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Response of California condor populations to reintroductions, reinforcements, and reductions in spent lead ammunition pollution

Bruce G. Marcot [a,*], Nathan H. Schumaker [b], Jesse D'Elia [c]

[a] U.S. Forest Service, Pacific Northwest Research Station, Portland, OR, United States
[b] U.S. Environmental Protection Agency, Pacific Ecological Systems Division, Corvallis, OR, United States
[c] U.S. Fish and Wildlife Service, Portland, OR, United States

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ABSTRACT

The California Condor (CACO; *Gymnogyps californianus*) is a critically-endangered apex scavenger with multiple reintroduction sites providing population reinforcement. Spent lead ammunition pollution in CACO food (i.e., carrion and gut piles) was most likely responsible for the decline of CACO populations in the twentieth century and continues to be the leading source of condor mortality. To aid condor recovery decisions for the California population, numbering approximately 200 in early 2024, we present results from a female-only, individual-based life cycle model. We simulated future CACO population size under each of 25 scenarios representing combinations of 5 levels of reintroductions of captive-bred CACO released in California, and 5 levels of lead reduction, projected over a 25-year forecast. Under the scenario of no change in current reinforcements or lead occurrence, CACO populations are projected to increase to 259 females; under the worst-case scenario of halting all reinforcements and no decrease in lead pollution, populations are projected to decline to 49 females; and under the best-case scenario of fully-enhanced reinforcements and complete elimination of lead pollution, populations are projected to increase to 569 females, with other scenarios having intermediate results. Our model predicted substantial improvements in population size even with incremental reductions in lead ammunition pollution, although we caution that population size is an incomplete measure of population health. Our maps of simulated foraging movements suggest a widespread expansion of condors throughout California and southwest Oregon under the best-case scenario, and major reduction with no expansion in distribution under the worst-case scenario. Our model serves as a framework for evaluating the efficacy of alternative recovery actions, and could be further enhanced to include economic and socio-economic tradeoffs associated with condor recovery.

1. Introduction

Intensive management interventions – including captive breeding, reintroductions, and reinforcements[1] – saved the California Condor (CACO; *Gymnogyps californianus*) from extinction (Snyder and Snyder 2000). However, they remain critically endangered with ongoing threats and relatively small population size. In addition, CACO are long-lived, invest considerable resources in raising young, and have low fecundity and low natural mortality rates, all of which increase the challenges and time-horizon for reaching recovery targets.[2] At present, the main drivers of population change are reinforcing the population with additional captive-bred individuals in existing populations, creating new populations through the establishment of additional reintroduction sites, and reducing human-caused mortality (Bakker et al., 2024).

Despite considerable challenges, intensive management interventions over the past few decades – inclusive of captive-breeding, reintroductions, reinforcements, vaccinations, and monitoring and recapture to treat injured or sick individuals – have resulted in an increase in CACO numbers and their distribution (Bakker et al. 2024). At the start of 2024, according to the CACO studbook, the total population of wild CACO in California was

* Corresponding author.
E-mail address: bruce.marcot@usda.gov (B.G. Marcot).

[1] Here, we use the term reintroduction to mean releasing individuals into an area without an established population, and the term reinforcement to mean releasing individuals into an area with an established population.

[2] The 1996 CACO recovery plan of U.S. Fish and Wildlife Service outlined criteria for downlisting from Endangered to Threatened status for the species, and is most recently summarized in the 2023 5-Year Review: https://ecosphere-documents-production-public.s3.amazonaws.com/sams/public_docs/species_nonpublish/7272.pdf

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197 (77 females, 101 males, and the rest of unknown sex), having increased from 16 CACOs in the wild 1996 – the first year they were present in central and southern California populations (USFWS 2023). As the population has grown, individuals have begun foraging over larger areas. Expansion of foraging areas means that CACOs, are returning to historically occupied areas with associated contributions to maintaining ecological health and possibly preventing disease spread (reviewed by Santangeli et al. 2024), and enhancing human communities that value the ability to view rare and iconic wildlife. However, this expansion is simultaneously making monitoring and management more costly. Therefore, deciding how to best allocate limited resources is becoming more critical. Where to allocate resources in species translocation programs is often a multi-dimensional decision problem (Keating et al. 2023), and models can help inform decision-makers of likely tradeoffs and risks when evaluating translocation options (e.g., Martínez-Meyer et al. 2006, Ransom et al. 2023, Bakker et al. 2024).

Severe impacts on CACO health and mortality from lead occurring in carrion and gut piles have been well established (Bakker et al. 2017, 2023; Church et al. 2006; Finkelstein et al. 2012, 2015). Within the range of California condors in the United States, both regulatory and voluntary approaches to reducing lead contamination have been implemented (reviewed by Shultz et al. 2023). Throughout most of the United States, lead is still used in ammunition for big game hunting, predator control, and in 0.22 caliber bullets used to plink ground squirrels and other small mammals. In 2019, California was the first state to require nonlead ammunition when taking any wildlife with a firearm throughout the state. Meanwhile, Oregon has adopted a voluntary approach to the reduction of lead available to scavengers by signing on to the North American non-lead partnership along with a number of other organizations.[3]

Yet, CACO continue to be poisoned by lead throughout their range and the threat has proven to be difficult to abate. Because condors will feed socially multiple birds can be poisoned by the remains of a single large mammal or offal pile contaminated with lead ammunition. Past analyses have shown that CACO remain reliant on management interventions, including continued addition of reinforcements for population growth (Finkelstein et al. 2012; Bakker et al. 2024). However, these analyses did not consider the spatial distribution of lead in the environment juxtaposed with individual condor movement, and any emergent properties of the population from combined effects that may become apparent only through the use of a spatially-explicit individual-based model (IBM, Heinrichs and Marcot 2019). To address this issue, we build upon our previous CACO models of landscape use, habitat connectivity, and movement and population dynamics (D'Elia et al. 2015, 2019, 2022). Our objectives are to determine, through use of an IBM, the potential effects on population size, dynamics, structure, and landscape use, of varying the levels of population reinforcements of existing reintroduction sites, the addition of a new reintroduction site, and of potential reductions in lead ammunition pollution.

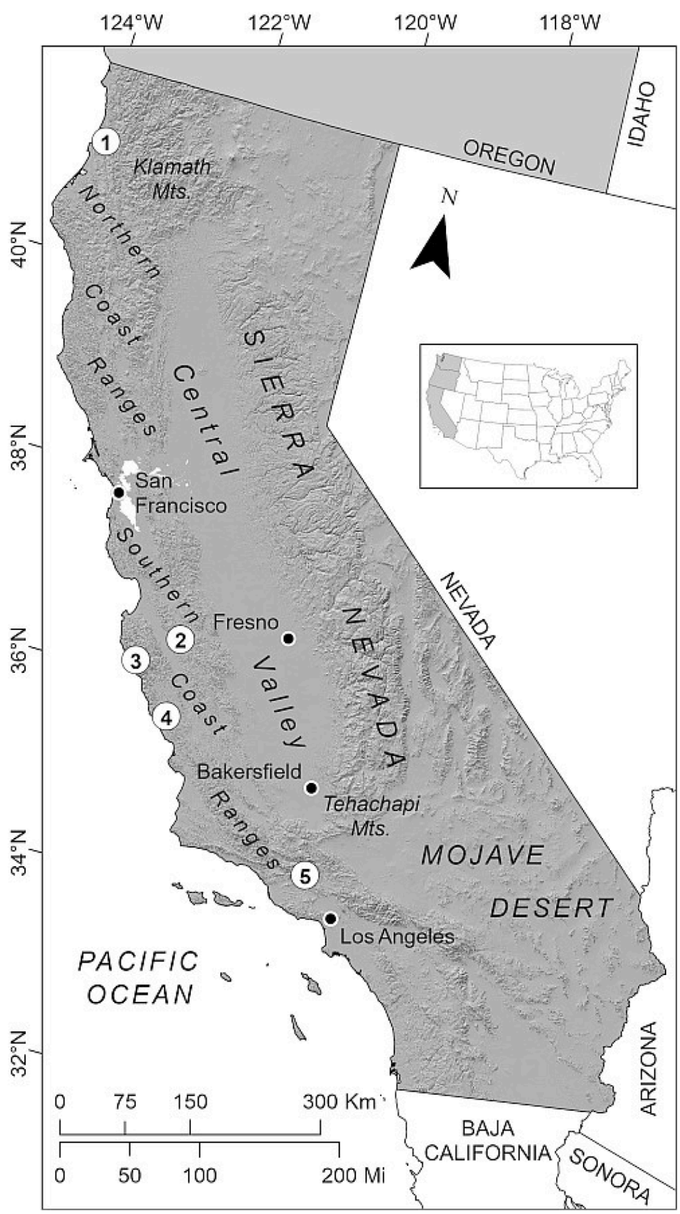

Fig 1. Locations of California condor (*Gymnogyps californianus*) release sites in California, and as used in the movement simulation model: (1) Yurok Tribe/Redwood National Park, (2) Pinnacles National Park, (3) Big Sur, (4) San Simeon, (5) Bitter Creek National Wildlife Refuge.

2. Methods

2.1. Study area

Our study area included the current range of CACO in California, USA (Fig. 1). We included in our modeling forecasts 5 sites with current or recent annual CACO reinforcements located in California: Pinnacles, Big Sur,[4] San Simeon, Bitter Creek, and Redwood (Bald Hills) .[5] We also included Oregon and Washington within our modeling domain, as they are part of the species' historical range (D'Elia and Haig 2013), and because CACOs released from the Redwood release site are expected to expand their distribution north of the state boundary in the future (D'Elia et al. 2019). Data limitations precluded enlarging our modeling domain to potentially disjunct CACO populations in other areas, including where they currently breed in the wild in Arizona, Utah, and Baja California, Mexico.

In California, the current range of CACO extends from the mountains and foothills of the southern part of the state to the north coastal redwood (*Sequoia sempervirens*) forests where a new coastal reintroduction site was recently established in 2022 in the Yurok Tribe's ancestral territory in the Bald Hills of Redwood National Park, and is jointly

[3] https://nonleadpartnership.org/

[4] In 2020, the Dolan Fire destroyed the condor release facility at Big Sur, which was in the process of being rebuilt during the course of our study; for simplicity, we retained this release site throughout our 25-year model projections in all simulations).

[5] Our hindcast model (D'Elia et al. 2022) also included three additional sites that were used only historically and where condors are not longer released: Castle Crags, Lion Canyon, and Hopper Mountain. Hopper Mountain was historically used for releasing cohorts of immature condors, but is now used primarily as a site for annual retrapping of condors for health checks, and the southern California cohorts are released at the adjacent site of Bitter Creek.

operated by the Yurok Tribe and National Park Service. Reinforcement translocations from the captive breeding population of CACO occur, or have recently occurred, at four other release sites, with one in southern California operated by the U.S. Fish and Wildlife Service, two in central California along the Pacific coast operated by Ventana Wildlife Society, one inland central California site operated by Pinnacles National Park (Fig. 1). The California portion of our study area is highly variable with a Mediterranean climate along the southern California coast, an alpine climate in the mountains of the high Sierra, a desert climate in the Mojave Desert east of the Tehachapi Mountains, and a coastal temperate climate with coniferous forests in northwestern California. Variability in climate across these regions corresponds with significant variation in vegetation and ecological communities.

2.2. Population structure and model updates

Our forecasting models began with a CACO population obtained from a previous application of our life cycle simulator that accounted for the full history of condor reintroductions and reinforcements taking place between 1995 and 2019 (D'Elia 2022). That simulator, and our new model, both track daily and annual life-cycle events such as survival, reproduction, and foraging. The models record individual condor ages in years, but also place condors into functional stage classes. We thus began our forecasting simulations in year 2020 using this simulated population, whose size and distribution agreed well with empirical data collected in California.

We modeled population structure and dynamics with the IBM HexSim (Schumaker and Brooks 2018), expanding on our hindcast-calibrated CACO-specific HexSim model of D'Elia et al. (2022). We structured the CACO HexSim IBM as a female-only model, with 5 population stage classes: fledgling (0 to <1 year), immature chick (1 to <2 years), mature chick (2 to <3 years), subadult (3 to <6 years), and adult (6+ years). We defined a maximum lifespan as 60 years, where any individuals exceeding that age were removed from the population in the model. Each stage class was assigned rates of survivorship and fecundity as described in D'Elia et al. (2022) (see Table 1). As in our previous work, a female-only model is justified because of no significant difference between the sexes in their movement behavior and home range size (D'Elia et al. 2022), although female CACOs may incur a slightly higher mortality rate over males (Bakker et al. 2023). See D'Elia et al. (2022) for further details of model structure and parameters.

Our previous hindcasting model simulated CACO spatial population dynamics for years 1995–2019 (D'Elia et al. 2022). Those hindcasting simulations began with no CACOs in the wild and the initial population resulted entirely from reintroductions of captive-bred individuals. Here, we started our current CACO forecasting model runs in year 2020, which picked up where the hindcast model left off. To do so, we made use of a HexSim utility that stores the full state of one model, and uses this information to initialize another model. We thus captured ending conditions of a specific hindcasting replicate having a particularly good fit to the actual 2019 end of year CACO population size, stage class distribution, and spatial distribution, and used this state data to initialize the forecasting model. All forecasting simulations therefore began with identical conditions corresponding to the spring of 2020, prior to the release of CACOs at the Redwood release site.

Two other key differences exist between our former hindcasting and current forecasting models. First, we simulated the actual release history in our hindcasting model, which involved changing the numbers and locations of introduced CACOs through time. In our forecasts, we use distinct models to examine a range of different release scenarios. But for any one model, the number of CACOs introduced per release site remains fixed for the duration of a simulation. Second, to account for a small reduction in the rate of lead induced CACO mortality, we slightly lowered our lead rate coefficient from 0.79 (hindcasting model) to 0.73 (forecasting model) so as to best replicate the past population size. This modification left the spatial distribution of lead unchanged, but lowered

Table 1
Demographic parameters by stage class of the California Condor individual-based simulation model. Values of annual survival rate exclude effects of lead ammunition pollution and senescence, which are accounted for separately in the model.

Stage class	Annual survival rate	Reproduction rate (no. females per female)
Fledgling (0 to <1 year)	0.879	0
Immature (1 to <2 years)*	0.825	0
Mature (2 to <3 years)	0.912	0
Subadult (3 to <6 years)	0.965	0
Adult (6+ years)	0.973	0.105

*Released CACOs were added to the simulations on November 1st of their second year of life, making them immature chicks of age 22 months. Survival rates for released immature CACOs were prorated to reflect their being subjected to mortality in the wild during just the last 2 months of the immature stage (D'Elia et al. 2022). As a result, they were assigned a higher annual survival rate of 0.971 for the remainder of their initial year of release, as compared with the annual survival rate of 0.825 assigned to wild immature chicks that were exposed to potential mortality in the wild for the entire year.

the number of carrion meals with lead, per carrion item. When our HexSim simulation added carrion to the landscape, each food item was assigned both a number of meals and a number of meals contaminated with lead. This latter value was obtained from the product $\alpha \times \beta \times M$, where α represents the mapped lead potential, β is the lead rate of addition, and M is the number of meals present in the carcass. Both acute and chronic levels of lead exposure were tracked separately for each simulated condor; and, each value could lower survival probabilities. See D'Elia et al. (2022) for additional details.

2.3. Scenarios for population analyses

We developed 25 scenarios of potential future conditions, representing combinations of 5 levels of population reinforcements and 5 levels of lead ammunition pollution reduction. The levels of population reinforcements were gauged as percentages of current levels, and included −100 % (no further CACO releases at any site), −33 % (6 females released per year), 0 % (9 females released per year), +33 % (12 females released per year), and +66 % (15 females released per year) (Table 2).

The levels of lead ammunition pollution reduction were also gauged as percentages of current levels, and included 0% (no reduction over current levels), −25 %, −50 %, −75 %, and −100 % (no further introduced lead). We did not entertain increases in lead over current levels, given the recent policy moves to reduce or eliminate lead ammunition pollution available to scavengers as discussed above. As per our previous work (D'Elia et al. 2022), we modeled the acute and chronic impact of lead ammunition in carrion on the probability of condor mortality as a function of the number of standard carrion meals containing lead consumed by individual condors.

We determined the effective modeled time horizon by plotting the running standard error (SE) of population size, from the hindcast simulations, as a function of model simulation years starting 1996, and evaluated the change in SE of population size over time. We ran initial population projections, consisting of 50 replicate model runs, and determined that variations in populations stabilized by year 25 or sooner, within some general stochastic variation (Appendix Figure A1). From this, we chose 25 years as the simulation time horizon for the current forecast model runs.

We conducted 100 replicate runs for each of our 25 scenarios. For each replicate simulation, we recorded the population size, stratified both by stage class and status (wild vs. released). We also tracked current and cumulative lead exposure, which was recorded as the number of meals contaminated with lead (the same units used in our hindcasting model). We also tracked mortality, stratified by stage class, status, and lead exposure, and observed reproductive rates. We developed and compared population pyramids – numbers of wild and released CACO by stage class – at the end of the 25-year simulation runs, for 6 selected scenarios representing worst, current, and best cases of reinforcement and lead reduction levels. Finally, we recorded the cumulative number of times each landscape location (hexagon) was visited during foraging, and used this information to develop maps of potential connectivity (*sensu* Schumaker 2024), which we previously referred to as "dispersal flux" (D'Elia et al. 2022). For each scenario, we used the 100 replicate-specific maps of potential connectivity to develop a single map showing the mean values distributed across the study area.

3. Results

3.1. Population response to reinforcements and lead reduction

We projected the combined effects of annual CACO reinforcement levels and lead reduction levels on population size and trend over our 25-year forecasting time frame. Mean population trajectories were nearly linear, including current and extreme cases (Fig. 2). Stochastic variation remained low among the 100 replicate simulations for each scenario and across the 25-year projections (Fig. 2); although, as we note in the methods, we maintained static numbers of CACOs released in each scenario throughout the simulation period which means that the real-world variation in the number of CACOs released each year is not reflected in our model outputs. Regardless of scenario, none of the simulated condors experienced senescence; all birds died prior to age 60, either from natural causes (annual mortality) or lead poisoning.

Under current conditions (scenario A0), our model suggests that the CACO population in California will increase from 100 to 259 females after 25 years. Under our worst case conditions (scenario B0) of no reintroductions or reinforcements and no reduction in lead available to scavengers, the simulated CACO population decreased from 100 to just 49 females, 19% of that expected under current conditions. Our best case conditions (scenario E4) of 66% additional reinforcements and zero lead ammunition pollution, the CACO population is anticipated to increase from 100 to 569 females or 220% of that expected under current conditions. The outcomes from all other scenarios fall between these worst and best case forecasts (Table 3).

Comparisons of 25-year outcomes among the 25 scenarios suggest greater effects among the lead-reduction scenarios than among most of the condor reintroduction and reinforcement scenarios, with some important considerations. For lead reduction among the condor reintroduction and reinforcement scenarios, the greatest improvement to the projected total population size at year 25 appears with the first step in reduction of lead ammunition pollution to −25 % of current levels (lead reduction scenario 1; Table 2, Fig. 3 *top*), leading to a 42% increase in year 25 CACO populations averaged across the 5 condor reintroduction and reinforcement scenarios (also see Appendix Figure A2). A further reduction from −25 % to −50 % of lead ammunition pollution yields a smaller but still positive dividend of an average 14 % further increase in year 25 CACO populations averaged across the 5 condor reinforcement scenarios. The population increase dividends then decline to averages of 2 % and 0 % for the next two increments of lead reduction of −75 % and −100 %, respectively.

However, as averaged across the 5 CACO reintroduction and reinforcement scenarios, reducing lead from current levels to −25 %, −50 %, −75 %, or −100 % at the beginning of the simulation, is projected to increase CACO year 25 populations by 118 %, 132 %, 134 %, and 134 %, respectively, the last three of these sets not being statistically different and with substantial overlap of model result outcomes (Fig. 3, *top*). Looked at another way, with no reduction in current levels of lead ammunition pollution, adding a reintroduction site and increasing CACO reinforcement from starting levels (scenario A0) to best-case levels (scenario E0) is projected to increase year 25 CACO populations by a further 55 %. Alternatively, retaining current CACO reinforcement levels but eliminating lead ammunition pollution, is projected to increase the year 25 CACO population by 58 % (Table 3). Further, across all the lead reduction scenarios, there is a major, consistent increase in the year 25 CACO population comparing the −100 % condor reinforcement level (scenario B) to the −33 % condor reinforcement level (scenario C). There are also lesser but still significant increases in population levels for each subsequent condor reinforcement level (scenarios A, D, E) (Fig. 3, *bottom*).

Our results also show that, for each lead reduction scenario, year 25 CACO population levels are statistically different among the 5 condor reinforcement levels (Fig. 3, *bottom*). Also, the 1SD variations (among the 100 model replicate runs) in year 25 CACO population levels are quite similar across all 25 scenarios, with smaller variations in a few scenarios such as B0 and C0 (Fig. 3, *top*). However, the coefficient of variation, which normalizes SD to the mean values, is greatest under worst-case scenario B0 (CV = 29.2 %) with −100 % reduction in CACO reinforcement levels and no reduction in lead ammunition pollution levels (Table 3c), as compared with the normative scenario A0 (CV = 8.7 %) and best-case scenario E4 (CV = 4.7 %). Implications with smaller year-25 population outcomes are that, although there is lower variation in absolute numbers, as shown by SD values, there is far greater variation relative to the mean outcomes, as shown by CV values. The greater variation suggests less certainty in reaching and retaining mean values of smaller population sizes.

Pyramid structures of year 25 populations suggest similar relative proportions of the 5 stage classes among six selected scenarios (Fig. 4), averaging 6 % fledglings, 7 % immature chicks, 6 % mature chicks, 15 % subadults, and 66 % adults. The numbers of individuals in each stage class are smallest under the worst-case scenario (B0), largest under the best-case scenario (E4), and in between under the current scenario (A0). Proportions in the numbers of wild vs. released birds at year 25 varied among scenarios. The worst-case scenario B0, with no Redwood release site and no further CACO reinforcements, results in the lowest proportion of released birds at 13 %; scenarios A4 and E0 having the highest at 55 %; and the current (normative) scenario A0 having 51 %.

3.2. Maps of foraging movements

We recorded the spatial patterns of CACO foraging movements in maps of what is termed dispersal flux in the HexSim model. For simplicity, we illustrate only the maps of dispersal flux for the worst (B0), normative (A0), and best (E4) scenarios, as these illustrate the most pronounced differences in foraging dispersal distributions (Fig. 5). In general, foraging dispersal flux is greatest nearest the CACO release sites (cf. Fig. 1) and lessens with more remote exploratory foraging movements. This result is expected, as each condor's foraging trips begin and end at its nesting or roosting site.

With greater degrees of reduction in lead ammunition pollution and greater levels of CACO reinforcement, we observed incremental changes in the CACO's projected geographic distribution. Scenarios that included the recent addition of a release site in northern California showed that a significant portion of California is projected to be explored by dispersal movements (Fig. 5). Under the best-case scenario E4, most of northern California and significant parts of southwest Oregon potentially become foraging exploratory zones, but are lost to exploration under the worst-cast scenario B0, which did not include the reintroduction effort in northern California. Note also the outlying exploratory boundaries (colored gray in Fig. 5) showing where at least a few foraging explorations can substantially increase the overall distributional range of the species.

4. Discussion

We previously developed a spatially-explicit, individual-based,

Table 2
Parameters and code names for 25 scenarios for the California Condor individual-based simulation model. Scenarios included 5 levels of population reinforcement and 5 levels of reduction of environmental lead. Also shown are the lead rate coefficients and the population reinforcements (numbers of female condors released) per year for each of 5 release sites as used in the model.

		Population Reinforcement (Additional Condors)					
Lead Reduction		B −100%	C −33%	A 0%	D +33%	E +66%	Lead Rate Coefficient
0	0%	B0	C0	A0	D0	E0	0.7000
1	−25%	B1	C1	A1	D1	E1	0.5475
2	−50%	B2	C2	A2	D2	E2	0.3650
3	−75%	B3	C3	A3	D3	E3	0.1825
4	−100%	B4	C4	A4	D4	E4	0.0000
Release Site		No. Condors Released Per Year By Site					
Redwood		0	2	3	4	5	
Pinnacles		0	0	1	1	1	
Big Sur		0	1	1	2	2	
San Simeon		0	1	1	1	2	
Bitter Creek		0	2	3	4	5	
TOTAL RELEASED		0	6	9	12	15	

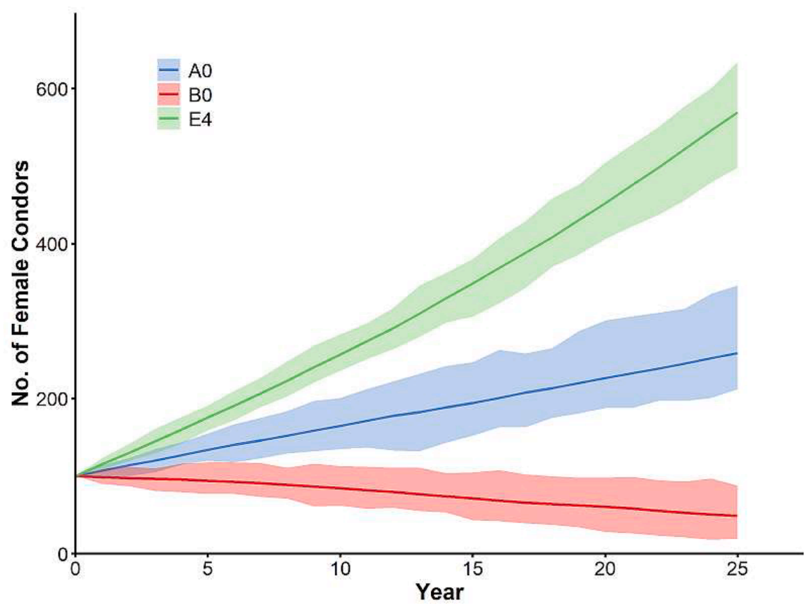

Fig. 2. California Condor population size over 25-year forecast simulations under current (normative) conditions (Scenario A0, 0 % additional condor reinforcements and 0 % reduction in environmental lead), worst-case conditions (Scenario B0, −100 % condor reinforcements and 0 % reduction in environmental lead), and best-case conditions (Scenario E4, +66 % condor reinforcements and −100 % environmental lead). Shaded areas encompass the range of values among each of the 100 simulation runs. See Table 2 for scenario parameters.

California condor hindcasting model, and illustrated its utility by simulating the species' reintroduction into California (D'Elia 2022). Here, we extend that work by constructing a CACO forecasting model, and use it to examine population response to hypothetical future changes to the captive-release program and to the amount of lead present in the environment. Our current results can be used alongside other complementary modeling efforts (e.g., Bakker et al. 2024) to advise on implications for interpreting and continuing modeling CACO populations, and for management of CACO sites in California and potentially beyond. In particular, our individual-based and spatially-explicit results offer a window into projected condor movements and spatial distribution that cannot be gleaned through matrix-based population projections.

4.1. Model implications

Our model results show that any level of reduction in lead ammunition pollution, particularly initially moving at least to −25 % and −50 % of current levels, will provide for significant positive future increase of CACO populations over current levels. As well, enhancing current levels of population reinforcement can result in significant increases in future population levels. Reductions of reinforcements from current levels, on the other hand, generally result in lower future population levels, at least and unless lead ammunition pollution also is substantially reduced.

The spatial nature of our model also provides a means to experiment with simulations of more geographically targeted lead reduction approaches that might be necessary to balance threat reduction with costs in real-world applications. For these simulations to be useful, it will likely require development of more accurate spatial layers quantifying the distribution of bioavailable lead across the landscape. Whereas developing a landscape-scale geospatial layer of bioavailable lead in carcasses and gut-piles would be costly, such geospatial information is likely to benefit a number of species that continue to be affected by lead poisoning from spent ammunition (e.g., Slabe et al. 2022).

In general, different population structures of wild-hatched and released CACOs result from different scenarios, with strong implications

Table 3
Results at the final forecast year 25 averaged over 100 replicate HexSim model runs, for model scenarios of additional California Condors (A-E) and lead reduction (0–4). Scenario A0 (outlined in bold) represents the current (normative) situation of 0% additional condors and 0% lead reduction. Cell colors are conditional formatting with green representing higher numbers of females and lowest variation (highest stability) in numbers of females among the model run replicates. (a) Mean total numbers of females. (b) Relative numbers of females compared as percent of the current (normative) scenario A0. (c) Coefficient of variation of total number of females among the model replicate runs. See Table 2 for scenario code parameters.

(a) Numbers of Birds		Additional Condors				
		B	C	A	D	E
Lead Reduction		-100%	-33%	0%	+33%	+66%
0	0%	49	184	**259**	331	401
1	-25%	136	293	373	445	525
2	-50%	174	332	404	486	561
3	-75%	176	333	415	491	565
4	-100%	178	332	409	491	569

(b) Percent of Current		Additional Condors				
		B	C	A	D	E
Lead Reduction		-100%	-33%	0%	+33%	+66%
0	0%	19%	71%	100%	128%	155%
1	-25%	52%	113%	144%	172%	203%
2	-50%	67%	128%	156%	188%	217%
3	-75%	68%	129%	160%	190%	218%
4	-100%	69%	128%	158%	190%	220%

(c) Coefficient of Variation		Additional Condors				
		B	C	A	D	E
Lead Reduction		-100%	-33%	0%	+33%	+66%
0	0%	29.2	9.5	**8.7**	7.4	6.7
1	-25%	15.9	7.4	7.2	6.4	5.2
2	-50%	12.2	6.2	6.0	5.1	4.6
3	-75%	11.8	7.0	6.8	5.2	5.4
4	-100%	11.7	6.8	5.4	5.6	4.7

for future population sizes and trends. The population pyramids resulting from our model projections (Fig. 4) mostly suggest constrictive or stationary or near-stationary conditions, with the great majority of individuals in the adult stage class of 6+ years old. The most constrictive pyramid condition appears most saliently with worst-case scenario B0, having extremely few birds in the three youngest stage classes. More stationary conditions, suggesting stable age distributions and population trends, occur with greater levels of population reinforcement and of reduction in lead ammunition pollution. Overall, despite substantial differences in model type, structure, and parameterization, our results are consistent with the conclusions of Finkelstein et al. (2012) and Bakker et al. (2024) that captive releases currently play a critical role in maintaining population growth and it will be important to reduce lead-related mortality to move toward self-sustaining populations.

Our model included only a single threat factor and did not consider catastrophes. Additional stressors on CACO populations, inclusive of catastrophes (e.g., avian influenza H5N1, and wildfires), may become manifest over time and could disrupt population growth and restrict positive responses to reinforcements and reduction in lead ammunition pollution (Bakker et al. 2024). Principally, the emergence of highly pathogenic avian influenza H5N1 in the Southwest CACO population, as well as widespread presence of the disease in other bird species throughout California, has raised alarms for spread to the California CACO population and beyond, leading to efforts for early disease detection (Straub et al. 2015) and for the unprecedented vaccination of CACO against the pathogen (Kozlov 2023). Other factors not considered in our model, but which could be added if sufficient data were available, include periodic catastrophes from wildfire or other environmental stressors, changes in fecundity based on DDE uptake from marine mammals, impacts of poaching on survival (e.g., a recent incident in Colorado[6]), and changes to survival and fecundity from modifying the intensity of monitoring efforts or management interventions.

Failing to track individual variation in modeling small populations can lead to unexpected bias (Armstrong et al. 2021). In our simulation

[6] https://coloradosun.com/2024/09/20/poached-california-condor-killed-colorado/

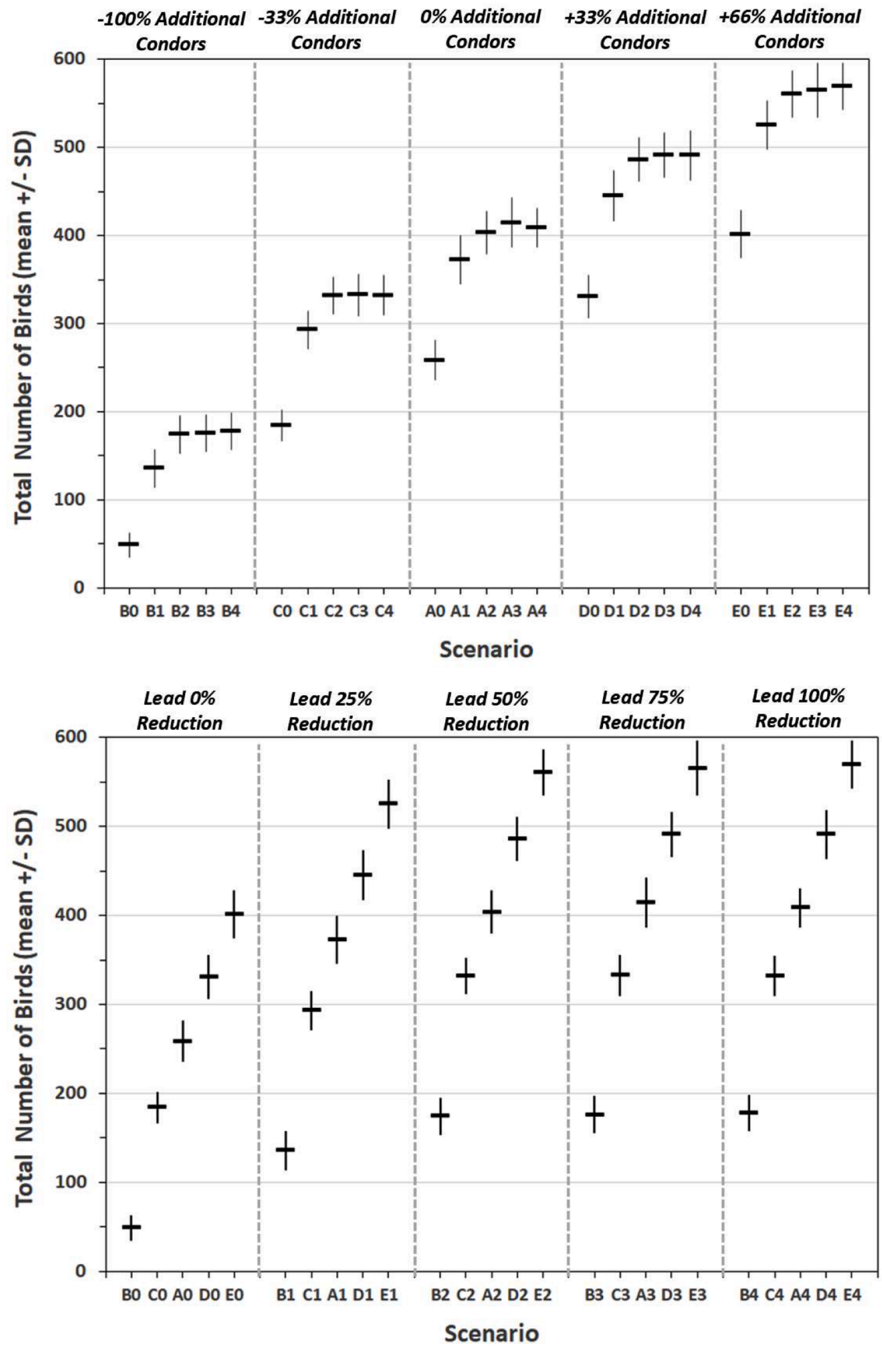

Fig. 3. California Condor simulation results with mean (horizontal bars) and ± 1SD (vertical bars) of total number of females at the final forecast year 25 over 100 replicate model runs, for each of 25 scenarios of population reinforcement and lead reduction (see Table X). *Top*: scenarios sequenced first by 5 population reinforcement levels (sequenced B, C, A, D, E) and then by 5 lead reduction levels (sequenced 0, 1, 2, 3, 4); *bottom*: scenarios sequenced first by lead reduction levels, and then by population reinforcement levels.

system, individual variation is tracked in terms of age, guided stochastic foraging movements, and cumulative encounters of food resources including those containing lead ammunition pollution, all potentially affecting survival and fecundity. Our modeling provides a fresh framework for projecting the interactive implications of reintroductions, reinforcements, and environmental stressors on survival and fecundity within a time-dynamic, individual-based movement simulation system. In particular, we based model parameters of fecundity on empirical observations, including those of habitat selection, so as to provide more realism in results, although we acknowledge potential sources of influence on fecundity not included in our model such as from variations in latitude and climate, and potential individual variations in lifespan, breeding propensity, and age of first reproduction (Etterson et al. 2011). We also opted for a dynamic stochastic approach rather than a deterministic stage-based population matrix model (e.g., Maestri et al. 2017) so as to estimate the degree of variation of outcomes among replicate stochastic model runs for a suite of scenarios, and to provide results as spatial representations of occurrence and distribution.

4.2. Management implications

Our work provides a platform for evaluating tradeoffs between CACO reintroductions, reinforcement, and lead ammunition pollution reduction actions, and which levels of each could provide for meeting a

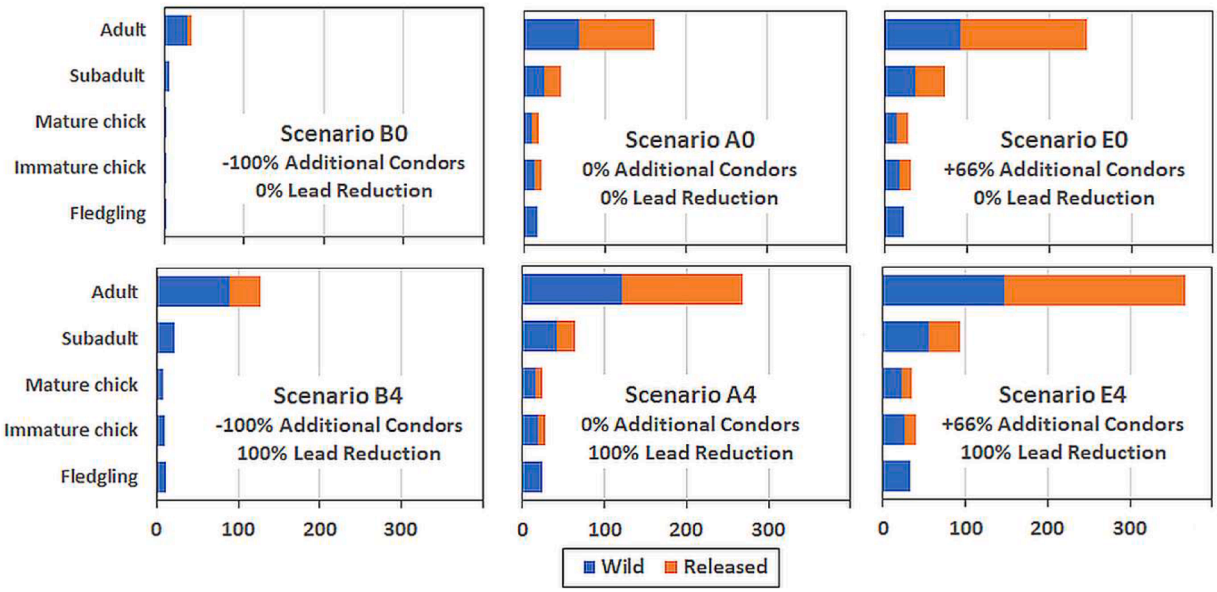

Fig. 4. Population pyramid structures of number of California Condors by 5 stage classes and wild and released categories, projected to year 25 from the HexSim simulation model, for 6 selected scenario outcomes. Wild refers to all females, alive by year 25, that were born in the wild over the course of the model simulation, plus any females that were already introduced at the onset of the simulation. Released refers to females introduced from release sites on and before year 25, if still living by year 25.

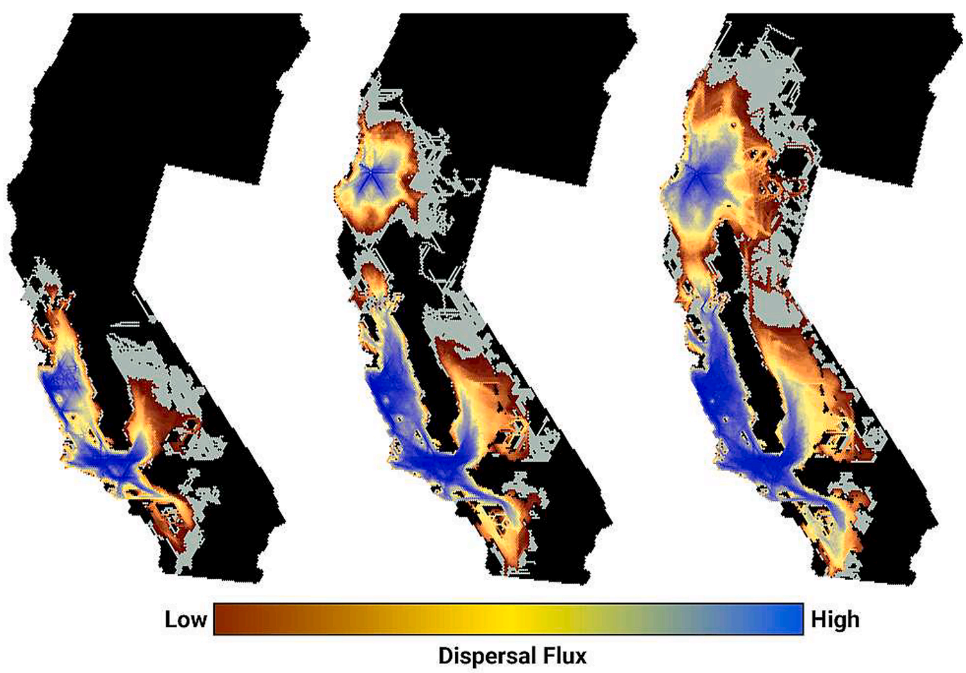

Fig. 5. Foraging dispersal flux maps of California and southern Oregon at the final simulated forecast year 25. *Left*: worst-case scenario B0 (−100 % additional condors, 0 % lead reduction); *middle*: current condition A0 (normative) scenario (0 % additional condors, 0 % lead reduction); *right*: best-case scenario E4 (+66 % additional condors, −100 % lead reduction). Gray represents areas visited, on average, less than once per model simulation replicate, suggesting intermittent peripheral condor foraging explorations.

population size objective. For example, if a management objective was to provide an increase in the California population of CACO from its 2023 level of 195 CACOs (for the sake of simplicity, approximately 100 female birds, assuming a 1:1 sex ratio) to, say, 300 females by year 25, one could use Fig. 3 to determine which scenarios may provide for meeting that goal. In this example, all scenarios under D and E (CACO reinforcements of +33 % and +66 %, respectively), all scenarios under current reinforcement levels (scenario A) that provide some reduction of lead ammunition pollution, and even scenarios under C (with −33 % reinforcement) but with at least a 50 % reduction in lead ammunition pollution, could potentially meet this objective of >300 females by year 25.

Our model results also suggest that the greatest benefit to condor population size from reduction in lead ammunition pollution appeared at the 50 % reduction level, with smaller incremental benefits thereafter. However, we strongly caution against reading this as a target for lead reduction efforts. Sub-lethal lead exposures were still recorded in our modeled population with a 75 % reduction in lead ammunition pollution, indicating there are impacts to population and individual CACO health that are not fully reflected in model outputs. Indeed, the non-linear demographic effects of lead reduction to population size, despite ongoing lead exposures, suggest that population size is only one of several factors likely to be relevant in assessing CACO population health when setting species recovery targets. In addition, our methods for modeling the distribution of lead across the landscape—and the subsequent ingestion by condors—are approximations, and the lookup table relating acute and chronic lead exposure to CACO mortality could underestimate the lethality of low chronic doses of lead or individual acute doses of lead. Therefore, our model is better considered a tool for investigating the relative benefit of lead removal versus reinforcements, and less appropriate for quantifying the exact population response to any specific hypothetical level of lead removal.

Our results also suggested greater certainty if higher population levels are reached, as indicated by lower values of coefficient of variation in condor numbers among model runs, and as might be achieved with higher levels of reinforcement and lower levels of lead ammunition pollution. We fully caution, however, to treat any such use of our modeling results as testable management hypotheses fully requiring monitoring and adaptive management adjustment as needed.

Projecting potential response in condor geographic distribution provides additional information to consider in recovery planning that is not available from non-spatial population models. For example, changes to the number of condor reinforcements or lead ammunition pollution at existing sites suggested incremental changes in overall population distribution with the potential for larger distributions and greater connectivity as reinforcements are increased and the amount of lead ammunition in the environment is reduced. The addition of a new reintroduction site in Redwood National Park in northern California resulted in the most substantial increase in condor distribution regardless of modeled changes in reinforcements or levels of lead ammunition pollution (Fig. 5). Further exploration of the geographic outputs of the model can highlight specific areas that may require additional monitoring and focused monitoring and lead-abatement efforts under various release and lead-reduction scenarios.

A further expansion of assessing tradeoffs between management actions could include economic or socio-economic analyses to further prioritize management scenarios of reintroductions and reinforcement (Dunham et al. 2016). Adding economic considerations could allow for refined cost-benefit analyses to further evaluate alternative management strategies. Our model does not provide an economic analysis but can serve as the basis for one. Our projections of foraging dispersal flux further suggest how establishment of a new reintroduction site, changing the level of reinforcements, and of reduction of lead ammunition pollution can have major effects on the expected geographic distribution of CACOs, particularly whether distributions would extend into northern California and southwest Oregon or beyond. Thus, tradeoff analyses could weigh the biological and socio-economic benefits of having condors in these projected geographic expansion areas against any anticipated biological or socio-economic costs, including opportunity costs.

The addition of a reintroduction site in the Pacific Northwest in our simulations resulted in a dramatic increase in the predicted distribution of CACO foraging movements (Fig. 5). We recognize there are substantial planning and implementation costs associated with setting up and operating a new release site; however, those costs must be weighed against the benefits to condors, recipient ecosystems, and human communities from releasing condors into parts of their historical range where they have been extirpated. Although we did not attempt to quantify those costs or benefits, our modeling framework establishes a foundation for future research into this aspect of condor recovery planning.

Our modeling framework could also be expanded to consider potential new release sites and movement patterns within and beyond California. Given the substantial costs for establishing and managing reintroduced populations and for monitoring condor movements (e.g., Lamb et al. 2023, Poessel et al. 2018, Stoms et al. 1993), evaluating and comparing options in a simulated environment provides a valuable tool to explore alternatives for achieving population and distribution goals. Further modeling explorations could explore such additional reintroduction sites throughout the West, such as Hells Canyon along the Oregon-Idaho border where the Nez Perce tribe has actively been exploring the feasibility of reintroducing condors. In addition, simulations that span longer time-horizons could also evaluate the potential for existing populations to expand and serve as founder populations as CACOs encounter a greater variety of landscapes and discover new foraging and perhaps nesting sites (Hall et al. 2021).

5. Conclusions

We provide a framework using individual-based movement simulations to model potential response of the CACO population to adding a reintroduction site, changing the number of condors released for population reinforcement, and changes to the amount of bioavailable lead from carrion and gut piles. We found that various combinations of population reintroductions and reinforcements along with reduction in lead ammunition pollution could provide for greater future CACO population levels in California than with current status quo "normative" conditions. Greater levels of reinforcement combined with substantial lead reduction levels were projected to result in CACO use of much of the state for foraging dispersal movements, especially expanding into significant areas of northern California and also into southwest Oregon.

Our modeling framework could be expanded and used as a basis for evaluating biological, economic, and socio-economic tradeoffs for CACO recovery planning. True sustainability of future CACO populations will depend not just on population reinforcement and reduction or elimination of environmental hazards, particularly lead in carrion, but on an array of governmental, tribal, non-profit, and social support systems. Such support systems may include monitoring population levels and CACO foraging movement patterns, decisions on maintaining or expanding reintroduction sites and captive-breeding facilities, and continuing regulations and incentive-based efforts to deter and reduce environmental stressors on CACO populations in their current and future geographic distributions. Ecological modeling approaches that incorporate spatial dynamics will continue to play an important role in making informed and transparent decisions in the face of these complex eco-social issues, competing priorities, and limited resources.

CRediT authorship contribution statement

Bruce G. Marcot: Writing – review & editing, Writing – original draft, Supervision, Methodology, Formal analysis, Conceptualization. **Nathan H. Schumaker:** Writing – review & editing, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Jesse D'Elia:** Writing – review & editing, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2024.111002.

Data availability

The model and data are freely available on public domain at https://www.hexsim.net/downloads under the California Condor Forecasting Model workspace.

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