Biological Conservation 291 (2024) 110447

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Practical models to guide the transition of California condors from a conservation-reliant to a self-sustaining species

Victoria J. Bakker[a,*], Myra E. Finkelstein[b], Daniel F. Doak[c], Steve Kirkland[d], Joseph Brandt[d], Alacia Welch[e], Rachel Wolstenholme[f], Joe Burnett[g], Arianna Punzalan[d], Peter Sanzenbacher[h]

[a] Department of Ecology, Montana State University, Bozeman, MT 59717, USA
[b] Microbiology and Environmental Toxicology Department, University of California, Santa Cruz, CA 95064, USA
[c] Department of Environmental Studies, University of Colorado, Boulder, CO 80309, USA
[d] US Fish and Wildlife Service, Ventura, CA 93003, USA
[e] National Park Service, Pinnacles National Park, Paicines, CA 95043, USA
[f] National Park Service, San Francisco, CA 94104, USA
[g] Ventana Wildlife Society, Monterey, CA 93940, USA
[h] US Fish and Wildlife Service, Palm Springs, CA 92262, USA

ARTICLE INFO

Keywords:
California condor
Population viability management
Conservation reliance
Lead
Tradeoffs
Catastrophes

ABSTRACT

California condors (*Gymnogyps californianus*) are a conservation-reliant species, needing ongoing management to prevent extinction in the wild. The free-flying California population depends on captive releases to achieve population growth, and lead poisoning from ingestion of spent lead ammunition is their primary threat. We used a population viability management approach to assess status and compare management actions to increase population growth and achieve self-sustainability. Specifically, we investigated how to optimize captive-breeding resources by comparing: the replacement of failed wild-laid eggs with captive-laid eggs vs. releases of captive-bred juveniles, releases of captive-bred juveniles in concentrated vs. dispersed timeframes, and releases of captive-bred juveniles vs. reductions in lead-related mortality. Releasing captive-bred juveniles bolstered the growth rate more than replacing eggs, and dispersed releases outperformed concentrated releases when population growth rates were lower, such as in current conditions. Importantly, even small, durable reductions in lead mortality outpaced annual releases, and the relative benefit of such reductions increased as the population grew. Further underscoring the importance of reducing adult mortality, we estimated that 2–3 captive-bred juveniles are needed to offset the loss of one free-flying adult. To assess population status and gauge recovery success, we recommend 3–4 years of time-averaged monitoring data. Finally, our analyses showed that recovery will require robustly growing populations to withstand catastrophic events. Overall, we illustrate the key role the captive-breeding program plays in the growth of the free-flying condor population in California and that a self-sustaining population is achievable through reductions in lead-related mortality.

1. Introduction

The majority of species listed as endangered under the U.S. Endangered Species Act (ESA) are considered conservation-reliant (Scott et al., 2010), such that over the long-term their threats “cannot be eliminated, but only managed” (Goble et al., 2012). While the term and its legal implications have been debated and refined since its introduction in 2005 (Goble et al., 2012; Rohlf et al., 2014; Scott et al., 2005), the strain that conservation-reliant species impose on the resources of management agencies and society in general remains undebatable (Scott et al., 2010). Transitioning species from conservation-reliance to self-sustainability frees up these resources and achieves the definition of recovery under the ESA (Doak et al., 2015; Rohlf et al., 2014).

Critically endangered California condors (*Gymnogyps californianus*) are a well-recognized conservation-reliant species (Scott et al., 2010). Extirpated in the wild in 1987, releases of captive-bred condors were initiated in 1992, and the global free-flying population increased to ~345 individuals by the end of 2022. Population growth has been achieved through a recovery strategy that rests on two pillars: a captive-breeding program, which provides juveniles for release to supplement

* Corresponding author.
E-mail address: vjbakker@gmail.com (V.J. Bakker).

https://doi.org/10.1016/j.biocon.2024.110447
Received 16 May 2023; Received in revised form 8 December 2023; Accepted 2 January 2024
Available online 15 February 2024

wild reproduction, and a threat management program, which implements strategies to increase wild survival and reproduction (USFWS, 2021). From 1992 to 2022, the predominant cause of mortality in free-flying condors (~50 % of known causes) has been lead poisoning from ingesting lead-based ammunition in terrestrial carcasses (Finkelstein et al., 2012; Rideout et al., 2012; Viner et al., 2020). After lead poisoning, the second leading anthropogenic cause of mortality was electrocutions and collisions at utility infrastructure (i.e., power lines and poles, Rideout et al., 2012).

Strategies to increase condor survival include outreach efforts aimed at decreasing the presence of lead-based ammunition in the environment and removal of hazards (e.g., power line burial) coupled with behavioral training (e.g., aversion training to inhibit landings on power poles, Mee and Snyder, 2007). Strategies to increase reproduction include replacing wild eggs with eggs from captive stock. Management of wild condors is facilitated by near-daily monitoring (via visual, camera, radio, and GPS tracking), regular health checks (including blood lead testing), and veterinary treatment when needed. Despite these efforts, California condor population growth has been reliant on releases of captive-bred individuals (Finkelstein et al., 2012).

Because condors are a classic *K*-selected species with a long lifespan, a low reproductive rate, and a generation time of 25 years (Bakker et al., 2022), attaining population sizes on a scale consistent with long-term self-sustainability will be a lengthy process regardless of whether it is achieved via captive releases or wild reproduction. However, unlike other conservation-reliant species that are expected to require management in perpetuity (e.g., Black-footed ferret, Kirtland's warbler, Rohlf et al., 2014), successful implementation of just one action, the societal switch to non-lead ammunition, would transition condors to self-sustainability (Finkelstein et al., 2012). Socio-political barriers to this switch have rendered California condors conservation reliant for the past 30 years, suggesting that this transition may occur on the timeframe of human generations (Cromie et al., 2019).

Compounding these challenges is the recent emergence of catastrophic mortality events linked to climate change and globalization. In 2020, 12 condors in California USA (> 10 % of the central California flock) were killed when a wildland fire burned through condor nesting and roosting habitat. In 2023, highly pathogenic avian influenza (HPAI) was confirmed or suspected of killing 21 condors in Arizona/Utah USA (~20 % of the Southwest flock, as of Dec 1, 2023).

Here we use a population viability management (PVM) approach (Bakker and Doak, 2009) to provide recommendations for maximizing the efficacy of actions to increase the wild California condor population in California. PVM is a process by which a collaborative team of modelers and managers use monitoring data to parameterize a population model that accounts for uncertainty and deploy this model to compare management actions using biologically meaningful metrics (e.g., population growth rate, see Bakker et al., 2009, Bakker and Doak, 2009). We used data on reproduction (Bakker et al., 2023) and on mortality from lead and other causes to parameterize a stochastic demographic matrix model for condors and used this model to predict their future status and to assess recovery actions. Specifically, we investigated: (1) how to maximize the value of captive-breeding resources, comparing egg replacements vs. juvenile releases and time-dispersed vs. time-concentrated releases, (2) how to maximize the efficacy of recovery actions, comparing allocation of management resources to captive breeding vs. lead reduction efforts, (3) how to mitigate anthropogenic mortality by estimating the number of captive juvenile releases required to compensate for the loss of an adult, (4) how to efficiently monitor population status, and (5) how to assess the potential effects of future catastrophes. All scenarios considered were identified as priorities for evaluation in collaboration with stakeholders (i.e., personnel from governmental, tribal, and non-profit organizations invested in condor conservation). To maintain focus on direct measures of recovery, we used demographic metrics (Bakker and Doak, 2009) rather than costs to compare recovery actions. Ultimately, we identify the conditions necessary to transition California condors from a conservation-reliant to a self-sustaining species.

2. Methods

2.1. Study system

During the study period, the free-flying California population of condors consisted of two somewhat distinct flocks, a southern California flock (hereafter, southern) managed by the U.S. Fish and Wildlife Service and a central California flock (hereafter, central) managed by Pinnacles National Park and Ventana Wildlife Society. Although the central and southern flocks are largely independent, there are occasional management transfers and interflock movements of individuals. Monitoring was conducted as part of ongoing management efforts under the authority of the U.S. Fish and Wildlife Service and was unique in its intensity. During the study period, all individuals were tagged with a vinyl tag on at least one wing, and most were given radio- or GPS-transmitters. Attempts were made on a near-daily basis to locate each individual visually, via telemetry, or on remote cameras at proffered feeding stations. Thus, all deaths were documented, and all recovered carcasses underwent necropsy. In addition, all nesting attempts were identified and monitored (Bakker et al., 2023). We parameterized our models with data from 1996, the first year that condors were present in both flocks, through August 2018; during this time the wild California population grew from 15 to 176 condors (Fig. 1).

2.2. Drivers of demographic rates: survival

We separated survival into two types: 1) *lead* survival (S_{Pb}), defined as $1 - M_{Pb}$, the annual probability of mortality determined by a pathologist to be lead-related, and 2) *other* survival (S_{other}, Green et al., 2022), defined as $1 - M_{other}$, the annual probability of mortality from all other causes, including missing in the wild. Assigning missing in the wild to S_{other} is a conservative assumption about total lead effects, since some missing birds almost certainly died from lead exposure. We used known fate models and fit additive age, sex, breeder class, and time-since-release effects with full and reduced model structures for annual and flock variance in S_{Pb} and S_{other} using Program MARK with bimonthly mortality data. We used the best AIC_C-supported models to estimate mean S_{Pb} and S_{other} for future simulations and used full year- and flock-varying models to estimate stochastic variance in annual survival rates (Bakker et al., 2009). We used a biological year (bioyear) increment starting at the approximate time condors fledge (Sep 1), which corresponds to the annual increment of our population model. Our survival analyses were based on data for all free-flying condors in California from bioyear 1996 (Sep 1996 – Aug 1997) through bioyear 2017 (Sep 2017 – Aug 2018). See Appendix A for additional details on survival analyses.

2.3. Drivers of demographic rates: reproduction

California condor reproductive rates over 20 years (1999, the first year that breeding-age birds were present, to 2018) were recently reported from the central and southern flocks (Bakker et al., 2023), and we used those rates here. We summarized annual reproduction as the number of female fledglings produced per female, broken down as the product of several individual probabilities: (*Recruit* or *Rebreed*) × *Clutch* × *Hatch* × *Fledge* × *Female.* To contribute a female offspring, a female must breed (i.e., lay an egg, clutch size is one) by recruiting into the breeding population (*Recruit*) or rebreeding as a recruited breeder (*Rebreed*). California condors recruit into the breeder class at ≥ 5 years and typically breed every other year (Bakker et al., 2023). The female and her mate must then successfully incubate the egg to hatching (*Hatch*) and rear the chick to fledging (*Fledge*). We assumed a 50 % probability that a fledged chick was female (*Female*). Foraging on marine mammals by central flock condors (Kurle et al., 2016) depresses

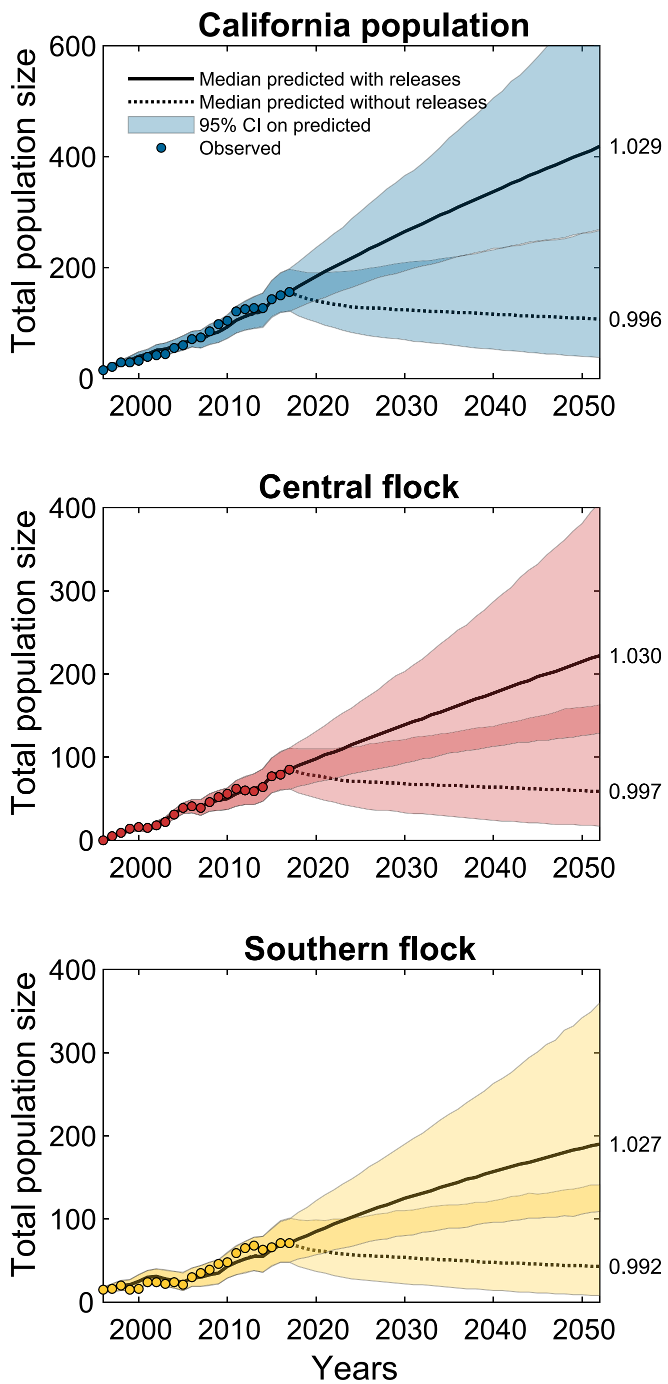

Fig. 1. Current status of California condors in California. Plots show model performance relative to observed population sizes for the California population of California condors using observed release rates of captive-bred juvenile condors for 1996–2018. Also shown are predicted future trajectories if current conditions persist, with and without ongoing releases at the *current release rate* (~8 per flock per year) for: (a) overall, (b), central flock, and (c) southern flock. Based on 5000 replicate runs for each scenario, text labels indicate median female λ_{ft}, (i.e., λ_{f34}, 2018–2052, for the ongoing release scenarios, solid line, and λ_{f25}, 2027–2052, for no-release scenarios, dotted line, starting 9 years after last release in 2018 to minimize effects of age structure skewed by juvenile releases). Shaded regions depict 95 % confidence intervals, or the 2.5th and 97.5th percentile of simulated population sizes for each year. Darker shaded regions represent overlap in confidence intervals.

Hatch (Bakker et al., 2023), presumably due to DDE-related eggshell thinning (Burnett et al., 2013). For model simulations, we assumed no effects of coastalness (an index of marine mammal feeding, Bakker et al., 2023) on *Hatch* in the southern flock, while in the central flock we assumed ongoing effects at the mean observed coastalness rate. We used the best AIC$_C$-supported models to predict the mean and variance of reproductive rates in simulations, and where supported, used the variance from random year effects to simulate environmental stochasticity. See Bakker et al. (2023) for additional details on reproductive rate analyses.

2.4. Population model overview

Using the survival and reproductive rates described above, we built a stochastic demographic matrix model that incorporated parameter uncertainty (Bakker et al., 2009) to predict future trajectories for the southern and central condor flocks separately as well as combined. The model assumed a fledging-time census with a Sep – Aug model year and consisted of a female-only matrix that tracked females by age and breeder class (similar to Bakker et al., 2018) (for female matrix see Appendix B, Table B3). We also tracked males in a separate matrix by age class, but given the observed male sex skew in the flocks (Bakker et al., 2023), we assumed males did not limit mate pairing, and thus we did not track male breeder class (for male matrix see Appendix B, Table B4). In summarizing simulation output, we refer to short-term realized stochastic lambda as λ_t, where t represents the number of years over which λ is summarized (i.e., $\left(\frac{N_t}{N_0}\right)^{\left(\frac{1}{t}\right)}$). We also summarized net gain in condors over the same timeframe as $N_{gained} = N_t - N_0$. For most simulations we focused on λ over 25 years or one condor generation (Bakker et al., 2022). In general, for simulations initiated at the stable age distribution, we track total population λ_t (males and females combined), but for simulations initiated at the observed population, which is male skewed, we track female lambda, λ_{ft}, to avoid the effects of changing sex skew on λ_t. Note that in most cases these parameter values are very similar. For each scenario considered, we ran 500–20,000 simulations, with differences in each simulation arising from parameter uncertainty, demographic stochasticity, and random year effects in reproduction and age-dependent S_{Pb} and S_{other}. Confidence bands on simulated trajectories represent the 2.5th and 97.5th percentile of simulated annual population sizes. To assess model fit, we simulated trajectories from 1996 onward, using observed releases, removals, coastalness, and nest management and compared predicted and observed population sizes. To assess the current status of condor flocks, we simulated future trajectories at current conditions from September 2018 onward with and without releases. See Appendix B for additional details on population model and scenarios.

2.5. Simulating futures with and without releases.

When projecting current conditions into the future with ongoing releases, we specified the *current release rate* as random draws from the observed sex- and flock-specific release schedules for bioyears 2014 through 2018. We chose to use 2014–2018 release rates to match the simulated demographic rates, which were also estimated from this time period. During this time, the mean annual total release rate was 7.6 in the central flock and 8.6 in the southern flock; releases were male skewed, and the mean annual female release rate was 3.4 for both flocks. The release rates from 2014 to 2018 were similar to those from 2019 through 2022, when the mean annual total release rate was 9.5 in the central flock and 6.3 in the southern flock.

When simulating future population dynamics following the cessation of releases and with populations initiated at the observed age distribution, we started tracking female λ_{f25} 9 years after releases ceased to avoid the transient effects of young-skewed age distributions; newly released birds and birds < 10 years post-fledge have lower survival than older adults (this analysis, Bakker et al., 2017). As such, these simulations ended in 2052 (2018 + 9 + 25). We compared these population dynamics to those with ongoing releases at the *current release rate*, for which we calculated lambda over the entire 34-year (9 + 25) timeframe (λ_{f34}).

As detailed below, for simulations based on a range of captive releases, we initiated populations at the stable age distribution, and we released equal numbers of males and females, with demographic stochasticity, to evaluate population dynamics at specified release numbers and without the influence of sex-skewed releases and thus summarized growth using total lambda (λ_{25}). While actual releases have been male-biased, we conducted these simulations without this bias to more clearly assess the effectiveness of releases in bolstering population numbers.

2.6. Maximizing the value of captive-breeding resources: egg replacements vs. juvenile releases

We compared predicted futures under a range of egg replacement and juvenile release scenarios. Specifically, we simulated from 0 to 16 eggs replaced in failed nests annually by increments of 2 eggs (hereafter denoted as minimum:increment:maximum, or 0:2:16 eggs) and from 0 to 16 captive juveniles released annually (0:2:16 releases). Simulated replacement eggs are assumed to hatch and have the same fledge probabilities as wild laid eggs (Bakker et al., 2023). We ran 500 replicates for each scenario (9 egg-replacement scenarios × 9 captive-release scenarios = 81 scenarios). We initiated the population at the stable age distribution estimated from mean vital rates, with 300 condors in each flock to ensure up to 16 failed nests in most years to accept replacement eggs. We recorded the number of eggs replaced annually and summarized the mean number replaced over 25 years (N_{eggs}), along with the number of captive-bred condors released annually ($N_{released}$). For each run, we also recorded total population λ_{25} and numbers of condors gained, N_{gained}. We fit general linear models (MATLAB fitglm) to predict λ_{25} and total N_{gained} based on N_{eggs} and $N_{released}$, comparing linear and interactive models via AIC, and plotted the best models to assess tradeoffs.

2.7. Maximizing the value of captive-breeding resources: dispersed vs. concentrated releases

We compared the relative effect of releasing captive juveniles at a constant annual rate (time-dispersed) to releasing the same number all at once (time-concentrated). Specifically, we simulated from 0 to 9 captives released annually for 25 years (note this maximum is close to the current annual release rate), by increments of 1 (0:1:9 releases) and from 0 to 225 captives released in year t_0 (i.e., 0:1:9 releases × 25 years). While the highest number of concentrated releases simulated is not feasible, this range of scenarios helps to highlight the tradeoff of dispersed vs. concentrated release strategies. For each scenario we varied the growth rate of the wild population by simulating a range of S_{Pb} and S_{other}, with proportional change, P, from 0 to 2 times the current mortality rates (0:0.25:2) ($S = 1 - (P \times (1 - S))$) for S_{Pb} and S_{other}. We ran 500 replicates for each scenario (10 dispersed scenarios + 10 concentrated scenarios = 20 scenarios × 9 mortality scenarios = 180 scenarios). We initiated the central and southern flocks at the observed total population sizes and age and sex distributions in late summer 2018, which were similar to current flock sizes ($N_{start\_ceca} = 89$ vs. 94 as of the end of 2022, $N_{start\_soca} = 87$ vs. 89 as of the end of 2022). We summarized results as the change in total flock size, N_{change}, over 25 years. We explored how the effectiveness of the two release strategies varied with the observed mortality rate for older adults (≥ 10 years post-fledge, $M_{oldAdult}$), which we focused on to discount the effects of higher mortality for newly released and younger individuals, and calculated the mean observed annual older adult mortality for each replicate. To quantify the relationship between older adult mortality and change in flock size for each release strategy, we fit an exponential function, $N_{change} = a \times e^{-b\, M_{oldAdult}}$, where a and b are coefficients (MATLAB fit, nonlinear least squares method and predint).

2.8. Maximizing the efficacy of recovery actions: captive juvenile releases vs. lead mortality

We compared the relative effects of increasing the numbers of juveniles released vs. decreasing lead mortality rates by simulating futures under a range of scenarios. Specifically, we simulated from 0 to 16 captive juveniles released annually (0:2:16 releases) and proportional change in the *lead* mortality rate ($S_{Pb} = 1 - (P \times (1 - S_{Pb}))$, where $P =$ 0:0.25:2), and initiated each flock at the stable age distribution at two population sizes, 100 and 300 condors, with 500 replicates for each scenario (9 captive scenarios × 9 *lead* mortality scenarios × 2 starting population sizes = 162 scenarios). We considered two population sizes because, unlike our other analyses, the actions compared here each scale differently with population size, and thus different actions might be supported at low vs. high population sizes. We summarized results using the methods described in *Egg replacements* vs. *juvenile releases*.

2.9. Mitigating anthropogenic mortality – the California condor replacement ratio (CCRR)

To inform conservation actions, we estimated the CCRR, or the number of releases of captive-bred juveniles required to compensate for the loss of one adult. To do so, we initiated each flock at 300 condors at the stable age distribution in year t_0 and simulated the removal of 10 females at year t_7 and the release of a range of captive-bred female juveniles in year t_7, including 0 (no replacement), 10 (1:1 rate of replacement with captive-bred juveniles), and higher replacement rates up to 34 (3.4:1 replacement rate). For computational efficiency, the specific range was informed by preliminary model runs and varied by scenario. We established the CCRR as the ratio of captive-bred juveniles per adult for which the number of total females and the number of adult (≥ 6 years post-fledge) females remained equal to or greater than the number in the absence of removals. We simulated two removal scenarios, a precautionary scenario in which females removed were assumed to be older adults (≥ 10 years post-fledge) successfully rearing a chick, and a random scenario in which females removed were taken at random from the adult (≥ 6 years post-fledge) breeder classes (e.g., successful breeder, failed breeder, skipper) proportional to class abundance. For all scenarios, we assumed that the loss of a successful breeder resulted in the loss of a chick. We assessed the CCRR based on the medians of 20,000 runs for each scenario for 25 years after the surviving released juveniles entered the older adult age class (i.e., $t_{17} - t_{42}$ for adult females). To represent uncertainty, for every year of each scenario, we drew 20,000 bootstrapped samples and took the difference of medians for release and baseline scenarios (i.e., no removals). Bootstrapped 95 % confidence intervals represent the release scenario for which the 2.5th and 97.5th percentile of number of females and adult females was greater than or equal to the baseline scenario.

2.10. Future monitoring

We investigated how to assess condor population status under a range of survival and reproductive rates in conditions otherwise similar to those of the current California population. We initiated flocks at the 2018 size, age, and sex distribution and simulated the *current release rate*. We proportionally altered S_{Pb} and S_{other} from 0 to 2 times the current mortality rate ($S = 1 - (P \times (1 - S))$, where $P =$ 0:0.25:2). Similarly, we varied hatch and fledge success by proportionally changing the hatch and fledge failure rate from 0.5 to 1.5 times the current rate (0.5:0.25:1.5). We ran 500 replicates for each scenario (9 mortality scenarios × 5 reproductive rate scenarios = 45 scenarios). We saved total annual observed adult mortality ($M_{adult} = N_{adultdied}/N_{adultstart}$) and nest success ($N_{succ}/(N_{succ} + N_{fail})$) at fledging time. We used these observed data to build logistic models to predict the probability the population would be self-sustaining (stable or growing). Because we simulated futures with releases, we were unable to use realized stochastic λ_{25}, which is based on changes in total numbers, as a measure of population health, as this parameter can indicate a positive population growth due to releases, even if without releases the population would be declining. Thus, we defined a self-sustaining population as one in which the mean stochastic log lambda, $\bar{\lambda}_{f\_i}$, over each 25-year run, $\bar{\lambda}_{f\_i} = e^{\mathrm{mean}(\log\lambda_{f\_i})}$, was > 1, where λ_{f_i} is the dominant eigenvalue of the annual female population matrix. The mean of the log of these growth rates provides a simple estimate of mean stochastic growth rate, which includes stochastic variance in demographic rates, but excludes demographic stochasticity and is not influenced by release rates or varying age structure. We used AIC to identify the best models to predict $\bar{\lambda}_{f\_i}$ (i.e., survival, nest success, or linear or interactive combinations) when monitoring all (100 %) or a random subset (25, 50, 75 %) of the population and when using annual or time-averaged data. We compared model performance in correctly predicting growing ($\bar{\lambda}_{f\_i} > 1$) or declining ($\bar{\lambda}_{f\_i} < 1$) populations in two ways: (1) *high-confidence* assessments, in which model predictions of $P(\bar{\lambda}_{f\_i} > 1) > 0.8$ were predictions of growth and predictions of $P(\bar{\lambda}_{f\_i} > 1) < 0.2$ were predictions of decline, and (2) *best-estimate* assessments, in which 0.5 was used as the threshold probability to predict growth or decline.

2.11. Catastrophic events

To assess the effects of catastrophic events, which can kill multiple individuals in a short timeframe, we simulated catastrophe scenarios given current conditions in two ways. First, we ran scenarios from 1996 to 2052, similar to those used to assess population status, with catastrophes starting after 2018 at a mean frequency of 2, 4, and 8 years, with and without future releases at the *current release rate*. Catastrophes occurred immediately after fledging and releases and removed 20 % of the population randomly in proportion to the sex, age, and breeder class distribution, with demographic stochasticity.

Second, we evaluated the relationship between catastrophic intensity and frequency with and without future releases. To simulate catastrophes with releases, we initiated populations at the 2018 size and age and sex distribution and simulated future trajectories with the *current release rate* and recurring catastrophes. We simulated a range of catastrophic intensities (proportion of population removed: 0.0:0.05:0.30) and frequencies (mean return frequency: 2:2:12 years, where annual event probability is return frequency^{-1}) with 500 replicates for each scenario (2 release scenarios × 7 intensities × 6 frequencies = 84 scenarios). For scenarios in which releases ceased in 2018, we calculated female λ_{ft} starting 9 years after releases ceased (see *Simulating futures with and without releases*). For these simulations without future releases, we initiated runs at three times the 2018 population size but at the observed sex, age, and breeder class distribution to avoid numerous extinctions for the most severe catastrophic scenarios. We compared the relative influence of catastrophe frequency and intensity on λ_{ft} using a cubic spline to interpolate contour lines (MATLAB griddata).

3. Results and discussion

3.1. Survival: lead continues to be the leading cause of mortality for free-flying California condors

Lead accounted for 25.9 % of 158 total deaths of condors in California for bioyears 1996 through 2017. *Other* mortality was attributed to: missing in the wild (24.1 %), undetermined (12.0 %), predation (10.8 %), collision and electrocution related to utility infrastructure (7.0 %), drowning (4.4 %), disease and poor condition (3.8 %), fire (3.8 %), shooting (3.2 %), trauma (not related to utility infrastructure or vehicles, 2.5 %), entanglement (1.3 %), poisoning (not lead, 0.6 %), and vehicle trauma (0.6 %). Many factors predisposing individuals to *other* mortality are associated with naiveté. Consistent with this hypothesis, S_{other} increased with age and time-since-release, both of which are experience-related. The best age and time-since-release structure for S_{other} included a continuous age effect until 1-year post-fledging ($age_{TrendTo1}$), a continuous time-since-release effect until 2 years after release ($tsr_{TrendTo2}$) and a negative juvenile (1 to 5 years post-fledge) effect for females (*f:juvenile,* See Appendix A, Table A1 for variable definitions and Appendix B, Table B2 for regression coefficients used to estimate survival and reproductive probabilities to parameterize population matrix). Thus, survival increased with age until 1 year post-fledge and then stabilized, except for juvenile females, which had lower survival. Survival of captive-bred birds increased until 2 years from initial release, after which time their survival equaled that of wild birds of the same age. There was no support for an interaction between $tsr_{TrendTo2}$ and age, suggesting the mortality hazard for released birds reflected inexperience in the wild, regardless of age (while most birds were released at age 1.5 years, ages of released birds in the dataset ranged from 0.5 to 36 years). There was no detectable effect of being a recruited breeder, breeding in the previous year, or currently rearing an egg or chick. The best temporal models included early trends in S_{other} for the newly established flocks (until 2001 in central, $yr_{TrendTo2001:ceca}$ and 2004 in southern, $yr_{TrendTo2004:soca}$), followed by constant survival, with higher S_{other} in the central flock (Table A5, overall best-supported model for $S_{other} = Flock + yr_{TrendTo2001:ceca} + yr_{TrendTo2004:soca} + tsr_{TrendTo2} + age_{TrendTo1} + f{:}juvenile$). We used the mean S_{other} after initial trends stabilized to simulate S_{other} for our population model.

Unlike $S_{other,}$ we found no experience-related gains in S_{Pb} (Table A7-A8). The best model for S_{Pb} was $S_{Pb} = youngAdult$ (Table A10), indicating lower S_{Pb} for young adults (6 to 10 years post-fledge) with no temporal variance. In general, *lead* mortality was more of an equal-opportunity killer than *other* mortality, with constant risk exhibited across sexes, flocks, and time. Although the cause of higher *lead* mortality for young adults is unknown, it may arise from subtle behavioral differences, selective loss of birds physiologically more vulnerable to lead toxicity, or other unknown factors. Likewise, we do not know why female juveniles experienced lower S_{other}, but since this effect was associated with an increased incidence of going missing in the wild, it may be due in part to unattributed lead poisoning. Others have reported age- and sex-related differences in survival in related species and hypothesized anthropogenic causes such as contaminants (Andean condors, Lambertucci et al., 2012; Egyptian vultures, Sanz-Aguilar et al., 2017). Together, the observed patterns of S_{Pb} (lower for young adults) and S_{other} (lower for early post-fledges and juvenile females) result in higher overall survival for older adults. *Lead* mortality represented a substantial fraction of the mortality rate across all adult age groups and flocks (ranging from 0.33 for southern older adults to 0.58 for central young adults).

Due to early fluctuations in the small flock sizes, we only used data from the second half of the time series (2007–2017) to estimate stochastic variance for our future projections, which we based on models with full flock × year variance and additive age effects (Table A7).

A prior survival analysis (Bakker et al., 2017) analyzed data through 2013 and did not separate S_{Pb} and S_{other} but focused on drivers of total survival and incorporated condor behavior (e.g., observed rate of feeding on proffered carcasses) to identify survival trends after accounting for behavior changes. With the current analysis, we added 5 years of data, substantially increasing the sample size, which allowed us to test for finer-scale differences in survival with age, sex, and time since release. Individuals bred in captivity often have lower survival when first introduced to the wild (Evans et al., 2009), and we also used our larger database to refine the length of the time-since-release effect detected previously (Bakker et al., 2017).

3.2. *Population status: growth of the free-flying condor population relies on captive-bred releases*

Consistent with prior models (Finkelstein et al., 2012), we found that growth of the condor population in California continues to be dependent upon the release of captive-bred juveniles (Fig. 1). In the absence of management or releases, our models predict that overall, the California population of condors is slightly declining ($\lambda_{f25} = 0.996$), and that both flocks show these declining trends (central $\lambda_{f25} = 0.997$, southern, $\lambda_{f25} = 0.992$), although confidence bands span one in all cases (Fig. 1). Continuing releases at the *current release rate* results in increasing population growth ($\lambda_{f34} = 1.029$, 1.030, and 1.027 for overall, central, and southern flocks respectively).

A prior demographic model indicated that, in the absence of releases, the condor population was stable (female deterministic lambda, $\lambda_{f\,det} = 1.0003$, Finkelstein et al., 2012) while our current model indicates the population is slightly declining. However, the two models generate remarkably similar findings considering their differences in structure and analysis methods. In particular, our current model increased realism in two ways. First, we included demographic and environmental stochasticity as well as parameter uncertainty in survival and reproductive rates, while the 2012 model excluded these effects, an approach known to bias growth rates high (Caswell, 2001; Morris and Doak, 2002). Excluding demographic and environmental stochasticity and parameter uncertainty from our current model runs increased population growth rate estimates by ~0.004 (California population $\lambda_{f25} = 0.999$, central $\lambda_{f25} = 1.001$, southern, $\lambda_{f25} = 0.996$). Second, the 2012 model analyzed reproductive rates without accounting for management interventions that maximize reproduction, and thus that study's 'no management' predictions implicitly assumed the continuation of nest management. In contrast, we used analyses that accounted for nest management (i.e., by classifying nests receiving intensive management as failures, Bakker et al., 2023) and thus our 'no management' predictions assume the cessation of nest management. Despite the different models and assumptions, both analyses emphasize the pivotal role that captive releases play in maintaining population growth and the importance of reducing lead-related mortality to transition condors from conservation reliant to self-sustaining.

3.3. *Maximizing the value of captive-breeding resources: juvenile releases increase population growth more than egg replacements*

Across a broad range of mortality conditions, the release of a captive-bred juvenile had almost double the effect on realized stochastic growth rate compared to the use of an egg laid in captivity to replace a failed wild egg (Fig. 2a-d). The annual captive production required to increase the flock size by 50 birds over one generation for the central flock was five captive eggs vs. three captive-bred juveniles and for the southern flock was six captive eggs vs. three to four captive-bred juveniles (Appendix B, Fig. B1). Thus, given limited resources, investing in rearing captive juveniles for release boosts the population more than using those

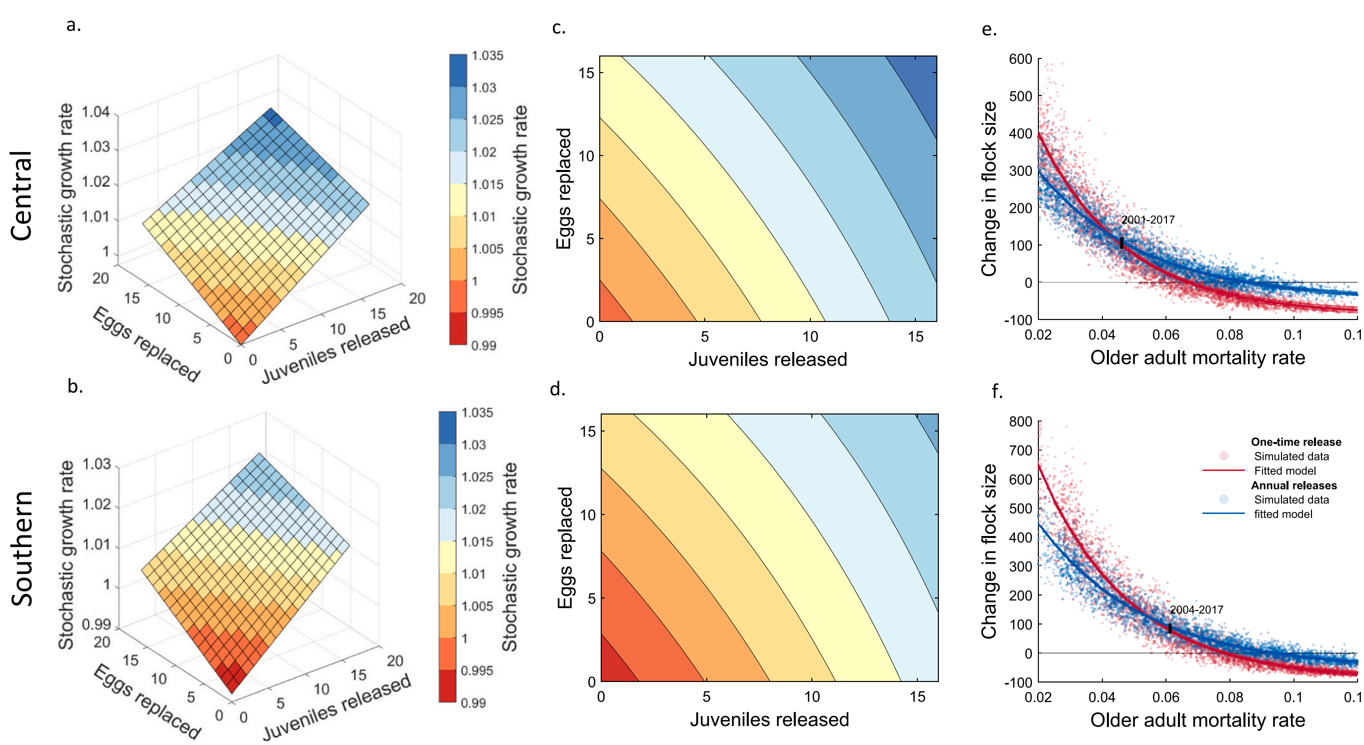

Fig. 2. Maximizing the value of captive-breeding resources. Three-dimensional planes in left panels (a, b) show tradeoffs in realized total stochastic growth rate, λ_{25}, when allocating captive propagation towards replacing failed eggs in wild nests vs. releasing captive-bred juveniles for: (a) central and (b) southern flocks, while middle panels (c, d) use contour plots to convey the same tradeoffs. (See Appendix B, Fig. B1 for tradeoffs in numbers of condors gained over 25 years.) Right panels (e, f) show tradeoffs in total flock size when releasing a total of 200 captive-bred juveniles at a constant annual rate of 8 birds over 25 years (i.e., time-dispersed, shown in blue) vs. releasing the same total number of juveniles (200) in a one-time release (i.e., time-concentrated, shown in red) across a range of older adult (≥ 10 years post-fledge) mortality rates for the (e) central and (f) southern flocks, with 95 % prediction intervals. Vertical black line represents overall older adult mortality rate for the years 2001–2017 (e, central flock) and 2004–2017 (f, southern flock). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

resources to produce captive-laid eggs to replace failed wild-laid eggs. We do not have the information to directly compare the financial and personnel costs of these management interventions, but tradeoffs are complex. Rearing a bird to be released as a juvenile is more resource intensive for captive breeding facilities than producing an egg, but exchanging eggs is also resource intensive, requiring regular monitoring of wild nests, including potentially difficult nest entries to detect failed nests, and a second entry for egg placement. As a result of on our finding that juvenile releases had a higher value to population growth, condor recovery personnel ceased to use egg replacements as a management strategy in the case of egg failure in most circumstances by 2015 (Appendix B, Fig. B2).

3.4. Maximizing the value of captive-breeding resources: benefits of concentrated vs. dispersed juvenile releases dependent upon population growth rate

The efficacy of time-concentrated vs. time-dispersed release strategies was governed by the mortality rate. The relative efficacy of the two strategies was essentially the same across the range of release rates simulated, and thus we illustrate the predicted trade-offs with 200 one-time released birds (concentrated) vs. 8 birds released annually (dispersed, and comparable to *current release rate*) (Fig. 2e-f). A time-concentrated release was more effective if the older adult mortality rate was very low; releasing captive individuals in a single event was always more effective than a time-dispersed release if the mean older adult mortality rate was < 0.043 in the central flock and < 0.055 in the southern flock. Ultimately, these thresholds correspond to the transition between increasing and decreasing population growth rates, as would be expected by theory: a concentrated release is favored in a growing population because birds released early will contribute to future population growth, whereas a dispersed strategy is favored in a declining population because birds released later have more relative value. The slightly lower mortality cutoff for the central flock results from its lower reproductive rate, due to DDE-associated impairment in hatching (Bakker et al., 2023; Burnett et al., 2013), necessitating lower mortality to achieve the same population growth as the southern flock. The current observed older adult mortality rate for both flocks is close to the breakeven point for these two approaches but favors dispersed releases as the population is currently declining (Figs. 1, 2e-f). While the concentrated release strategy is likely infeasible for all but the low end of the release range (e.g., 1–2 birds released annually vs. 25–50 released all at once), we simulated a wider range to better elucidate tradeoffs in concentrated vs. dispersed release strategies with increasing numbers of released individuals. The consistency of our conclusions across the range of releases examined clarified that this contrast is invariant to release

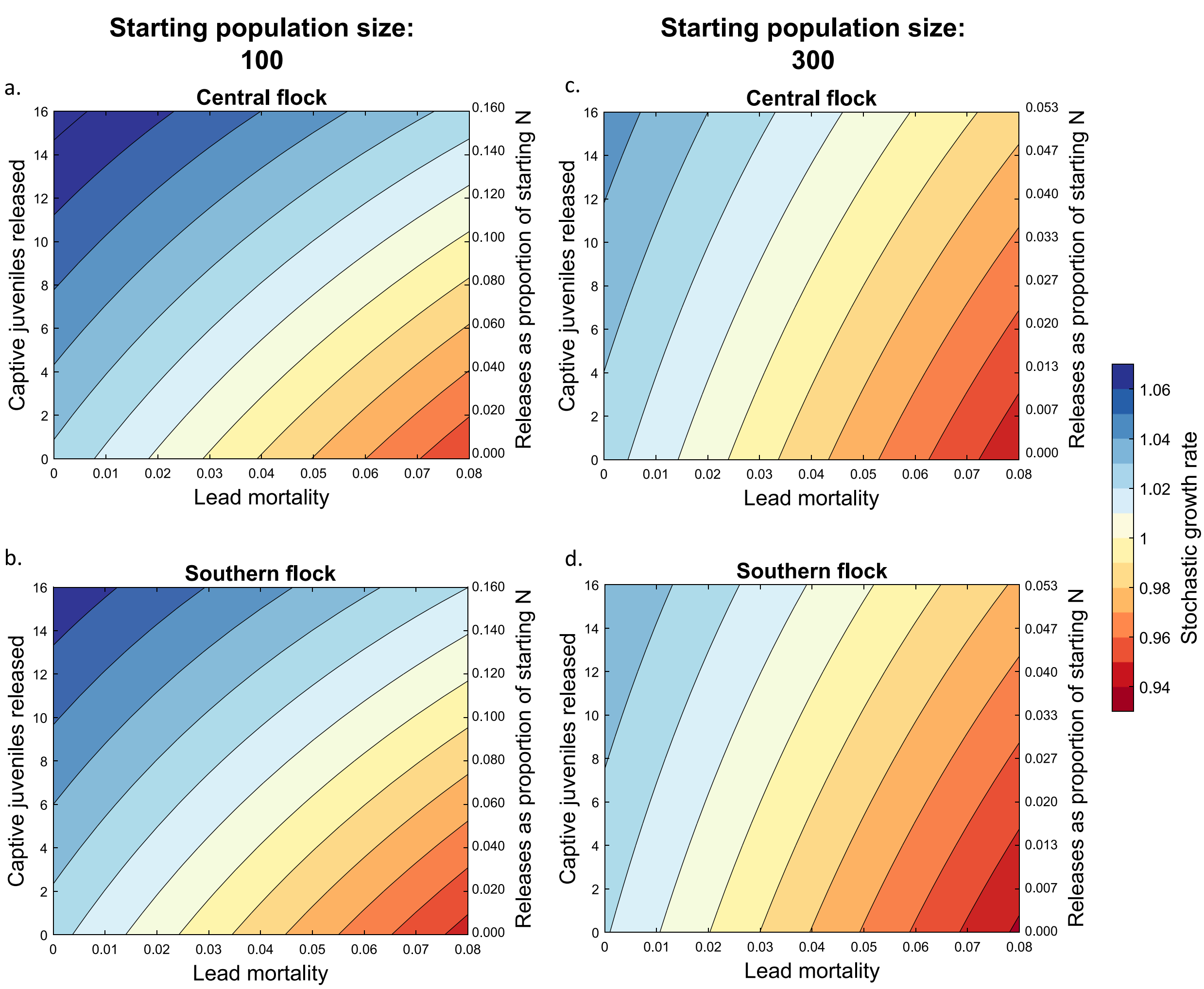

Fig. 3. Maximizing the efficiency of recovery actions. Panels compare strategies focused on enhancing survival (reducing lead mortality) vs. reproduction (increasing captive breeding). Shown are the tradeoffs in realized total stochastic growth rate, λ_{25} for the (a, c) central and (b, d) southern flocks when reducing lead mortality vs. increasing releases of captive-bred juveniles for flocks initiated at population sizes of 100 and 300 condors at the stable age distribution. X-axis depicts mean annual total observed lead mortality rate across 25 years, left y-axis depicts the number of captive-bred juveniles released annually, and right y-axis expresses annual releases as a proportion of starting population size.

number, underscoring the primacy of the lead mortality threat for condor recovery and contextualizing the value of releases in different demographic settings.

3.5. Maximizing the efficacy of recovery actions: small reductions in the lead mortality rate can increase population growth more than releasing captive-bred juveniles

In both central and southern flocks, decreasing lead mortality by 0.01 yields gains in λ_{25} that are comparable to increasing the annual release of captive-bred juveniles by 2 to 3 birds with flock sizes similar to current numbers ($N_{start} = 100$, Fig. 3a-b). The effect of reducing lead mortality scales with population size in a way that increasing releases does not, which leverages its relative efficacy at larger population sizes. Thus, when starting flock sizes are 300 (Fig. 3c-d), annual releases of $\sim$7 captive juveniles per flock are needed to equal the benefits of reducing lead mortality by 0.01. By comparing a reduction in lead-related mortality to captive juvenile releases, our analyses provide a tangible measure of the potential efficacy of interventions that achieve even small durable changes in the amount of lead on the landscape. Given the substantial resources required to produce captive condors for annual release, our analyses suggest that efforts to reduce lead on the landscape could yield ongoing dividends for condor conservation. Ultimately, reductions in lead mortality can replace zoo-derived population growth with intrinsic wild population growth and thus transition condors from conservation reliant to self-sustaining.

3.6. Mitigation for anthropogenic mortality – the estimated California Condor Replacement Ratio (CCRR) indicates 2 – 3 captive-bred juveniles are required to offset the loss of one adult

Captive-bred juveniles cannot compensate for the loss of adults in a 1:1 ratio for several reasons. Released juveniles have lower survival relative to wild juveniles for 2 years after release and also experience lower survival as juveniles and young adults relative to older adults (Appendix A). Juveniles also require at least 3.5 years before recruiting into the breeder class, and breeding success increases with age up until the older adult age class (Bakker et al., 2023). Thus, we used the CCRR to estimate the combined effects of these differences between captive-bred juveniles and free-flying adults. The California condor replacement ratio, or the number of released captive-bred juveniles required to offset the loss of one adult (with bootstrapped 95 % CIs) was 2.6 (2.2–3.0) and 2.0 (1.8–2.4) in the central flock and 3.0 (2.6–3.4) and 2.6 (2.0–2.6) in the southern flock for precautionary (Appendix B, Figs. B3, B5) and random removal assumptions (Figs. B4, B6), respectively. The greater CCRR for the southern flock derives from its lower survival rates (this analysis) and higher reproductive rates (Bakker et al., 2023) that increase the relative impact of removing adults. The CCRR analysis complements our other analyses weighing trade-offs in lead mortality vs. captive releases by reinforcing the importance of adults relative to captive-bred juveniles for population growth. The CCRR approach has recently been used to establish offsets for potential adult mortality in permitting wind energy facilities, with managers favoring precautionary assumptions to buffer against uncertainty and future changes in population status (ICF and WEST, 2022). This mitigation is expected to be achieved via the expansion of capacity at captive breeding facilities (Avangrid, 2021; ICF and WEST, 2023).

3.7. Future monitoring should emphasize time-averaged survival

Time-averaging of monitored demographic rates, consistent with recovery monitoring approaches for other species (Bakker and Doak, 2009), increased the ability to distinguish growing populations from declining populations by reducing the noise arising from annual stochastic fluctuations (see Appendix B for full results). However, gains in model performance began to slow after three years of time averaging suggesting that three years was an optimal balance between speed and accuracy in assessment of current trends. While we did not simulate changing conditions, we recommend time averaging over the shortest timeframe possible (e.g., 3 years) to achieve desired status assessment goals while avoiding errors from unforeseen influences on demographic rates. Below we provide examples of optimal sampling strategies, which maximize model performance (correct status assessment rate > 0.8 using *best-estimate* methods) by time-averaging over the shortest timeframe, and alternative strategies that achieve similar performance by averaging data over longer timeframes:

Central

- Optimal: survival sampling rate: 100 %, nest sampling rate: 25 %, 3-year averaging
- Alternative: survival sampling rate: 75 %, nest sampling rate: 50 %, 4-year averaging

Southern

- Optimal: survival sampling rate: 100 %, nest sampling rate: 0, 3-year averaging
- Alternative: survival sampling rate: 75 %, nest sampling rate: 25 %, 4-year averaging

3.8. Recent catastrophic events heighten the importance of maintaining positive growth for the wild population

If catastrophic events that killed 20 % of individuals occurred every 4 years, the California population, which is currently exhibiting moderate growth due to releases ($\lambda_{f34} = 1.029$), would essentially cease to grow even with releases ($\lambda_{f34} = 1.002$, Fig. 4a). In the absence of releases, a slowly declining California population ($\lambda_{f25} = 0.996$) would become a rapidly declining one ($\lambda_{f25} = 0.941$) (Fig. 4b).

The recent emergence of wildland fires and HPAI, which killed 10–20 % of individuals in the central California and Southwest flocks, underscores the need to manage condors for growth and resilience (Fig. 4c-d). Indeed, our simulations predicted that a stable or slightly growing population would not withstand recurring catastrophes, such as zoonotic diseases and wildland fire, which are expected to increase due to climate change (IPCC, 2022). Because HPAI is an emerging threat, and we do not yet know the frequency or intensity of future outbreaks (Harvey et al., 2023), we did not attempt to simulate realistic within-flock spread or temporal dynamics. HPAI, along with wildland fires, serve as examples of the types of catastrophic mortality events that can and will periodically affect California condor flocks, in addition to documented ongoing mortality.

3.9. Applying the Population Viability Management (PVM) process to California condors and other conservation-reliant species

A PVM approach (Bakker and Doak, 2009) can be particularly effective for guiding the ongoing management of conservation-reliant species because their population health is, by definition, reliant on conservation actions in perpetuity. PVM is inherently iterative, and here we present one cycle in this process (see Appendix B, Fig. B10 for a detailed explanation of the steps in the PVM process and their specific application to California condors). Analyses such as the ones we present here can be used to identify and prioritize management actions that maximize demographic gains. Future iterations can account for changing threats, demographic rates, and management options. Where feasible, including cost estimates can further increase efficient use of limited conservation resources. For California condors, the PVM process clarified that reducing lead poisoning to low levels would end its conservation reliance and thus provides a critically important example for the management of other endangered species.

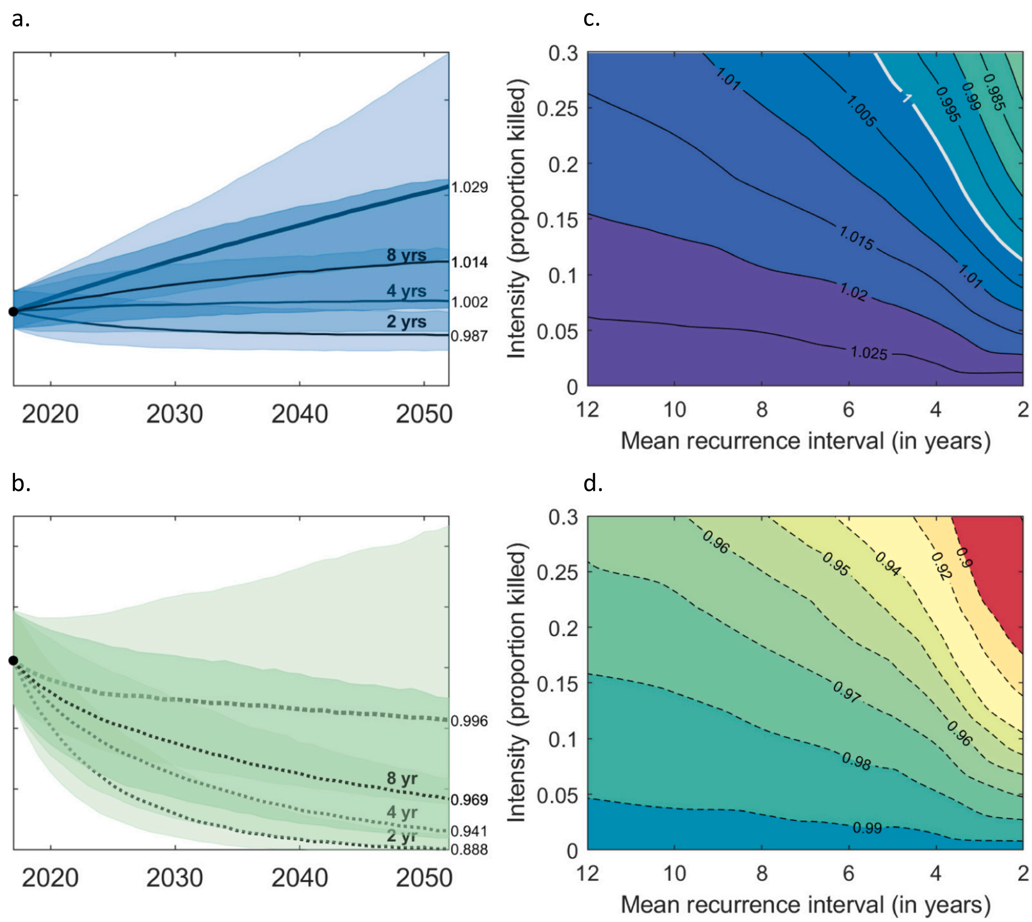

Fig. 4. The effect of catastrophes on the population growth rate of California condors in California. Left panels (a, b) depict observed trajectories of the California population (a) with and (b) without ongoing releases at the *current release rate* and with catastrophes randomly removing 20 % of the population at a mean recurrence interval of 2, 4, and 8 years. Solid and dotted black lines represent the medians of 5000 replicate simulations. Shaded regions depict 95 % confidence intervals, or the 2.5th and 97.5th percentile of simulated population sizes for each year, and darker regions represent overlap in confidence intervals. Right panels (c, d) depict the relative effects of the intensity and frequency of catastrophes on λ_{ft} (c) with and (d) without ongoing releases at the *current release rate*. For all panels, text labels indicate median female realized stochastic lambda λ_{ft}, (i.e., λ_{f34}, 2018–2052, for ongoing release scenarios and λ_{f25}, 2027–2052, for no-release scenarios, starting 9 years after last release to minimize effects of age structure skewed by juvenile releases).

4. Conclusion

Over the past 15 years, two policy changes in California restricted the use of lead-based ammunition (i.e., Ridley-Tree Act, AB711), but they have not eliminated all uses of lead-based ammunition within the state. In addition, studies examining regulations on lead-based ammunition elsewhere documented only partial compliance (e.g., Cromie et al., 2015; Widemo, 2021). We found that condors in California continue to be lead-poisoned at a rate that prevents recovery. Condors exhibiting more 'wild' behaviors, such as roaming far from the management area (i.e., area where food was proffered or daily monitoring occurred) experience higher mortality, and these behaviors have increased over time as the flocks have grown in size and contain more older and experienced individuals (Bakker et al., 2017). Thus, changing condor behaviors are likely an important factor offsetting the gains of policy changes and outreach activities. The ongoing lead-related mortality renders the California population of condors conservation reliant, and we used our models to identify conservation actions that maximize population growth. Our simulations showed that releasing captive-bred juveniles yields more growth than replacing eggs, that time-dispersed releases currently outperform concentrated releases, and that 2–3 captive-bred juveniles are needed to offset the loss of one free-flying adult condor. We also highlight the need for a robustly growing condor population to withstand catastrophic mortality events, such as the recent wildland fire and HPAI outbreak. Finally, we contrast lead reduction and captive release strategies and demonstrate that even small declines in lead mortality rates can substantially reduce reliance on captive breeding. Taken together, our analyses underscore the need to prioritize lead-reduction efforts while continuing the efficient use of captive-breeding resources to maintain a growing wild condor population. Indeed, we show that unless lead-related mortality is reduced, California condors in California will remain conservation reliant.

CRediT authorship contribution statement

Victoria J. Bakker: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Writing – original draft, Writing – review & editing. **Myra E. Finkelstein:** Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Project administration, Writing – original draft, Writing – review & editing. **Daniel F. Doak:** Conceptualization, Methodology, Writing – original draft, Writing – review & editing. **Steve Kirkland:** Conceptualization, Funding acquisition, Methodology, Writing – review & editing, Data curation. **Joseph Brandt:** Conceptualization, Data curation, Methodology, Writing – review & editing. **Alacia Welch:** Conceptualization, Data curation, Funding acquisition, Writing – review & editing, Methodology. **Rachel Wolstenholme:** Conceptualization, Data curation, Funding acquisition, Methodology, Writing – review &

editing. **Joe Burnett:** Conceptualization, Data curation, Methodology, Writing – review & editing. **Ariana Punzalan:** Conceptualization, Data curation, Methodology, Writing – review & editing. **Peter Sanzenbacher:** Conceptualization, Data curation, Funding acquisition, Methodology, Writing – review & editing.

Declaration of competing interest

The authors declare no competing interests.

Data availability

Data and code used to generate the results are listed in Appendix C and available from the corresponding author upon request.

Acknowledgements

We thank the following individuals and institutions for support, guidance, and data collection efforts: Don Smith, Nacho Vilchis, Tim Huntington, LightHawk, Pinnacles National Park, Ventana Wildlife Society, U.S. Fish and Wildlife Service, Los Angeles Zoo, Oakland Zoo, Oregon Zoo, San Diego Zoo Global, Santa Barbara Zoo, and The Peregrine Fund. This article benefited from the constructive feedback of two anonymous reviewers. Our work was funded in part by the U.S. Fish and Wildlife Service and Pinnacles National Park.

Author statement

The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the National Park Service or the U.S. Fish and Wildlife Service.

Appendices A - C. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2024.110447.

References

Avangrid Renewables LLC, Dudek and Nossaman LLP, 2021. Manzana Wind Power Project California Condor Conservation Plan. May.
Bakker, V.J., Doak, D.F., 2009. Population viability management: ecological standards to guide adaptive management for rare species. Front. Ecol. Environ. 7, 158–165.
Bakker, V.J., Doak, D.F., Roemer, G.W., Garcelon, D.K., Coonan, T.J., Morrison, S.A., Lynch, C., Ralls, K., Shaw, M.R., 2009. Incorporating ecological drivers and uncertainty into a demographic population viability analysis for the island fox. Ecol. Monogr. 79, 77–108.
Bakker, V.J., Smith, D.R., Copeland, H., Brandt, J., Wolstenholme, R., Burnett, J., Kirkland, S., Finkelstein, M.E., 2017. Effects of lead exposure, flock behavior, and management actions on the survival of California condors (*Gymnogyps californianus*). EcoHealth 14, 92–105.
Bakker, V.J., Finkelstein, M.E., Doak, D.F., VanderWerf, E.A., Young, L.C., Arata, J.A., Sievert, P.R., Vanderlip, C., 2018. The albatross of assessing and managing risk for long-lived pelagic seabirds. Biol. Conserv. 217, 83–95.
Bakker, V.J., Finkelstein, M.E., D'Elia, J., Doak, D.F., Kirkland, S., 2022. Genetically based demographic reconstructions require careful consideration of generation time. Curr. Biol. 32, R356–R357.
Bakker, V.J., Finkelstein, M.E., Doak, D.F., Wolstenholme, R., Welch, A., Burnett, J., Punzalan, A., Brandt, J., Kirkland, S., Seal Faith, N.E., Lehnert, E.R., Sandhaus, E.A., 2023. 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. Ornithol. Appl. 125, 1–13.
Burnett, L.J., Sorenson, K.J., Brandt, J., Sandhaus, E.A., Ciani, D., Clark, M., David, C., Theule, J., Kasielke, S., Risebrough, R.W., 2013. Eggshell thinning and depressed hatching success of California condors reintroduced to central California. Condor 115, 477–491.
Caswell, H., 2001. Matrix Population Models: Construction, Analysis and Interpretation,, 2nd edition. Sinauer Associates, Sunderland, Massachusetts.
Cromie, R., Newth, J., Reeves, J., O'Brien, M., Beckmann, K., Brown, M., 2015. The sociological and political aspects of reducing lead poisoning from ammunition in the UK: why the transition to non-toxic ammunition is so difficult. In: Proceedings of the Oxford Lead Symposium. Lead Ammunition: Understanding and Minimising the Risks to Human and Environmental Health. ed. C.J.S. R.J. Delahay. Edward Grey Institute, University of Oxford, Oxford, pp. 104–124.
Cromie, R., Newth, J., Strong, E., 2019. Transitioning to non-toxic ammunition: making change happen. Ambio 48, 1079–1096.
Doak, D.F., Himes Boor, G.K., Bakker, V.J., Morris, W.F., Louthan, A., Morrison, S.A., Stanley, A., Crowder, L.B., 2015. Recommendations for improving recovery criteria under the US Endangered Species Act. Bioscience 65, 189–199.
Evans, R.J., Wilson, J.D., Amar, A., Douse, A., Maclennan, A., Ratcliffe, N., Whitfield, D. P., 2009. Growth and demography of a re-introduced population of White-tailed Eagles *Haliaeetus albicilla*. Ibis 151, 244–254.
Finkelstein, M.E., Doak, D.F., George, D., Burnett, J., Brandt, J., Church, M., Grantham, J., Smith, D.R., 2012. Lead poisoning and the deceptive recovery of the critically endangered California condor. Proc. Natl. Acad. Sci. 109, 11449–11454.
Goble, D.D., Wiens, J.A., Scott, J.M., Male, T.D., Hall, J.A., 2012. Conservation-reliant species. Bioscience 62, 869–873.
Green, R.E., Pain, D.J., Krone, O., 2022. The impact of lead poisoning from ammunition sources on raptor populations in Europe. Sci. Total Environ. 823, 154017.
Harvey, J., Mullinax, J., Runge, M., Prosser, D., 2023. The changing dynamics of highly pathogenic avian influenza H5N1: next steps for management & science in North America. Biol. Conserv. 282, 110041.
ICF and WEST, 2022. Wind Energy Condor Action Team (WECAT) – Condor Conservation Plan. Draft. December. (ICF 556.20.) Sacramento, CA. Prepared for WECAT, Jacksonville, OR.
ICF and WEST, 2023. Wind Energy Condor Action Team (WECAT) – Condor Conservation Plan. Sacramento, CA. Prepared for WECAT, Jacksonville, Oregon.
IPCC, 2022. Climate Change 2022: Impacts, Adaptation, and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [H.-O. Pörtner, D.C. Roberts, M. Tignor, E.S. Poloczanska, K. Mintenbeck, A. Alegría, M. Craig, S. Langsdorf, S. Löschke, V. Möller, A. Okem, B. Rama (eds.)]. Cambridge University Press. Cambridge University Press, Cambridge, UK and New York, NY, USA, 3056 pp. https://doi.org/10.1017/9781009325844.
Kurle, C.M., Bakker, V.J., Copeland, H., Burnett, J., Jones Scherbinski, J., Brandt, J., Finkelstein, M.E., 2016. Terrestrial scavenging of marine mammals: cross-ecosystem contaminant transfer and potential risks to endangered California condors (*Gymnogyps californianus*). Environ. Sci. Technol 50, 9114–9123.
Lambertucci, S.A., Carrete, M., Antonio Donazar, J., Hiraldo, F., 2012. Large-scale age-dependent skewed sex ratio in a sexually dimorphic avian scavenger. PLoS One 7, e46347.
Mee, A., Snyder, N.F.R., 2007. California condors in the 21st century - conservation problems and solutions. In: Mee, A., Hall, L.S. (Eds.), California Condors in the 21st Century. American Ornithologists Union, Washington, DC, pp. 243–279.
Morris, W.F., Doak, D.F., 2002. Quantitative Conservation Biology: Theory and Practice of Population Viability Analysis. Sinauer and Associates Inc., Sunderland, MA.
Rideout, B.A., Stalis, I., Papendick, R., Pessier, A., Puschner, B., Finkelstein, M.E., Smith, D.R., Johnson, M., Mace, M., Stroud, R., Brandt, J., Burnett, J., Parish, C., Petterson, J., Witte, C., Stringfield, C., Orr, K., Zuba, J., Wallace, M., Grantham, J., 2012. Patterns of mortality in free-ranging California condors (*Gymnogyps californianus*). J. Wildl. Dis. 48, 95–112.
Rohlf, D.J., Carroll, C., Hartl, B., 2014. Conservation-reliant species: toward a biology-based definition. Bioscience 64, 601–611.
Sanz-Aguilar, A., Cortes-Avizanda, A., Serrano, D., Blanco, G., Ceballos, O., Grande, J.M., Tella, J.L., Donazar, J.A., 2017. Sex- and age-dependent patterns of survival and breeding success in a long-lived endangered avian scavenger. Sci. Rep. 7, 40204.
Scott, J.M., Goble, D.D., Wiens, J.A., Wilcove, D.S., Bean, M., Male, T., 2005. Recovery of imperiled species under the Endangered Species Act: the need for a new approach. Front. Ecol. Environ. 3, 383–389.
Scott, J.M., Goble, D.D., Haines, A.M., Wiens, J.A., Neel, M.C., 2010. Conservation-reliant species and the future of conservation. Conserv. Lett. 3, 91–97.
U.S. Fish and Wildlife Service [USFWS], 2021. Hopper Mountain National Wildlife Refuge Complex: California Condor Recovery Program 2021 Annual Report. Ventura, CA.
Viner, T., Kagan, R., Rideout, B., Stalis, I., Papendick, R., Smith, M.E., Burnham-Curtis, M., Hamlin, B., 2020. Mortality among free-ranging California condors (*Gymnogyps californianus*) during 2010–2014 with determination of last meal and toxicant exposure. J. Vet. Foren. Sci. 1, 15–20.
Widemo, F., 2021. Shooting habits and habitats- effects of education and legislation on the phasing out of lead shot. Environ. Sci. Pol. 118, 56–62.