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Two decades of cumulative impacts to survivorship of endangered California condors in California

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ABSTRACT

We investigated threats to the California condor (*Gymnogyps californianus*), a flagship endangered species, using individual data on survival during a 20 year period of intensive recovery efforts. Over the two decades of reintroductions, condors in California had an estimated median survival time of 7.8 years suggesting that 50% of condors are expected to survive in the wild long enough to contribute to recruitment. In general, annual mortality rates exceeded levels necessary for a stable population; however, mortality declined, reaching levels needed for population stability, during the second decade of re-establishment. Intensive management practices, including utility pole aversion training and clinical interventions to prevent lead-related deaths likely contributed to the decrease in mortality rates. Utility line collision and/or electrocution was an important factor causing mortality over the two decades; though, this threat has largely been mitigated through management and targeted efforts in high-risk areas. In the past, wildfires were not considered a major threat to survival of free-flying condors. However, our analyses suggest that forest fires are significantly linked to the hazard of death, and increased wildfire activity in California highlights this population's vulnerability to catastrophic losses from forest fire. Lead poisoning, which was a major driver in the population's decline, was a leading cause of death accounting for the greatest adult mortality, and lead exposure remains the most significant threat. Recent lead ammunition reduction efforts in the condor range in California hold promise for improving the recovery potential for this population.

1. Introduction

Inadequate mitigation of threats, especially those that lead to a species decline, is the primary factor limiting recovery of endangered species. The last California condors (*Gymnogyps californianus*) were removed from the wild in the late 1980s in a desperate, yet extraordinary effort to save the species (Grantham, 2007; Snyder and Snyder, 2000). At the time, human disturbance at nesting sites, direct persecution through shooting and poisoning, food scarcity, wildfire, and eggshell thinning as a result of DDE contamination were some of the factors hypothesized to have led to the species decline (Snyder and Snyder, 2000; Wilbur, 1978). However, evidence suggests that lead poisoning was the major driver of the precipitous decline, and near extinction, of the California condor population in the 1980s (Janssen et al., 1986; Meretsky et al., 2000; Snyder, 2007). Reintroduction efforts starting in 1992 have been largely successful. Since 2011, over 200 individuals are free-flying (Mace, 2012) in California, Arizona, Utah, and Baja California, Mexico (Walters et al., 2010). Nevertheless, free-flying condor populations are far from self-sustaining in the wild.

The leading cause of mortality in the reintroduced condor populations is lead poisoning from ingestion of spent lead ammunition in animal remains (Finkelstein et al., 2012; Rideout et al., 2012; Walters et al., 2010). Lead poisoning has resulted in intensive management practices (Walters et al., 2010), including annual to semiannual sampling of the entire population for lead exposure, and frequent and costly clinical interventions for lead poisoned individuals (Hall et al., 2007; Sorenson

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and Burnett, 2007). In addition, California condors have been regularly provisioned with food at the release sites since reintroductions began, primarily as a means to transition young captive-reared juveniles to the wild and capture individuals for routine management and monitoring (Walters et al., 2010). Supplemental feeding has been associated with lower lead levels in condors (Kelly et al., 2014). Adherence to food subsidies was greatest early in the reintroduction program. Reliance on provisions has decreased over time as condors have increased their flight range and become more experienced at finding non-proffered food sources (Hall et al., 2007), leading to greater risk of lead exposure (Kelly et al., 2014). In California, lead poisoning in condors has led to non-lead ammunition outreach programs and in 2008, regulations prohibiting the use of lead ammunition for big game and nongame hunting activities within the condor range (California Fish and Game Commission, 2009; Ridley-Tree Condor Preservation Act, 2008). In addition, a bill recently passed that will phase out the use of lead ammunition for all types of wildlife shooting statewide in California by 2019 (California State Assembly, 2013).

Acknowledging the enormity of the lead threat and other hurdles to recovery, some scientists have suggested that extirpation from the wild may be plausible if lead from spent ammunition continues to contaminate the condor's natural food sources (Walters et al., 2010). Given that condor life history is characterized by slow maturation and low reproductive rates, annual adult mortality must necessarily be low for stable wild populations (Meretsky et al., 2000). Causes of mortality for the reintroduced condor population have been well documented and include lead poisoning, utility line collision and/or electrocution, inanition, and predation (Rideout et al., 2012). However, assessment of factors influencing survival time of California condors in the wild in California is needed given obvious constraints in population growth. A comprehensive evaluation of threats will also prioritize monitoring and management actions needed for recovering the population. Longitudinal studies using detailed individual-level data, including intensive field observations and information on causes of mortality of free-ranging individuals can provide insight into population health that was impossible before modern tracking technology (Johnson et al., 2009). Such study designs provide a robust method to utilize individual-level data for estimating population trends and assessing causal factors (Murray and Patterson, 2006). Here, we present a 20 year investigation using detailed individual-based approaches to assess threats to condor survival and evaluate whether recovery may be possible even with long-standing intensive management actions aimed at reducing mortality in the population.

2. Materials and methods

2.1. Study population

We utilized a 20 year longitudinal dataset containing demographic, behavioral, environmental, and health information for the condor population in California to assess patterns in annual mortality and investigate factors that are likely to influence survival time in the wild. The study population consisted of 220 free-flying California condors in California from 1992–2011 (n = 191 released individuals, n = 29 wild-fledged individuals). California condors have been released from the captive breeding program into their historic range at seven different release sites in California: five sites in southern California beginning in 1992, and two in central California (Big Sur area since 1997 and Pinnacles National Park since 2003). In 2004, the first California condor chick successfully fledged from a nest in California. Since then, natural recruitment has occurred in both southern and central California.

2.2. Data sources

Each condor was identifiable by patagial tags and monitored via VHF transmitters and visual observation using both mobile and stationary tracking (Grantham, 2007). When condors made significant movements or were undetected for two or more days, management activities were coordinated across sites to locate birds. Mixing of birds from different release sites first occurred in 2000 when condors released in Big Sur started to fly back and forth to southern California. These movements became less frequent in 2005 and since then, condors infrequently fly between these two sites (Grantham, 2007). However, significant mixing occurred between birds released at the two sites in central California (Big Sur and Pinnacles National Park). Most individuals spent time at both sites, with the exception of newly released or fledged condors and a few individuals that demonstrated site fidelity. In order to assess regional variation in survival, the percentage of daily intervals that a condor was detected within southern and central California was calculated. Condors were classified into a primary region of residence (southern or central California) based on where the majority of detections occurred.

Because monitoring for lead exposure is an integral component of the recovery effort, condors generally underwent lead testing in conjunction with evaluations prior to their release to the wild and were routinely monitored for lead exposure at least annually and more recently, two to three times a year (Hall et al., 2007). In addition, condors suspected of exposure and exhibiting signs of illness were captured and screened for lead poisoning. The capture and handling of condors was approved by institutional, state, and federal agencies. Lead analysis was conducted on-site using a portable lead analyzer (Lead Care Blood Lead Testing System, ESA Inc., Chelmsford, MA), which enabled assessment of the need for clinical intervention consisting of hospitalization, chelation therapy, and occasionally surgical management (Hall et al., 2007). Blood samples were also shipped to multiple commercial laboratories (Antech Diagnostics, Irvine, CA; Louisiana Animal Disease Diagnostic Laboratory (LADDL), Baton Rouge, LA; California Animal Health and Food Safety Laboratory (CAHFS), University of California, Davis, CA) for lead analysis as previously described (Kelly et al., 2014).

Briefly, at LADDL, blood samples were analyzed for lead levels using graphite furnace atomic absorption spectrophotometry (GFAAS) via a PerkinElmer Analyst 800 instrument. Blood samples were diluted 16-fold and red blood cells were lysed using a solution of 0.01% Triton X-100 and compared to aqueous standards. A whole blood reference sample (Seronorm Trace Elements Whole Blood — Level 2, SERO AS, Billingstad, Norway) provided a control for each blood lead assay. The analysis was performed twice on each batch of samples and controls. Average recovery of the control was 97% with a coefficient of variation of 6.3%. At the CAHFS laboratory, blood lead measurements were determined using GFAAS via a Perkin Elmer Analyst 800 instrument. Sample preparation consisted of diluting 0.05 ml of blood to 1.00 ml. The diluent was made up by 0.6% Triton X-100, 0.2% HNO3, and 0.2% NH4H2PO4 matrix modifier. Each batch of samples was analyzed with quality control samples consisting of a method blank, method detection limit spike, sample duplicates, and a certified reference material. A Wisconsin State Laboratory of Hygiene (WSLH) lead proficiency testing blood sample served as the reference material. Analyses of the method detection limit spikes produced acceptable results (within ±10% of the 50 ppb spiked level). Results from the analyses of the reference material were all within the acceptable range as determined by WSLH (mean, ±2 s.d.). Sample duplicates produced results that were all within 10% of each other. At Antech, blood lead levels were determined using anodic stripping voltammetry (ASV) via an ESA 3010B Trace Metals Analyzer (Environmental Science Associates) with a mercury-coated graphite electrode, a Ag/AgCl reference electrode, and a platinum counter electrode. Samples were prepared by mixing 0.05 ml of blood with 250 μL of dilute hydrochloric acid solution in water (0.1 mol/L). Calibration of the instrument was performed with each use and calibration of the ASV was carried out with calibrators made from bovine blood. The relative standard deviation for this method was < 10% with a 3% relative error. ASV technology (3010B) and GFAAS have shown good correlation for determination of blood lead concentrations, and can therefore be

considered comparable methods for blood lead analysis (Bannon and Chisolm, 2001).

Only laboratory-determined blood lead measurements obtained from the condors were used for the analyses (n = 1825). Blood lead levels ranged from non-detectable concentrations (<6 μg/dL) to 610 μg/dL with a median of 13 μ/dL. Excluding baseline blood lead levels measured at release to the wild, the annual prevalence of elevated lead exposure (i.e., the percentage of sampled condors with blood lead ≥10 μg/dL (Cade, 2007) in a given year between 1992 and 2011) ranged from 61–91% and the annual prevalence of lead poisoning (i.e., the percentage of sampled condors with blood lead ≥ 45 μg/dL (Finkelstein et al., 2012) in a given year between 1992 and 2011) ranged from 0–44% (median 20%).

Mortality data for condors that died from 1992 to 2009 were obtained from Rideout et al. (2012). Causes of death for condors that died in 2010 and 2011 were assigned by the same veterinary pathologist using methodology as previously described (Rideout et al., 2012). Causes of death were based on history, and diagnostic test results in conjunction with a complete postmortem examination. Condors were assigned an unknown cause of death when the condor disappeared in the wild (n = 19) or when a particular cause could not be determined due to factors such as autolysis of tissues or partial scavenging of the carcass (n = 12). Data were included in this study if the condors were found dead in the wild, were brought into captivity from the wild for a life-threatening illness or injury and died while undergoing treatment of causes directly or indirectly related to the medical problem, or disappeared in the wild and were presumed dead, as previously described (Rideout et al., 2012). Data from condors surviving to the end of the study were also included in the analyses. Mortality data from condors that were brought in from the wild for management-related purposes (e.g. captive breeding, temporary or permanent removal from wild for human-oriented behaviors) and died while in captivity were not included. However, data from these condors up to the time they were brought into captivity were included.

Mortalities occurring in the wild were identified by lack of variation in VHF transmitter signal strength or direction, or activation of a transmitter fatality sensor. Because the population was tracked daily and condors only went undetected for a few days at a time, the date of death for condors dying in the wild is generally accurate to within a few days. Condors that disappeared were presumed to have died, and the day following the last day of detection was assigned the date of death (Woods et al., 2007). Given the intensity of tracking efforts and high site fidelity of condors to the release and food provisioning locations (Grantham, 2007), it is unlikely that disappearances were the result of condors emigrating out of the area undetected. For condors that were brought into captivity as a result of a life-threatening medical problem and died while undergoing treatment of causes related to the illness or injury, the last day in the wild was used as the date of death.

2.3. Proportionate mortality ratios and annual mortality rates

To assess the extent to which certain causes of death contributed to condor mortality during the study period, proportionate mortality ratios were calculated by dividing the number of mortalities from a specific cause by all mortalities with a definitive cause. Because the daily fate of each individual in the free-flying population was known, mortality rates could be calculated precisely using the numbers of days each individual was free-flying in the wild in a given year (Woods et al., 2007). Unadjusted annual survival rates (ASR) over the study period were estimated using data from each individual in the free-flying population: $(\mathrm{ASR}) = \left(1 - \sum_{i=1}^{K}(y_i) / \sum_{i=1}^{K}(x_i)\right)^{n}$, where K is the total number of condors, y_i is 1 if condor i died during the study period and 0 if condor i is still alive at the end of the period, x_i is the total number of days in the wild during the period for condor i, and n is the average number of days in a year (365.25; Trent and Rongstad, 1974; Small and DeMaster, 1995; Woods et al., 2007). The summation of y over all condors is the number of deaths that occurred. The summation of x over all condors is the total number of condor-days in the wild. Annual mortality rates were then calculated as the inverse of ASR (AMR = 1 − ASR). Rates were calculated for the population and for immature and adult condors, separately. For this study, a condor ≥6 years old was categorized as an adult.

Mean annual mortality rates generated for this study were qualitatively compared to mortality rates previously estimated for establishment of a stable California condor population using simple population demographic models (Meretsky et al., 2000). Demographic parameters closely approximating observed demographic rates for the reintroduced population in California were assessed in these demographic models (Meretsky et al., 2000). Specifically, a reproductive rate of 0.23 fledglings per adult female per year used by Meretsky et al. (2000) closely approximates the mean rate of 0.21 fledglings per adult female per year observed in the reintroduced population (Finkelstein et al., 2012). Similarly, an assumption used by Meretsky et al. (2000) that 50% of the adults in the population breed with a 40% breeding success is comparable to what has been observed in the reintroduced population in California over the past 20 years (48% of adults bred with a breeding success of 43%; USFWS unpublished data). The assumption of a 0.25 probability of renesting in a single nesting season by Meretsky et al. (2000) is slightly higher than what has been observed in the reintroduced condor population (15% of condors renesting; USFWS unpublished data). Additionally, an assumed age of 8 years for first breeding in the demographic models (Meretsky et al., 2000) is slightly higher than the mean of 6 years observed in the reintroduced population (USFWS unpublished data). The population demographic models were relatively insensitive to the age of first breeding and probability of renesting (Meretsky et al., 2000). Given the minor difference in these parameters in the demographic models and the corresponding values observed in the reintroduced population, comparison of our annual mortality estimates to those estimated for stability in condor populations by Meretsky et al. (2000) will provide insight into sustainability of the current population.

2.4. Multivariable analyses

To investigate factors that influence survival time in the wild for the California condor population, we utilized computations in the survival library in R (R Development Core Team, 2012; Therneau and Lumley, 2011) to fit extended Cox regression models based on the counting process formulation of the Cox Model (Andersen and Gill, 1982; Therneau and Grambsch, 2000). Survival time was measured from the time of release or fledge to death or disappearance in the wild (n = 76). Survival data from condors surviving to the end of the study period (n = 119), and condors permanently returned to captivity or transferred to a site outside of California (n = 25) were censored at the time of these events. Individuals with censored data contribute information to the survival analyses up to the time of censoring, and therefore all available data are included in calculations of median survival time and assessments of factors influencing survival (Kleinbaum and Klein, 2005; Murray and Patterson, 2006). We used the Efron approximation to the partial likelihood and robust variance estimation to account for ties in mortality events (i.e., multiple deaths on the same day) and potential correlation in survival time, respectively. The counting process formulation allowed for time-varying risk factors and discontinuous intervals of risk when condors were in captivity for management or health-related concerns.

We constructed a null model to produce a baseline population survivorship function with unadjusted Nelson–Aalen survival estimates and respective 95% confidence limits. Models were then developed based on a-priori knowledge of the most common mortality factors (lead poisoning and utility line collision and/or electrocution; Rideout et al., 2012)

and putative risk factors for decreased survival time in the wild. Covariates assessed in the models included sex, source (captive-reared or wild-fledged), rearing status (parent or puppet-reared), baseline age (age at release or fledge), region of release or fledge, region(s) of residence, lead exposure, wildfire activity, utility pole aversion training, and lead ammunition regulations (Table 1). Utility pole aversion training was initiated in 1995 in an attempt to reduce condor perching on utility poles (Mee and Snyder, 2007). Power pole replicas that deliver a mild shock when condors land on them were placed in flight pens used to prepare condors for release to the wild and to capture free-flying condors for management purposes. Twelve condors were released into the wild in southern California prior to initiation of the training. The remaining 208 condors included in this study were released or fledged after training was implemented, and therefore received utility pole aversion training in the captive breeding facility prior to release and/or in the field pens during capture. To evaluate the effect of the lead ammunition regulations on survival, we included a covariate that took on a value = 0 during the time period up to two months following implementation of the regulations, and a value = 1 during the time period ≥2 months following implementation of the regulations. We incorporated the two month period immediately following the regulations in the pre-regulation period to account for mortalities associated with lead exposure that occurred prior to the regulations.

Factors specific to release of captive-bred condors, including the number of individuals released in a release cohort, release year (1992–2011), release age class, and original release site were assessed using a subset of data including only condors released to the wild (i.e. wild-fledged condors were excluded; n = 191). For this sub analysis, release age class was broken down into four categories (first year (≤365 days), second year (366–730 days), subadult (731–2190 days), and adult (≥2191 days)). Original release site was only assessed in southern California where condors were released at multiple sites within the region (Hopper Mountain Wildlife Refuge, Lyon Canyon, Castle Crags, and Bitter Creek National Wildlife Refuge).

In order to assess time-varying covariates measured on different time-scales (lead exposure and wildfire activity), we constructed two separate regression models. For the first model, the effect of lead exposure was assessed through blood lead levels, and time was comprised of intervals between blood lead measurements. For each interval, we incorporated the blood lead level (μg/dL) obtained at the beginning of the interval to represent the level of the variable until the next blood lead measurement was obtained. Because blood lead levels are dynamic in California condors with an estimated elimination half-life of ~13 days (Fry and Maurer, 2003) and condors were generally sampled 2–3 times per year over the study period, an inherent limitation of this approach was the incomplete history of exposure for each individual and the inability to account for change in lead levels between measurements. Nevertheless, this is a common approach used in survival studies when health parameters are measured intermittently (Therneau and Grambsch, 2000). All of the covariates in Table 1, with the exception of wildfire activity, were assessed in this model. Wildfire activity was not included as a risk factor in this model as it was measured on a daily time interval and assessment of the effect of wildfire activity on survival over intervals of time defined by blood lead measurements is not meaningful.

For the second model, time was comprised of daily time intervals and the effect of lead exposure was assessed through a covariate that reflected the cumulative percentage of blood lead levels ≥ 45 μg/dL for each daily time interval in the model. Lead levels ≥ 45 μg/dL are indicative of clinical lead poisoning in condors (Finkelstein et al., 2012). We categorized daily intervals during which condors were at risk of wildfire exposure based on the presence of condors, determined using observational data, within the final mapped perimeter of a forest fire during fire activity. Wildfire perimeter data were obtained from a statewide interagency geodatabase (California Department of Forestry and Fire Protection, 2012). Perimeters of wildfires occurring in California from 1992 to 2011 were overlaid on a map of the condor range using ArcGIS9.0. Condors with observations within the forest fire perimeter during the period of reported fire activity were considered at risk. Daily intervals for condors with undetermined locations were treated as missing data in this model. All of the remaining covariates listed in Table 1 were also assessed in this model.

For two individuals for which blood lead levels were lacking and lead poisoning was assigned the cause of death based on hepatic lead levels (Rideout et al., 2012), we used the median blood lead level derived from laboratory-based measurements around the time of death from individuals that died due to lead poisoning (150 μg/dL, range = 80–523 μg/dL; n = 9) as an estimate for the blood lead level at the time of death. For a third individual for which lead poisoning was assigned the cause of death and there was no associated blood lead level, we used a blood lead level of 60 μg/dL estimated from feather lead concentrations (Rideout et al., 2012) as the blood measurement at its time of death. The blood lead level was estimated from feather lead concentrations as previously described (Finkelstein et al., 2010).

Covariates were selected for inclusion in the multivariable models by first screening univariable models, and were retained if they were significant and reduced the model deviance. Biologically meaningful two-way interaction terms were tested between main effect variables. Akaike information criterion (AIC) calculated using the maximum partial likelihood and corrected for small sample sizes, was used for model comparison and selection. Variables that were significantly associated with survival and improved model fit as assessed through AIC were included in the final models. Hazard ratios and 95% confidence intervals for significant risk factors were estimated. For time-varying risk factors, hazard ratios were estimated as the average effect over the period of follow-up. Informative censoring was likely not a concern in our models because permanent return to captivity or transfer of condors to a field site outside of California were primarily the result of management needs and generally unrelated to their risk of death in the wild. Model adequacy was assessed by inspection of residual plots to evaluate overall fit, check the functional form of covariates, identify outliers, and assess the validity of the proportional hazards assumption.

Table 1
Demographic, behavioral, environmental, and health risk factors evaluated for their effect on survival time in the wild for California condors. Time-varying risk factors in the model reflect the level of covariate or risk factor for the condor during each time interval.

Risk factor	N	Risk factor description and categories
Time-invariant risk factors		
Sex	117	Male
	103	Female
Source	191	Captive reared
	29	Wild fledged
Rearing status	81	Puppet
	139	Parent
Baseline age	220	Age (in days) at release or fledge (median = 426 days)
Region of release or fledge	122	Southern California (SOCA)
	54	Big Sur (BS)
	44	Pinnacles National Park (PNP)
Region(s) of residence	123	Southern California
	97	Central California
Utility pole aversion training	12	Didn't receive utility pole aversion training
	208	Received utility pole aversion training
Time-varying risk factors[a]		
Blood lead level		Blood lead level (μg/dL)
Percentage of blood lead levels ≥45 μg/dL		Cumulative percentage of blood lead levels ≥ 45 μg/dL
Lead ammunition regulation		No lead ammunition regulation
		Lead ammunition regulation
Wildfire		Condor present within forest fire perimeter during fire activity
		Condor not present within forest fire perimeter during fire activity

[a] Time-varying risk factors in the model reflect the level of covariate or risk factor for the condor during each time interval.

3. Results and discussion

3.1. Mortality rates

Over the two decades of re-establishment, the estimated median survival time (unadjusted) for condors after release or fledge in the wild was 7.8 years (2850 days, 95% CI: 1886 days, NA). Because condors on average did not successfully fledge young until they had been free-flying in the wild for seven years (Mace, 2012), results suggest that 50% of condors within the 20 year period would be expected to survive long enough in the wild to fledge a chick (Fig. 1). Demographic constraints of such low recruitment to the breeding population were exacerbated by the fact that only 48% of breeding aged condors engaged in reproductive activities and condors fledged young from 43% of eggs laid (USFWS unpublished data). Furthermore, condor reproductive rates are naturally low with pairs generally producing one chick every two years (Meretsky et al., 2000; Snyder and Snyder, 2000).

During the 20 year study period, the overall mean annual mortality rates for adult and immature condors were 0.082 and 0.140, respectively. Annual mortality rates decreased to levels during the second decade of condor reintroductions that are permissible for population stability (Meretsky et al., 2000). Population demographic models using parameter inputs that closely approximate observed population demographic rates for the reintroduced condor population in California suggest that annual mortality rates must be ≤ 0.067 to sustain a stable population in the wild (assuming similar mortality rates for adult and immature condors; Meretsky et al., 2000). If annual mortality rates for immature condors were to be twice that of adults, the mortality rates required for a stable population are ≤ 0.053 and ≤ 0.106 for adult and immature condors, respectively (Meretsky et al., 2000). During the first decade of re-establishment, the mean annual mortality rate among immature condors decreased from 0.372 during 1992–1994 (range = 0.330–0.416) to 0.122 during 1995–2000 (range = 0–0.193), following initiation of utility pole aversion training. Over the second decade of reintroductions, the mean annual mortality rate for immature condors was 0.091 (range = 0–0.220). The annual mortality rate for adult condors was relatively high (0.380) in 2000, which was the first year adult condors were free-flying in the reintroduced population in California. From 2001–2011, during the second decade of re-establishment of condors in California, annual adult mortality rates ranged from 0 to 0.155 with a mean rate of 0.054.

Although annual mortality rates decreased to levels permissible for population stability (Meretsky et al., 2000) during the second decade of reintroductions (0.054 for adults and 0.091 for immature condors), the reduction in mortality was likely the result of intensive management practices, including utility pole aversion training and interventions to prevent lead-related deaths. Clinical interventions for lead poisoning include chelation therapy, hospitalization, and occasional surgical management (Hall et al., 2007). Over the study period, up to 48% (median 18%) of condors sampled for lead exposure in a given year were administered chelation therapy. Among the individuals who underwent chelation therapy, 95% survived treatment and were successfully released back into the wild. The results presented here and by Finkelstein et al. (2012) suggest that a stable condor population in California is dependent on continuation of the current level of management interventions, especially those required to mitigate lead poisoning. Finkelstein et al. (2012) used survival estimates generated from 2010 data to project an annual condor population growth rate of 1.003 (i.e., approximately stable), assuming no captive-reared releases and the current level of management actions for the population. Natural recruitment, largely hindered by high nestling mortality (Mee et al., 2007; Rideout et al., 2012), has yet to compensate for the level of mortality experienced in the population. As a result, continued releases from the captive breeding program have been necessary to promote growth.

3.2. Threats to survival

Lead poisoning remains a significant cause of mortality in the condor population and a pervasive threat to survival. Despite intensive management to prevent and treat lead exposure in the condor population,

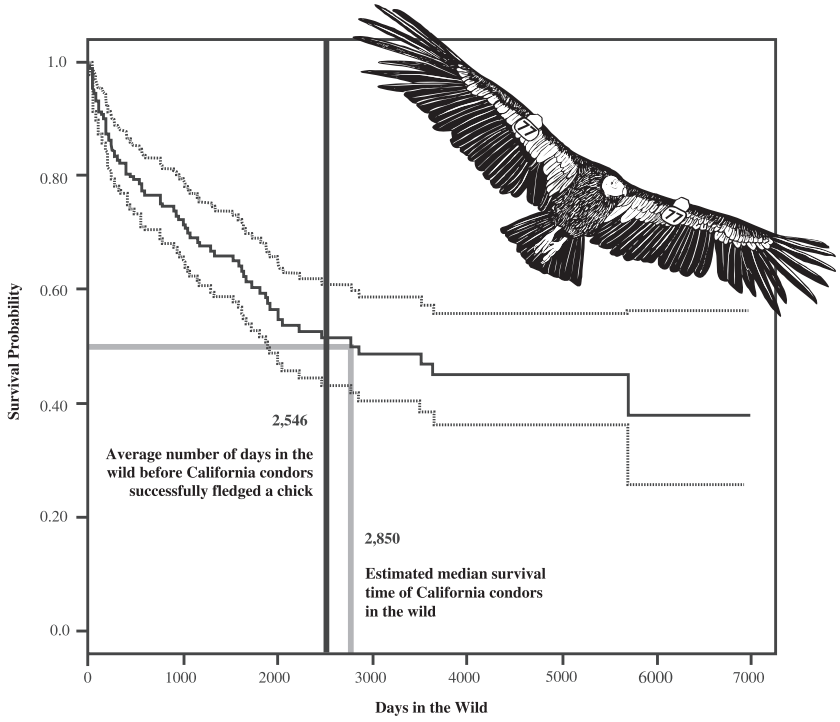

Fig. 1. The estimated unadjusted median survival time for California condors in the wild was 7.8 years (2850 days, 95% CI: 1886 days, NA; light gray line) during the two decades of reintroductions. Because California condors were free-flying in the wild for 7 years on average before they successfully fledged a chick (black line), findings suggest that 50% of condors released or fledged within the 20 year period would be expected to survive until the average time in which they successfully fledge their first chick, illustrating low recruitment to the breeding population.

27% of the 45 mortalities with known cause in California from 1992–2011 were attributed to lead poisoning. Lead accounted for 14% (5/35) of deaths with known cause in immature condors (<6 years old) and the majority of deaths in the adult age class (≥6 years; 70%, 7/10). Because mortality factors leading to the greatest numbers of adult deaths generally have the largest influence on overall rates of avian population change (Saether and Bakke, 2000), lead poisoning ranks highest among threats to the population. Since initiation of the reintroduction program in 1992 through 2009, lead poisoning was also the most important mortality factor for immature and adult condors in the combined free-ranging populations with 26% of juveniles and 67% of adults dying as a result of lead toxicosis (Rideout et al., 2012).

Proportionate mortality due to lead poisoning increased from 16% (5/32) prior to implementation of the lead ammunition regulations (January 1992–June 2008) to 50% (7/13) during the post-ban period (July 2008–December 2011). In addition, greater than 50% (7/12) of the lead-related mortalities in the 20 year study period occurred in the last 3.5 years. Further, we did not detect a significant association between the implementation of lead ammunition regulations and survival time in the wild in our regression models. Over the study period, the annual prevalence of elevated lead exposure (i.e., percentage of sampled condors with blood lead ≥10 μg/dL in a given year) ranged from 62 to 91% (median = 75%). During the post-ban period, the annual prevalence of elevated lead exposure ranged from 79% to 87% (Kelly et al., 2014). Over time, as reintroduced condors have matured and become more experienced in the wild, they have been detected less frequently near managed release sites, and become less reliant on food provisions (Kelly et al., 2014). These shifts toward greater natural foraging, which were most pronounced during the post-ban period, are associated with a higher probability of encountering carrion containing lead ammunition and therefore, a heightened risk of lead poisoning (Kelly et al., 2014). Persistence of lead ammunition in the condors' environment during the post-ban period could be the result of imperfect compliance and/or non-regulated shooting activities (i.e. small mammal game and upland game hunting, depredation killing of nuisance wildlife, poaching, and shooting of domestic animals). Because condors forage communally, multiple individuals can become lead poisoned from a single lead-contaminated carcass. Therefore, even with relatively high compliance, lead poisoning can be prevalent as a result of communal scavenging on carrion containing spent lead ammunition (Kelly et al., 2014).

The recent increase in lead-related mortality in the population may be due, in part, to enhanced detection of lead poisoning and related mortality during the post-ban period. Among condors with an undetermined cause of death as a result of disappearance (n = 19) or poor carcass condition at recovery (n = 12), the percentage of deaths with undetermined cause was lower during the post-ban period (32%) compared to the pre-ban period (44%). Logistical challenges associated with carcass recovery may lead to under-representation of causes of mortality that are more difficult to detect, such as lead poisoning (Rideout et al., 2012). Condors that die from lead poisoning are less likely to be recovered than condors that die from utility line collision and/or electrocution due to the proximity of utility lines to human infrastructure and roads. Because condor tracking effort using satellite telemetry increased after implementation of the lead ammunition regulations, it is likely that detection of lead-related mortalities was higher during the post-ban period.

Even with clinical interventions to mitigate lead poisoning, lead exposure was associated with an increased hazard of death for condors in our multivariable analyses. Our first regression model shows that the hazard of death was 4.6 times higher on average for every 100 μg/dL increase in blood lead level measured in an individual (Table 2). Similarly, our second regression model with time intervals defined on a daily scale reveals that for every 50% increase in the cumulative percentage of lead levels ≥ 45 μg/dL (threshold for clinical lead poisoning (Finkelstein et al., 2012)) over an individual's lifetime, the hazard of death increased by a factor of 3.0 (Table 3). Possible non-exclusive explanations as to why multiple blood lead levels ≥ 45 μg/dL might contribute to an increased hazard of death are three-fold. First, multiple lead poisoning events for an individual may reflect behaviors, such as a lower reliance on food provisions and greater natural foraging, that are associated with increased risk of lead exposure and a higher probability of an acutely toxic lead exposure event leading to death (Kelly et al., 2014). Second, lead has multi-organ system effects in birds (Beyer et al., 1988, 1998; Reiser and Temple, 1981) that can occur at blood lead levels < 45 μg/dL (Dey et al., 2000; Finkelstein et al., 2012). Finkelstein et al. (2012) showed that condors experience 90% δ-aminolevulinic acid dehydratase (ALAD) enzyme inhibition at blood lead concentrations < 45 μg/dL. Depressed ALAD activity is a sensitive bioindicator of sublethal lead toxicosis in humans and animals (Felitsyn et al., 2008; Flora et al., 2012; Hunt, 2012), is correlated with biomarkers for oxidative stress (Gurer-Orhan et al., 2004), and is associated with adverse health effects (Felitsyn et al., 2008; Hunt, 2012). Oxidative stress and tissue damage associated with chronic lead exposure (Bellinger, 2011; Dey et al., 2000; Felitsyn et al., 2008; Flora et al., 2012; Fowler et al., 2004; Hunt, 2012; McBride et al., 2004; Work and Smith, 1996) may result in a decreased ability to process subsequent lead exposures and an increased vulnerability to lead-related mortality. Third, chronic lead exposure may also lead to an increased risk of mortality due to other causes. For example, sublethal lead exposure in humans has been associated with higher all-cause mortality (i.e., mortality rate from all causes of death; Bellinger, 2011; Hunt, 2012). Long-term prospective studies conducted in cohorts drawn from the general population have reported an association between lead exposure and decreased survival. Deaths due to cardiovascular disease were largely responsible for the associations in these studies (Bellinger, 2011; Hunt, 2012).

There are reports of lower lead concentrations, especially with prolonged or repeated exposure, resulting in negative health effects in condors and other avian species, including impaired reproductive success (Buerger et al., 1986), growth rate of young (Custer et al., 1984; Hoffmann et al., 1985), neurobehavioral function (Burger and

Table 2
Extended Cox regression model adjusted hazard ratios and 95% confidence intervals for the association between survival time and risk factors for decreased survival in the wild in California condors in California, 1992–2011. Time intervals in this model are defined by the periods of time between blood lead measurements for each condor.

Risk factor	Coefficient	Hazard ratio (95% C.I.)	*P*
Blood lead level (μg/dL)	0.02	4.60 (2.30–9.30)[a]	<0.001
Region of residence			
Central California	Reference		
Southern California	0.59	1.80 (1.10–2.90)	0.02

[a] Calculation of adjusted hazard ratio was based on consideration of a meaningful unit change in the risk factor: 100 μg/dL increase in blood lead level. The median blood lead level detected at the time of death from individuals that died due to lead poisoning was 150 μg/dL (n = 9; range = 80–523 μg/dL).

Table 3
Extended Cox regression model adjusted hazard ratios and 95% confidence intervals for the association between survival time and risk factors for decreased survival in the wild in California condors in California, 1992–2011. Time intervals in this model are daily time intervals for each condor.

Risk factor	Coefficient	Hazard ratio (95% C.I.)	*P*
Observation in perimeter of forest fire during wildfire activity	3.02	20.60 (6.80–62.10)	<0.001
Percentage of blood lead levels ≥45 μg/dL	2.24	3.10 (1.82–5.17)[a]	<0.001
Region of residence			
Central California	Reference		
Southern California	0.50	1.70 (0.99–2.71)	0.05

[a] Calculation of adjusted hazard ratios were based on consideration of a meaningful unit change in the risk factor: 50% increase in percentage of blood lead levels ≥45 μg/dL.

Gochfeld, 2005; Kelly and Kelly, 2005), immunity (Redig et al., 1991; Snoeijs et al., 2004), and physiology (Carpenter et al., 2003; Finkelstein et al., 2012; Gangoso et al., 2009). Sublethal effects of lead and its contributing effects on mortality and population viability in wild bird populations are likely more prevalent than we are able to determine from studies of free-flying populations. An inherent limitation to assessing the association between sublethal lead exposure and decreased survival is the incomplete history of exposure for an individual. Blood lead analysis is the most commonly utilized method for assessing lead exposure, but it reflects only recent exposure because of the short half-life of lead in blood (estimated elimination half-life ~13 days; Fry and Maurer, 2003). Therefore, sampling a condor two to three times a year for lead exposure underestimates the frequency and magnitude of lead exposure (Finkelstein et al., 2010). Among condors dying from causes other than lead poisoning in our study, 12% had previous lead poisoning events detected through blood lead analysis. Competing risk models, which require larger sample sizes than this study, could be useful in the future when there are greater amounts of data for this population to investigate the relationship between condor lead exposure and hazard of death due to causes other than lead poisoning.

Utility line collision and/or electrocution was also a leading cause of mortality in this study, though less formidable in recent years. From 1992–2011, 24% (11/45) of mortalities for the population were attributed to this mortality factor. During the first three years of the reintroduction program when releases were only occurring in southern California, utility line electrocution mortalities were common among newly released condors (Snyder and Snyder, 2000). In 1995, utility pole aversion training was initiated, which decreased the incidence of condors perching on utility poles (Snyder, 2007), and subsequently the numbers of utility line injury-related deaths. The proportionate mortality for utility line collision and/or electrocution decreased from 66% (4/6) for condors released prior to implementation of utility pole aversion training to 18% (7/39) for condors released after initiation of training. Utility pole aversion training was not significantly associated with survival time in our regression model. However, only twelve condors were released prior to implementation of training and three of these individuals were permanently returned to captivity in 1994, and therefore lost to follow-up. So, the lack of detectable association between training and the hazard of death in the model was likely the result of such few individuals without training in the 20 year dataset.

The majority of utility line associated mortality following implementation of the aversion training occurred in a high risk area near the Big Sur release site as a result of inflight line collisions (Rideout et al., 2012), a problem not easily addressed through aversion training. After bird-flight diverters were installed on lines in this area, only one collision related mortality occurred at a utility line equipped with the diverters (Rideout et al., 2012). Further efforts to mitigate this problem involved burying a portion of the utility line in the high risk area. Condor mortalities as a result of utility line collision and/or electrocution are rare outside of California, with only one utility line collision related death reported in a condor in Arizona and no mortalities associated with utility lines in condors at the Baja California release site (Rideout et al., 2012). The difference in utility line related mortality in these populations is presumably the result of fewer utility lines surrounding the Arizona and Baja release sites. While the risk of utility line collision and/or electrocution related mortality has decreased substantially within the current condor range as a result of targeted mitigation efforts, this mortality factor may pose an increased threat to the population in the future as individuals expand their range and reoccupy areas of their historic range, which includes locations of existing and proposed energy developments with transmission lines (Barrios and Rodriguez, 2004; Carette and Sanchez-Zapata, 2010; Telleria, 2009).

Over the past two decades, seven condor deaths have been associated with wildfire activity in southern California and Big Sur. Although a definitive cause of death could not be determined, wildfire was presumed to have contributed to the death of these individuals because their disappearance coincided with wildfire activity in the surrounding area (Rideout et al., 2012). Condors were observed in areas with wildfire activity during four forest fires in California (1992–2011) and all of these fires were associated with at least one condor mortality. In the multivariable analyses, the hazard of death was on average 20 times higher for a condor last documented within the final forest fire perimeter (as defined in the California Department of Forestry and Fire Protection fire perimeter database) during reported fire activity compared to an individual not observed within the perimeter (Table 3) suggesting that wildfire was a significant hazard to free-flying condors. Wildfires have impacted condor nesting in California, but historically were presumed to have little effect on individuals that can fly away from locations with wildfire activity (Snyder and Snyder, 2000). Although our analyses provide evidence that wildfire threatens survival of free-flying condors in California, it is unclear how condors succumb to fire or die during periods of intense fire activity. Wildfire likely presents a hazard to condors when it burns through roosting and nesting areas at night and at rates that preclude escape (Brandt et al., 2010).

Since the 1980s, California has experienced increased wildfire frequency as a result of land-use and local climatic conditions (Westerling et al., 2006). Warming trends and drought are expected to result in longer fire seasons and higher incidence of large wildfires (Westerling et al., 2006). Wildfire has not been documented as a mortality factor in condors at the Baja California and Arizona release sites (Rideout et al., 2012) where nesting and roosting areas have been less impacted by forest fires. Increases in frequency of wildfire and fire season duration in California are emerging conservation concerns for the population. Similar to clustered mortality due to communal feeding on a contaminated carcass, small flocks, limited geographic distributions, and communal roosting increases the population's vulnerability to catastrophic losses from a single fire event.

Our regression models also revealed regional differences in survival time over the study period (Tables 2 and 3). On average, the hazard of death was approximately 1.8 times higher for condors in southern California compared to condors in central California. Low survival rates, particularly within the first year following release in southern California and to a lesser extent in Big Sur, were evident early in the reintroduction program. Condors were first reintroduced to the wild in southern California five years prior to initiation of reintroductions in central California. Utility line collision and/or electrocution, trauma, and starvation were particularly common causes of mortality for these newly released individuals.

Sex, age at release or fledge, source of the condor (i.e., captive-reared or wild-fledged), and having been reared by a parent or a hand puppet were not significantly associated with survival time in the multivariable analyses. In our sub analysis involving only captive-bred condors, we did not detect an association between survival and release year and numbers released in the cohort with the individual, nor did we detect an association between survival and original release site in condors released in southern California. Furthermore, survival was not influenced by the age class of the condor at release. In contrast, Woods et al. found that among California condors released in Arizona between 1996 and 2005, individuals that were less than one year old when they were released had a lower likelihood of survival than individuals that were released when they were greater than one year old (Woods et al., 2007). Differences in the influence of age at release on survival of condors in California and Arizona could be due to management and/or mortality factors important for first-year condors that are specific to these locations, especially early in the reintroduction programs.

4. Conclusion

Our results show that over the two decades of re-establishment, overall annual mortality rates for the California condor population in California exceeded levels necessary for a stable wild population. Annual mortality rates have decreased to levels during the second decade of

reintroductions that are required for stability; however, ongoing intensive management actions have been required to decrease mortality. Natural recruitment of fledglings has so far been too low to compensate for mortality rates. As a result, continued releases from the captive breeding program have been necessary to promote population growth.

Mortality in the reintroduced California condor population has largely been the result of anthropogenic impacts, which have had a cumulative impact on survivorship in the population. Utility line collision and/or electrocution was an important mortality factor early in this study period that has since been largely mitigated by utility pole aversion training, and more recently by placement of bird-flight diverters and burial of lines in high-risk areas. Historically, wildfires were presumed to pose minimal threat for free-flying condors that can move away from locations with wildfire activity; however, our analyses suggest that forest fires were a significant hazard for free-flying condors in California during the two decades of re-establishment. Increases in the incidence of wildfire and the length of the fire season in California emphasize the importance of this threat to the population as the limited geographic distribution and communal roosting behavior by condors put this population at risk of catastrophic losses from fire. Decreasing the population's vulnerability to wildfire will become even more important as drought conditions in California heighten the risk of wildfire.

Lead poisoning was the leading cause of death over the two decades, accounting for the greatest mortality among breeding aged adults. Because small populations are sensitive to slight changes in mortality rates among breeders (Saether and Bakke, 2000), mitigation of lead poisoning is critical to this species' recovery. Our analyses show that lead poisoning was a significant threat to survival even with clinical interventions for lead poisoned individuals. In addition, we found that lead-related mortality was higher in recent years in spite of lead ammunition regulations within the condor range in California. Shifts toward less reliance on food provisions and increased natural foraging among condors have increased their risk of lead poisoning (Kelly et al., 2014). Increasing independence in this population has contributed to recent increases in lead-related mortality, which are also likely evident from improved detection in the post-ban period with fewer deaths from undetermined causes. Similar to other vulture populations experiencing declines worldwide (Fisher et al., 2006; Ogada et al., 2012; Shultz et al., 2004), California condors are susceptible to large-scale poisoning events as a result of communal foraging behavior that puts several individuals at risk of exposure to a single contaminated carcass (Ogada et al., 2012). Progress toward recovery is not sustainable if the level of management required to ameliorate the threat of lead poisoning for the condor population remains the same, as the majority of investment has been put forth to reducing mortality rates rather than improving the viability of the reintroduced populations (Walters et al., 2010). Recent expansion of lead ammunition reduction efforts in California, including intensified outreach efforts, holds promise for new directions in management and an upward trajectory in survivorship and growth for this population (Johnson et al., 2013).

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