predictions with 90% confidence intervals for fixed effects (*ggpredict* in package *ggeffects*, Lüdtke 2018).

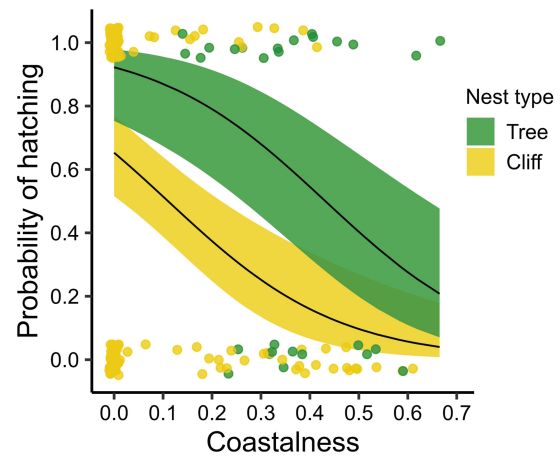


FIGURE 3. Relationship between coastliness, nest type, and probability of a female California Condor hatching an egg. The probability of a female hatching an egg decreased with her coastliness and increased if she nested in a tree cavity (model plotted is $Hatch \sim Coastliness + Tree$, [Supplementary Material Table S15](#)). Observed hatching data relative to coastliness and nest type indicated by points, with hatched eggs depicted at probability 1 and failed eggs depicted at probability 0, and points jittered for visibility. Plotted probabilities are population-level predictions with 90% confidence intervals for fixed effects (*ggpredict* in package *ggeffects*, Lüdtke 2018).

was positively associated with *Fledge* but was not included in the best-supported model ([Supplementary Material Table S18](#)). After accounting for age and *PreTrashMgmt*, there was also no difference in fledge success based on flock, nest type, or the female parent's breeder class, experience, proffered feeding rate, or past blood lead level ([Supplementary Material Table S18](#)). However, the proffered feeding rate (*Proffered*) of the male parent was positively associated with *Fledge* ([Supplementary Material Table S17](#)).

Female

The overall proportion of fledglings of known sex that were female was 0.46 (24F, 28M). The proportion female for birds of known sex by flock was 0.38 (8F, 13M) for the central flock and 0.52 (16F, 15M) for the southern flock. We were unable to test whether sex was a predictor of fledging because sex is frequently unknown for failed nests (i.e., sex was known for 54% of failed nests vs. 98% of successful nests).

Fertility Rates

Predicted reproductive rates using our best-supported statistical models yielded age-specific rates for *Recruit* and *Fledge*, age- and breeder-class-specific rates for *Rebreed*, and an age-invariant rate for *Hatch* ([Table 6A](#)). We summarized observed annual reproductive rates using comparable patterns for age- and flock-dependence to calculate observed fertility. Using the observed rates for *Hatch* (central: 0.41, southern: 0.64) and *Fledge* (0.66), observed breeding success ($Hatch * Fledge$) was 0.27 in the central flock and 0.42 in the southern flock. Based on the proportion of adults breeding at age 8 or greater (0.49), fertility, or the number of female fledglings per female, was 0.07 in the central flock and 0.10 in the southern flock, with the

Table 4. Predictors of hatch probability for female California Condors. Shown are estimated coefficients (*B*), standard errors (SE), and p-values (*P*) for the best-supported model (Supplementary Material Table S15) to predict the probability of a female condor hatching an egg, based on generalized linear mixed effects models with a binomial response (GLMER, R package *lme4*; Bates *et al.* 2015) using data collected from central and southern flocks in California (Figure 1) from 2001 to 2018. See Table 1 for variable definitions.

Random effects	Variance	N	
<i>ID</i>	0.854	53	
<i>Year</i>	0.314	18	
Variable	<i>B</i>	SE	<i>P</i>
Intercept	0.631	0.345	0.067
<i>Coastalness</i>	-5.728	1.660	<0.001
<i>Tree</i>	1.841	0.749	0.014

Table 5. Predictors of fledge probability for female California Condors. Shown are estimated coefficients (*B*), standard errors (SE), and p-values (*P*) for the best-supported model (Supplementary Material Table S18) to predict the probability of a female condor fledging a chick, given that her egg hatched, based on generalized linear mixed effects models with a binomial response (GLMER, R package *lme4*; Bates *et al.* 2015) using data collected from central and southern flocks in California (Figure 1) from 2001 to 2018. See Table 1 for variable definitions.

Random effects	Variance	N	
<i>ID</i>	0.372	46	
<i>Year</i>	0.301	18	
Variable	<i>B</i>	SE	<i>P</i>
Intercept	-1.376	1.268	0.278
<i>AgeTo11</i>	0.233	0.138	0.092
<i>PreTrashMgmt</i>	-3.059	1.227	0.013

lower fertility for the central flock due to lower rates of *Hatch* (Table 6B).

DISCUSSION

The reintroduced population of California Condors has grown through the release of captive-bred individuals (Finkelstein *et al.* 2012, USFWS 2013) but self-sustainability will require replacing captive propagation with wild reproduction. Here, we provide the largest and most comprehensive assessment of the first 20 years of wild California Condor reproduction in California, which can be used to inform recovery planning for this critically endangered species. Our analyses showed that several anthropogenic threats (lead, trash, DDE) were associated with lower reproductive output. In addition, we found that older birds had higher reproductive output, indicating that the young age skew of the reintroduced population also contributed to its lower overall fitness.

An important caveat to the interpretation and application of our results to other large scavengers is that, although the California Condor Recovery Program spans three decades, the condor population is still far from a stable age distribution. Due to the ongoing releases of captive-bred juveniles, the age distribution is skewed toward younger individuals resulting in a population-wide average age of 7 years old and a maximum age of 24 for female breeders, much younger than the estimated condor lifespan of ~70 years (Finkelstein *et al.* 2020). Furthermore, due to the long-term decline of California Condors, there are no data for a population in the

absence of anthropogenic threats and thus we were unable to assess the degree to which our reproductive rate estimates for the reintroduced population differ from a healthy population at a stable age distribution. However, the patterns we observed may nevertheless be typical of reintroduced populations with similar life histories.

Comparison with Published California Condor Reproductive Data

Reproductive rates estimated for historic California Condor populations were derived from very small sample sizes and often incomplete observations of declining populations (Wilbur 1978, Snyder 1983, Snyder and Snyder 1989). Thus, we cannot document true differences in reproductive rates between reintroduced and historic populations, but we do report several refinements in our general understanding of reproductive rates relative to those inferred from previous studies.

While previous studies assumed California Condors begin breeding at ages 6–8 (based largely on zoo observations) (Snyder and Snyder 1989, Meretsky *et al.* 2000), with our larger dataset, we documented a small proportion of females and males recruiting into the breeding population at age 5. The contribution of these younger individuals to the population growth rate was relatively low as probabilities of both rebreeding and fledging a chick increased with age. We also observed fewer instances of condors laying a replacement egg ($n = 3$ observations from 73 failed nests, 4%) relative to that observed by Snyder and Hamber (1985) ($n = 9$ eggs for 15

Table 6. Reproductive rates for California Condor flocks in central and southern California (Figure 1) based on data collected from 1999 to 2018. Shown are (A) predicted probabilities of *Recruit*, *Rebreed*, *Hatch*, and *Fledge* based on statistical models with the best-supported age, breeder class, and flock structure, and (B) observed reproductive rates. Observed adults breeding is the proportion of all adults breeding by age, regardless of breeder class. Breeding success is *Hatch* * *Fledge*, and fledglings/female/year is calculated as adults breeding * breeding success, using breeding rates for adults ≥ 8 years old. See Table 1 for variable definitions.

A. Predicted probabilities								
Age	Recruit ^a	Rebreed ^b			Hatch ^c		Fledge ^d	
		Failed	Skipped & Widow	Succeeded	Central	Southern		
5	0.06	–	–	–	0.41	0.64		0.47
6	0.24	0.78	0.10	0.02	0.41	0.64		0.51
7	0.41	0.78	0.17	0.03	0.41	0.64		0.55
8	0.41	0.78	0.26	0.05	0.41	0.64		0.60
9	0.24	0.78	0.37	0.08	0.41	0.64		0.63
10	0.24	0.78	0.51	0.13	0.41	0.64		0.67
≥11	0.24	0.78	0.64	0.21	0.41	0.64		0.71

B. Observed rates								
Age	Adults breeding	Hatch		Fledge ^e	Breeding success		Fledglings/female/year ^f	
		Central	Southern	Both flocks	Central	Southern	Central	Southern
≥5	0.39	0.42	0.64	0.65	0.27	0.42	0.13	0.20
≥6	0.44							
≥7	0.47							
≥8	0.49						Female fledglings/female/year ^f	
							Central	Southern
							0.07	0.10

^aBased on the model $Recruit = Age5 + Age7to8 + First4yrs$ and estimated for the time period after first 4 years (i.e., $First4yrs = 0$).

^bBased on the model $Rebreed = Succeeded + Failed \times Ageto11$.

^cBased on the model $Rebreed = Coastalsness$ and assuming mean annual *Coastalsness* of 0.31 for central flock and 0 for southern flock.

^dBased on the model $Fledge = Ageto11yrs + PreTrashMgmt$ and is estimated for time period after 2006, when trash management was initiated (i.e., $PreTrashMgmt = 0$).

^eObserved fledge censors 5 nests in which parents died between hatching and 2 months after fledge.

^fFledgling/female/year is calculated for females ≥ age 8 and does not include hatch year survival, and Female fledgling/female/year assumes *Female* = 0.5.

nest failures, 60%). In addition, Meretsky *et al.* (2000) assumed replacement clutches occurred at a rate of 25–75% in their population models, which, even given the wide range, is substantially higher than our observed rate. However, observations of replacement clutches may have been missed in our dataset and the practice of swapping captive-laid eggs into failed nests may have inhibited attempts at re-laying. Finally, Snyder and Hamber (1985) reported that breeders successfully fledging young early in the season were more likely to rebreed the following year, but we found no influence of fledging time on rebreeding probability (Supplementary Material Figure S3).

Importantly, several differences in our reproductive rate estimates resulted in lower fertility estimates than those reported previously (Snyder 1983, Snyder and Snyder 1989). Meretsky *et al.* (2000) assumed 80% of paired adults breed annually, while we found lower breeding probabilities, with ~60% of known breeders (i.e., paired adults) breeding in any year (Table 6). Breeding success was likewise lower than previously assumed. Meretsky *et al.* (2000) assumed 40–50% breeding success, including first year survival. In contrast, not including first year survival, we estimated 27% (central flock) to 42% (southern flock) success (*Hatch* * *Fledge*). The lower proportion of birds breeding combined with lower breeding success resulted in an estimated fertility (female fledglings

per adult female) of 0.07 in the central flock (affected by egg shell thinning, presumably from DDE, Burnett *et al.* 2013) and 0.10 in the southern flock (Table 6). Our estimated fertility was similar to 0.11 used by Finkelstein *et al.* (2012), but lower than 0.12–0.28 assumed by Meretsky *et al.* (2000). We note that our fertility rates characterize unmanaged nests; nests requiring intervention deemed necessary for egg or chick survival were considered failures or censored from our analyses (see Methods).

Anthropogenic Effects on Reproduction

We found that use of the coastal region by California condors was linked to reduced hatch success, presumably due to DDE exposure from feeding on marine mammal carcasses (Kurle *et al.* 2016). The use of tree cavities for nesting, which currently occurs only in the coastal region of the central flock, had a positive effect on hatch probability. Although we do not know why nests in tree cavities had higher hatch success, eggs from DDE-exposed coastal condors could potentially fare better in their softer nest substrate compared to cliff nests. Statistical models that assessed temporal trends indicated that hatch success was increasing in the central flock through 2014, when the trend plateaued. This positive temporal trend was however not supported in models that included annual coastalsness, and thus may reflect a change in coastal behavior as central flock

birds have become more wide-ranging (Bakker *et al.* 2017), which could result in reduced DDE exposure risk. Nonetheless, since condors are suspected to have DDE-induced egg shell thinning (Burnett *et al.* 2013), and beach-cast marine mammals along the central California coast continue to have high levels of DDE in their blubber (Kurle *et al.* 2016), we recommend continued monitoring of condor DDE levels, coastal behavior, and hatching success.

Trash ingestion had a significant effect on fledgling success and represented a novel problem to the reintroduction program. The strong positive influence of trash management implemented in 2007 on fledgling success underscores the effectiveness of the management response. Interestingly, the negative effects of trash appear to have diminished over time as trash management was progressively scaled back starting in 2015 with no observed decrease in California Condor fledgling success. We attribute the recent reductions in trash-related chick mortality to a dilution by new breeders entering the breeding pool that are not frequenting trash-impacted areas or are not prone to trash collection behavior. As such, although trash ingestion was cited as a primary cause of reproductive failure (Mee *et al.* 2007a) and chick mortality (Rideout *et al.* 2012), our analyses suggest trash ingestion is not currently a significant barrier to recovery.

Lead remains the number one mortality factor for free-flying adult and juvenile California Condors (Rideout *et al.* 2012, Viner *et al.* 2020), and our analyses showed that lead poisoning is also a direct and indirect cause of chick mortality. Blood lead data and necropsies confirm that lead poisonings of condors, linked to lead-based ammunition (Finkelstein *et al.* 2012, 2014, M. E. Finkelstein personal observation), persist despite a ban of lead-based ammunition in condor range in 2009 (Ridley-Tree Act) and a California statewide ban that took full effect in 2019 (AB711). Indeed, we documented 3 incidences of direct chick mortality due to lead toxicosis (determined via pathologist; [Supplementary Material Table S1](#)), presumably from parental provisioning of contaminated food. Direct lead-related chick mortality may also have been underestimated as deceased chicks were not recovered for pathological evaluation in at least 14 cases. Analysis of parental behaviors provided additional evidence that lead exposure can result in chick mortality. Low rates of proffered feeding and presence in the management area are both known correlates of high lead exposure (Bakker *et al.* 2017), and both were associated with lower fledge success. Lead can also indirectly cause chick mortality when a parent dies of lead poisoning. We documented the loss of a parent for 5 chicks in the rearing stage, and all 5 of these chicks also died, 3 in the nest and 2 shortly after fledging (10 and 48 days). Three of these parents died of lead-related causes and a fourth was missing in the wild, and thus lead exposure may have contributed to its death (the fifth parent died of predation). Finally, the high rate of lead-related mortality for adult California Condors (Rideout *et al.* 2012, Viner *et al.* 2020) is indirectly lowering overall wild reproductive output by limiting the number of older breeders, which have higher reproductive rates.

Effects of Age and Experience on Reproductive Rates

Probabilities of recruitment, rebreeding, and fledging generally increased with age, suggesting that experience boosted breeding success. Likewise, recruitment rates increased after

the first four years that breeding-age birds were present in each flock, which we attributed to increases in individual- and flock-level experience. Finally, male and female recruitment increased with the proportion of free-flying days over the previous year, while female rebreeding probabilities increased with the proportion of free-flying days in the previous eight weeks. These patterns suggest that experience with potential or established mates is important to breeding decisions and that removal of individuals from the wild for treatment of lead-poisoning or other purposes may negatively influence breeding behavior.

Male condors recruited at later ages than females, as has been observed in other monogamous raptors such as Cooper's Hawks, a pattern hypothesized to result from greater costs of breeding for younger males and female preference for more experienced males (Millsap *et al.* 2019). In populations with delayed male recruitment, male mate limitation can depress reproduction and thus alter female reproduction, potentially biasing population growth rate estimates based solely on female performance (Millsap *et al.* 2019). In the case of condors, however, the evidence suggested that males were available in excess and that the male recruitment delay we observed was because of this superfluity. Condors had male-biased sex ratios in both flocks (average annual sex ratio for breeding-age birds, males per total, for the last 10 years of 0.56 in central and 0.55 southern, with annual rates as high as 0.64 and 0.63, respectively) (V. Bakker, personal observation), likely in part due to the higher release rate for captive-bred males relative to females (central: 56 female:74 male; southern: 70 female:85 male). Of note, male-skewed adult sex ratios are widely reported in birds and more common in threatened species (Donald 2007) including Andean condors (Lambertucci *et al.* 2012).

We recorded a few instances of both male and female condors breeding at age 5, which is younger than previously reported (Snyder and Snyder 1989). Morandini *et al.* (2019) have shown that density-dependent reductions in age at first breeding increased growth rates and enhanced the success of reintroductions of long-lived raptors. Although we observed a limited number of these 5-yr-old breeders, the mean age at first breeding was 7.8 yr, similar to what Meretsky *et al.* (2000) assumed (breeding at 6–8). Thus, even though condors have a small population size, they are unlikely to be exhibiting density-dependent increases in their observed breeding rate.

Conclusion

We provide a compressive assessment of the intrinsic and extrinsic factors affecting the reproduction of California Condors that can help inform conservation efforts for this species and large scavenging species worldwide. Our analyses suggest that reproduction will increase as the condor population matures because of the higher reproductive rates of older breeders. We found that the effects of two main threats to reproduction—DDE-associated hatch failure and chick mortality from trash ingestion—appeared to be stabilizing or decreasing. Finally, we found that lead exposure, already recognized as a primary threat to juvenile and adult survival, also lowered reproduction both directly and indirectly. Consequently, reductions in lead-related mortality can play a key role in the successful recovery of California Condors, not only by increasing survival of free-flying birds but also by improving the fertility of breeders.

Supplementary material

Supplementary material is available at *Ornithological Applications* online.

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Ethics statement

All data collection was conducted under IACUC approval and required state and federal permits.

Author contributions

VJB, MEF conceived of the idea. AW, JB, AP, JB, EAS, ERL, NESF collected the data. VJB and MEF analyzed the data and wrote the paper. All authors reviewed and edited the manuscript.

Data availability

Data and code to analyze reproductive rates of California Condors in the first two decades of reintroduction in California is available at Bakker *et al.* (2023).

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