Contributed Paper

Spatiotemporal Patterns and Risk Factors for Lead Exposure in Endangered California Condors during 15 Years of Reintroduction

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Abstract: *Large-scale poisoning events are common to scavenging bird species that forage communally, many of which are in decline. To reduce the threat of poisoning and compensate for other persistent threats, management, including supplemental feeding, is ongoing for many reintroduced and endangered vulture populations. Through a longitudinal study of lead exposure in California condors* (Gymnogyps californianus), *we illustrate the conservation challenges inherent in reintroduction of an endangered species to the wild when pervasive threats have not been eliminated. We evaluated population-wide patterns in blood lead levels from 1997 to 2011 and assessed a broad range of putative demographic, behavioral, and environmental risk factors for elevated lead exposure among reintroduced California condors in California (United States). We also assessed the effectiveness of lead ammunition regulations within the condor's range in California by comparing condor blood lead levels before and after implementation of the regulations. Lead exposure was a pervasive threat to California condors despite recent regulations limiting lead ammunition use. In addition, condor lead levels significantly increased as age and independence from intensive management increased, including increasing time spent away from managed release sites, and decreasing reliance on food provisions. Greater independence among an increasing number of reintroduced condors has therefore elevated the population's risk of lead exposure and limited the effectiveness of lead reduction efforts to date. Our findings highlight the challenges of restoring endangered vulture populations as they mature and become less reliant on management actions necessary to compensate for persistent threats.*

Keywords: ecotoxicology, epidemiology, *Gymnogyps californianus*, scavenger, vulture, wildlife disease

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Patrones Espaciotemporales y Factores de Riesgo por Exposición a Plomo en Cóndores de California Durante 15 Años de Reintroducción

Resumen: *El envenenamiento a gran escala es común en especies de aves carroñeras que forrajean comunalmente, muchas de ellas en declinación. Para reducir la amenaza del envenenamiento y compensar otras amenazas persistentes, se realizan acciones de manejo, incluyendo la suplementación de alimento, con muchas poblaciones de buitres reintroducidas y en peligro. Mediante un estudio longitudinal del envenenamiento por plomo en cóndores de California (*Gymnogyps californianus*), mostramos los retos de conservación inherentes a la reintroducción de una especie en peligro cuando las amenazas principales no han sido eliminadas. Evaluamos patrones en los niveles de plomo en sangre de 1997 a 2011 y evaluamos un amplio rango factores putativos de riesgo demográfico, conductual y ambiental por exposición a niveles elevados de plomo en cóndores de California reintroducidos en California (E.U.A.). También evaluamos la efectividad de las regulaciones para el uso de municiones de plomo en el rango de distribución de Cóndores mediante la comparación de niveles de plomo en la sangre antes y después de la implementación de las regulaciones. La exposición a plomo fue una amenaza constante para los cóndores de California a pesar de las regulaciones que establecen el uso de municiones sin plomo. Adicionalmente. Los niveles de plomo incrementaron significativamente a medida que aumentaba la edad y la independencia de manejo intensivo, incluyendo el incremento del tiempo lejos de sitios de liberación, y el decremento en la dependencia en el aprovisionamiento de alimento. Por lo tanto, una mayor independencia en un mayor número de cóndores reintroducidos, a la fecha ha incrementado el riesgo de exposición a plomo en la población y limitado la efectividad de los esfuerzos para la reducción de plomo. Nuestros resultados resaltan los retos para el restablecimiento de poblaciones de cóndores a medida que maduran y se vuelven menos dependientes de las acciones de manejo necesarias para compensar las amenazas persistentes.*

Palabras Clave: Buitre, carroñero, ecotoxicología, enfermedad de vida silvestre, epidemiología, *Gymnogyps californianus*

Introduction

Global declines in vulture populations have brought awareness to the vulnerability of these populations to variation in food availability, subsequent shifts in food base, and the presence of toxicants and lead in food sources (Ogada et al. 2012). Well-documented poisoning events in vultures have been related to exposure to nonsteroidal anti-inflammatory drugs, predator bait poisons, and lead (Ogada et al. 2012). Because vultures scavenge communally, a single contaminated carcass can poison several individuals. Intensive ongoing management, including supplemental feeding, is used for threatened vulture species to reduce poisoning and compensate for other hazards (Houston 2006; Ogada et al. 2012). However, as individuals in these populations mature in the wild, they may gain independence from management actions, leading to greater risk from persistent threats. We illustrate this conservation challenge through a multidisciplinary investigation of pervasive lead poisoning in an intensively managed endangered species, the California condor (*Gymnogyps californianus*).

Lead poisoning from ingestion of spent lead ammunition in carrion (Hunt et al. 2006) poses a substantial threat to wildlife (Fisher et al. 2006; Rogers et al. 2009) and is of serious concern to the conservation of scavenging birds worldwide, including the California condor (e.g., Fisher et al. 2006; Nam & Lee 2009; Finkelstein et al. 2012). Condors are obligate scavengers and have evolved foraging strategies that allow them to utilize ephemeral and patchily distributed food resources. Historically, California condors fed on large mammalian wildlife, but overharvest and subsequent decline of many terrestrial and marine mammal species and agricultural intensification over the past few centuries encouraged greater dependence on agricultural animals as a food source (Koford 1953; Emslie 1987; Chamberlain et al. 2005). Populations of deer (*Odocoileus hemionus* spp.), elk (*Cervus canadensis* spp.), and many marine mammals have since rebounded and these, together with introduced pigs (*Sus scrofa*) and livestock, provide important natural food sources for the reestablishing California condor population (Chamberlain et al. 2005; Sorenson & Burnett 2007; Walters et al. 2010).

Evidence points toward lead poisoning as a major driver of population decline, and near extinction, of the California condor in the 1980s (Meretsky et al. 2000; Snyder 2007). After there were just 21 individuals remaining in the wild, the remnant population was brought into captivity in the late 1980s for captive breeding and reintroduction efforts. Reintroductions were initiated in 1992, and there are now over 100 free-flying condors in California (Mace 2011). However, condor populations are far from self-sustaining (Walters et al. 2010), and lead poisoning remains the greatest challenge facing recovery efforts despite intensive management actions aimed at reducing this threat (Finkelstein et al. 2012; Rideout et al. 2012). Condors are regularly monitored for lead exposure, and treatment is provided to poisoned individuals (Walters et al. 2010). The population is also regularly provisioned with food, primarily for the transition of young birds to the wild. Food provision has reduced foraging on natural food sources that may be contaminated with lead ammunition (Walters et al. 2010).The potential of food provisioning as a tool for reducing lead exposure was a justification presented for condor reintroduction in the 1990s (Snyder & Snyder 2000). Voluntary and mandatory nonlead ammunition programs have also been initiated in the California condor's range to reduce lead ammunition in natural food resources (e.g., California Department of Fish and Wildlife 2008; Institute for Wildlife Studies 2008; Ventana Wildlife Society 2012). Most notably, regulations on use of lead projectiles for big game and nongame hunting were implemented throughout the condor's range in California in 2008 (California Fish and Game Commission 2008; California State Assembly 2008). Most recently, California has broadened regulations that will eventually phase in restrictions on lead ammunition for take of all types of wildlife statewide.

The seriousness of the lead threat illustrates the need for an enhanced understanding of risk factors for lead exposure in California condors and the effectiveness of initial management actions aimed at reducing lead exposure in the population. We conducted a population-wide investigation into spatiotemporal patterns of lead exposure in condors free-flying in California and evaluated the putative demographic, environmental, and behavioral risk factors for elevated lead exposure.

Methods

Study Population

California condor reintroductions were initiated in southern California in 1992, Big Sur Condor Sanctuary in 1997, and Pinnacles National Park (hereafter Pinnacles) in 2003 (Fig. 1). Four release locations have been used in southern California (Hopper Mountain National Wildlife Refuge (Hopper Mountain NWR), Lion Canyon, Castle Crags, and Bitter Creek National Wildlife Refuge); condors were released at only one location at a time. Long range movements of condors occurred between Big Sur and southern California from 2000 to 2004, when a number of Big Sur condors spent time in southern California. However, use of the southern California site by condors released at Big Sur became less frequent in 2005. In contrast, since 2007 most condors released in central California have used both Big Sur and Pinnacles.

Data Collection

As part of the post-reintroduction intensive monitoring conducted by the condor recovery program, all California condors were fitted with numbered patagial tags for visual verification and VHF transmitters for radiotelemetry. In general, condor tracking was performed daily with radiotelemetry and visual observation (Supporting Information). In addition, global positioning system telemetry units were used on a portion of the population starting in 2003 to provide additional information on population movements (Grantham 2007), and breeding adults were tracked to monitor reproductive activities (Mee et al. 2007).

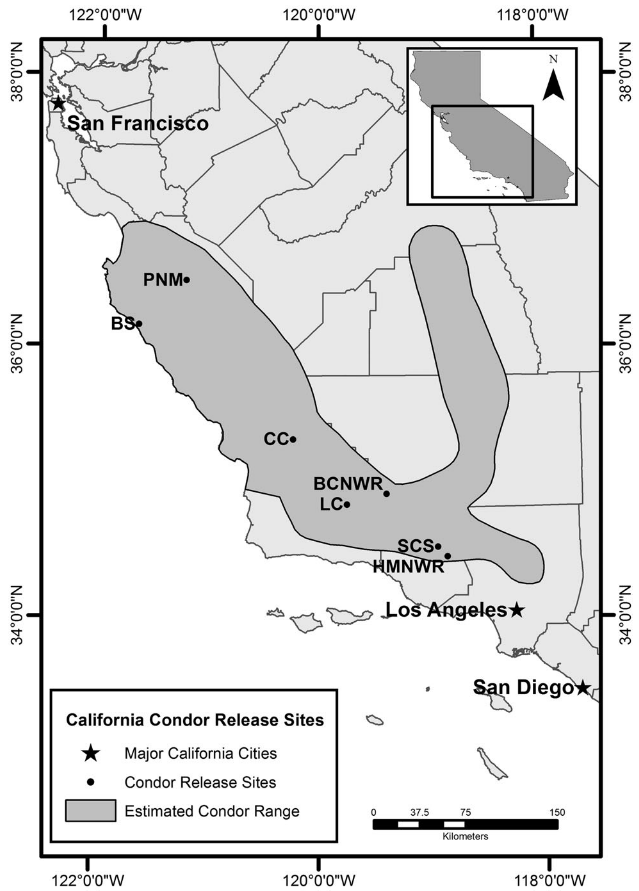

*Figure 1. Estimated California condor (*Gymnogyps californianus*) range and release sites in California (BCNWR, Bitter Creek National Wildlife Refuge; BS, Big Sur; CC, Castle Crags; HMNWR, Hopper Mountain National Wildlife Refuge; LC, Lion Canyon; PNP, Pinnacles National Park; SCS, Sespe Condor Sanctuary).*

California condors have been provided with carrion, generally every 3 d, at provisioning sites at or near release locations in southern and central California. We observed sites on days when food was provided and often more frequently (Hall et al. 2007; Sorenson & Burnett 2007). More recently, remote cameras have been used to collect data on feeding.

We sampled condors for lead exposure at least annually and more recently 2 to 3 times per year (Hall et al.

Table 1. Demographic, environmental, and behavioral risk factors evaluated for their relationship with blood lead level (μg/dL) in California condors (*Gymnogyps californianus*), 1997–2011.

Risk factor	*Risk factor subcategories*
Time—invariant	
sex	male
	female
source	captive reared
	wild fledged
original location of release or fledge	Hopper Mountain National Wildlife Refuge/Sespe Condor Sanctuary
	Castle Crags or Lion Canyon
	Bitter Creek National Wildlife Refuge
	Pinnacles National Park
	Big Sur
Time—varying[a]	
age class	≤2 years
	≥3 years
year of capture	year of capture for sampling
month of capture	month of capture for sampling
secondary site[b]	none
	Southern California
	Big Sur
	Pinnacles National Park
reliance on food provision[c]	percentage of days observed feeding on proffered food
time undetected	percentage of days not detected by VHF telemetry or observation
stage of parental care	not providing care to young
	providing care to nestling
	providing care to fledgling
home range[d]	home range (ha)
reason for sampling	routine lead monitoring
	suspect lead exposure

[a] *Risk factors characterized for each blood lead measurement during the exposure window.*
[b] *Where condor was detected in addition to its primary site during the exposure window.*
[c] *Data available only for central California (Big Sur and Pinnacles National Park).*
[d] *Estimates available for a subset of condors for which there was a monthly home range estimate overlapping in time with the exposure window.*

2007; Sorenson & Burnett 2007). Furthermore, we tested individuals that appeared to be ill and those suspected to have fed on lead contaminated carrion for lead exposure in addition to conducting routine monitoring. Lead levels in blood samples were analyzed at commercial laboratories (Supporting Information).

Data Analyses

We used longitudinal blood lead data collected from 1997 to 2011 from 150 condors to assess spatiotemporal trends in lead levels and putative demographic, behavioral, and environmental risk factors for lead exposure in the population (Table 1 & Supporting Information). Sequential lead levels separated by >2 months were included (i.e., approximately 5 half-lives of lead in condor blood) (Fry & Maurer 2003). These samples were considered independent in terms of a lead exposure event. Sequential lead concentrations obtained ≤2 months apart from an individual were also included when the lead level for the second blood sample was 10 μg/dL greater than the level for the first sample. The 10 μg/dL elevation in blood lead concentration signified that an exposure event occurred for the individual between sample collections (Supporting Information).

Time-varying risk factors were characterized for each lead measurement with individual-level data for the 4 weeks preceding capture (Table 1 & Supporting Information). This period reflected the time presumed to be most relevant when assessing time-varying risk factors for lead exposure. For 4 individuals with increasing sequential measurements obtained ≤2 months apart indicating an exposure event, time-varying factors were characterized for the shorter period between samples. We refer to the 4-week or shorter period between increasing sequential measurements as the exposure window. Monthly home range sizes (Supporting Information) overlapping with the exposure window were available for a subset of individuals, which allowed us to evaluate the relationship between home range and lead exposure.

We applied a natural logarithmic transformation to assist with normalization of the blood lead concentration data. Univariable generalized estimating equation (GEE) models (Hardin & Hilbe 2003) were developed to investigate the relationship between putative risk factors and blood lead concentrations. We also performed bivariate analyses to evaluate associations between risk factors. Factors that had a significant relationship with lead level ($p < 0.1$), potentially confounding variables, and biologically plausible interactions were then evaluated in multivariable GEE models; transformed blood lead concentrations was the dependent variable.

Because there was significant spatial variation in the effect of several risk factors on lead levels, we performed site-specific analyses. Although condors were most often detected at a single site during the exposure window, condors were sometimes detected at multiple sites during the window. Thus, we used the site (i.e., southern California, Pinnacles, or Big Sur) at which the condor had the majority of daily detections during the window to designate a primary site for that blood lead measurement. The primary site designation was used to group the blood lead data into 3 subsets according to the sites for spatially explicit analyses. In each site-specific model, we also assessed whether use of an additional site (i.e., secondary site) during the exposure window was a risk factor for elevated lead exposure. We also constructed GEE models including only data collected from 1 September 2008 to 31 December 2011 to specifically investigate risk factors during the post-ban period (Supporting Information).

Temporal clusters of elevated blood lead concentrations (i.e., defined outbreaks of lead exposure) were also detected through use of temporal scan statistics in SatScan version 9.0 (Kulldorff et al. 2009) (Supporting Information). To compare lead exposure between

Table 2. Unadjusted summary measures for blood lead levels (μg/dL) for California condors (*Gymnogyps californianus*) in California (1997–2011) before and after a ban on the use of lead ammunition for big game and nongame hunting activities in the condor range in California in 2008.

	n^a	*Proportion of blood lead levels ≥ 10 μg/dL*	*Median blood lead level in μg/dL (maximum)*[b]	*SD*
Total population				
overall	1291	0.64	14 (610)	56.40
pre-ban	565	0.67	14 (610)	44.97
post-ban	726	0.62	13 (580)	63.77
post-ban 2008	36	0.58	11.5 (320)	52.29
2009	223	0.60	12 (370)	57.22
2010	232	0.61	14.5 (570)	73.93
2011	235	0.63	13 (580)	60.18
Southern California				
overall	709	0.63	14 (580)	51.03
pre-ban	339	0.71	16 (523)	43.73
post-ban	370	0.56	11 (580)	56.49
post-ban 2008	36	0.58	12 (320)	52.29
2009	93	0.38	8 (120)	15.96
2010	120	0.58	15 (370)	65.47
2011	121	0.63	13 (580)	67.62
Big Sur				
overall	399	0.54	10 (610)	38.31
pre-ban	183	0.55	10 (610)	49.90
post-ban	216	0.53	10 (230)	24.53
2009	83	0.66	13 (230)	32.88
2010	67	0.46	9 (62)	11.71
2011	66	0.47	10 (110)	20.92
Pinnacles National Park				
overall	183	0.89	27 (570)	89.35
pre-ban	43	0.85	21 (200)	38.80
post-ban	140	0.90	33 (570)	98.10
2009	47	0.92	41 (370)	95.83
2010	45	0.91	36 (570)	119.46
2011	48	0.88	26 (440)	71.93

[a]*Number of independent blood lead measurements.*
[b]*The minimum blood lead level for each time period was below the reporting limit for the laboratory; therefore, only the median and maximum blood lead levels are reported.*

condors and sympatric scavenging birds sampled post-ban, we used a subset of data collected the first year after the ban so we could compare blood lead levels in condors with sympatric Golden Eagles (*Aquila chrysaetos*) and Turkey Vultures (*Cathartes aura*) (Kelly et al. 2011). All nonspatial analyses were performed in R (R Development Core Team 2011), and we used the geepack package (Hojsgaard et al. 2006) for the GEE models.

Results

Prevalence and Magnitude of Lead Exposure

The annual prevalence of elevated lead exposure (i.e., percentage of sampled condors with blood lead ≥10 μg/dL in a given year) among the 150 condors we sampled in California between 1997 and 2011 ranged from 62% to 91% (median = 75%). During a 3-year period following implementation of the ammunition regulations (i.e., 2009–2011), the annual prevalence of elevated lead exposure ranged from 79% to 87% (median = 81%). The frequency and magnitude of elevated lead exposure varied across sites; exposure was highest among condors at Pinnacles, followed by southern California and Big Sur (Table 2). Overall, lead concentrations (adjusted for month and reason for sampling) were significantly higher in condors at Pinnacles than in condors in southern California and Big Sur ($p < 0.001$, both comparisons). In addition, lead levels were higher in southern California relative to Big Sur over the study period ($p < 0.02$); however, post-ban lead levels were similar among condors at these 2 sites. Blood lead concentrations in California condors during the first year post-ban were similar to levels observed in sympatric Golden Eagles sampled concurrently in southern California; however, condor lead levels were slightly higher than levels in sympatric Turkey Vultures sampled concurrently in the Big Sur area ($p < 0.02$) (Supporting Information).

Relationships between Blood Lead Level and Risk Factors

Overall, univariable GEE models revealed that blood lead concentrations increased as reliance on food provision decreased ($p < 0.001$) and as the time the condor was undetected near provisioning and release sites ($p < 0.001$) during the exposure window increased. Overall, reliance on food provision decreased over time and was significantly lower during the post-ban period relative to the pre-ban period ($p < 0.01$). In addition, despite similar or increased monitoring efforts between the pre-ban and post-ban periods, time that a condor was undetected increased over the study period and was significantly higher post-ban ($p < 0.01$). Furthermore, lead levels increased as monthly home range size increased ($n = 61$; $p = 0.03$). Home range size and time undetected were positively correlated during the post-ban period ($n = 42$; $r = 0.3$; $p = 0.05$), suggesting that increased time undetected was due in part to wide ranging movements away from release and provisioning sites.

Condors ≥3 years old had higher lead levels relative to individuals ≤2 years old ($p < 0.001$). Condors in the older age class also had greater time undetected ($p < 0.001$) and were less reliant on food provision ($p < 0.01$) than condors ≤2 years old. The age distribution of the population increased throughout the study; condor median age during the post-ban period was significantly higher than during the pre-ban period ($p < 0.001$). Blood lead concentrations did not vary relative to sex, origin, rearing status, or whether the condor engaged in parental care during the exposure window.

Spatial Patterns of Risk Factors

Condors at Pinnacles had the greatest percentage of time undetected near release and provisioning sites during the exposure window (median = 23%), followed by Big Sur (median = 20%) and southern California (median = 17%). Condors at Pinnacles also had significantly lower reliance on food provision during the exposure window (median = 10%) than condors at Big Sur (median = 13%) ($p < 0.001$).

Blood lead levels among 90 condors in southern California ($n = 339$ pre-ban and 370 post-ban lead measurements) exhibited significant interannual and seasonal variation. Relative to the adjusted geometric mean blood lead level (hereafter mean lead level or concentration) during the pre-ban period, the mean lead level in 2009 was reduced in magnitude (50% decrease). However, in 2010 the mean lead concentration was higher relative to the pre-ban period and in 2011 there was no difference (Table 3 & Supporting Information). Lead levels were higher in July and August than at other times of the year (Table 3). Lead levels were also high in April and May; however, sample sizes were very low for these months ($n = 16$).Temporal scan statistics revealed significant temporal clusters of elevated blood lead concentrations, indicating outbreaks of lead exposure in August to September 2000 ($p < 0.01$) and during the post-ban period in November to December 2010 ($p < 0.001$). With the exception of one 2-year-old individual, this outbreak was limited to condors ≥3 years old.

Table 3. General estimating equation (GEE) model estimates for the relationship between blood lead level (μg/dL) and risk factors for lead exposure in California condors (*Gymnogyps californianus*) in southern California, 1997–2011.

Risk factor	*Coefficient estimate*[a]	*SE*[a]	*p*
Intercept	1.740	0.242	<0.001
Time of capture[b]			
pre-ban	Reference		
post-ban 2008[c]	0.064	0.183	0.728
2009	−0.573	0.102	<0.001
2010	0.239	0.122	0.049
2011	0.029	0.122	0.812
Month of capture			
February and March	Reference		
April and May	0.786	0.256	0.002
June	0.261	0.139	0.060
July and August	0.546	0.131	<0.001
September to November	0.053	0.122	0.666
December and January	0.241	0.142	0.090
Time undetected[d]	0.007	0.002	<0.001
Release or fledge location			
Bitter Creek National Wildlife Refuge	Reference		
Big Sur	0.335	0.316	0.290
Castle Crags or Lion Canyon	0.766	0.207	<0.001
Hopper Mountain National Wildlife Refuge	0.401	0.195	0.040
Age			
≤2 years	Reference		
≥3 years	0.295	0.124	0.018
Reason for sampling			
routine lead testing	Reference		
suspect lead exposure	0.177	0.162	0.274

[a] *Natural logarithmic scale.*
[b] *The use of lead projectiles for big game and nongame hunting was banned throughout the condor's range in California in 2008.*
[c] *Pre-ban: 1 January 1997 to 31 August 2008; post-ban 2008: 1 September to 31 December 2008. Blood lead levels obtained during the first 2 months post-ban were included in the pre-ban period because lead levels may reflect exposure that occurred pre-ban.*
[d] *Variable was centered.*

Blood lead concentrations increased as time the condor was undetected during the exposure window increased (Table 3 & Supporting Information). Condors that were undetected for 33% of the exposure window (i.e., upper quartile of the risk factor) had a mean lead level that was 1.2 times higher than condors that were undetected for 7% of the window (i.e., lower quartile of the risk factor).

Blood lead levels were highest in condors originally released at the Lion Canyon and Castle Crags locations (Table 3). Data from the 2 release cohorts were combined for analysis because the lead levels were similar in magnitude and the 2 cohorts had almost immediate interaction postrelease (Grantham 2007). Even after adjusting for age, condors released at these 2 locations had a mean lead concentration that was approximately 1.5

Table 4. General estimating equation (GEE) model estimates for the relationship between blood lead level (μg/dL) and risk factors for lead exposure in California condors (*Gymnogyps californianus*) in Big Sur, California, 1998–2011.

Risk factor	*Coefficient estimate*[a]	*SE*[a]	*p*
Intercept	1.244	0.172	<0.001
Time of capture[b]			
Pre-ban	Reference		
2009	−0.096	0.141	0.496
2010	−0.256	0.107	0.010
2011	−0.255	0.136	0.060
Month of capture			
February to April	Reference		
May to August	0.316	0.101	0.002
September and October	0.857	0.120	<0.001
November to January	0.579	0.145	<0.001
Secondary site			
none	Reference		
Pinnacles National Park	0.252	0.123	0.041
Southern California	0.645	0.171	<0.001
Reliance on food provisions[c]	−0.010	0.004	0.021
Age			
≤2 years	Reference		
≥3 years	0.660	0.153	<0.001
Reason for sampling			
routine lead testing	Reference		
suspect lead exposure	0.826	0.280	0.003

[a]*Natural logarithmic scale.*
[b]*The use of lead projectiles for big game and nongame hunting was banned throughout the condor's range in California in 2008.*
[c]*Variable was centered.*

Table 5. General estimating equation (GEE) model estimates for the relationship between blood lead level (μg/dL) and risk factors for lead exposure in California condors (*Gymnogyps californianus*) in Pinnacles National Park, California, 2005–2011.

Risk factor	Coefficient estimate[a]	SE[a]	*p*
Intercept	2.142	0.357	<0.001
Time of capture[b]			
Pre-ban	Reference		
2009	0.592	0.173	0.001
2010	0.451	0.289	0.119
2011	0.143	0.242	0.555
Month of capture			
February toApril	Reference		
December and January	−0.021	0.455	0.963
July to September	−0.011	0.247	0.966
May and June	0.224	0.283	0.428
October and November	0.699	0.285	0.014
Reliance on food provisions[c]	−0.031	0.001	0.004
Age			
≤2 years	Reference		
≥3 years	0.632	0.247	0.011
Reason for sampling			
routine lead testing	Reference		
suspect lead exposure	0.333	0.199	0.093

[a]*Natural logarithmic scale.*
[b]*The use of lead projectiles for big game and nongame hunting was banned throughout the condor's range in California in 2008.*
[c]*Variable was centered.*

times higher than condors released or fledged at Big Sur or Hopper Mountain National Wildlife Refuge (Table 3 & Supporting Information). The mean lead level during the post-ban period remained higher for individuals released at these 2 locations than for individuals released at all other locations (Supporting Information).

Blood lead levels among 67 condors at Big Sur ($n = 183$ pre-ban and 216 post-ban lead measurements) were similar among years during the pre-ban period, with the exception of 2005 when they were higher than all other years. In Big Sur, relative to the mean blood lead concentration during the pre-ban period, the mean in 2010 decreased (23% decrease), whereas in 2009 and 2011 the mean blood lead levels were similar to the pre-ban period (Table 4 & Supporting Information). Blood lead levels were highest in September and October at this site (Table 4). Blood lead concentrations among 44 condors at Pinnacles ($n = 43$ pre-ban and 140 post-ban lead measurements) were too sparse across the shorter pre-ban period for comparisons to be made between years. At Pinnacles in 2009, the mean lead level was higher than during pre-ban period (Table 5 & Supporting Information). Overall, blood lead levels were highest in October and November at this site (Table 5). A significant temporal cluster of elevated blood lead concentrations was detected among condors in central California in October to November 2009 ($p < 0.001$). This event was limited to condors ≥3 years old.

Blood lead levels were higher in Big Sur condors that were detected at a secondary site in addition to Big Sur during the exposure window, indicating that movements outside the Big Sur area were associated with higher lead levels (Table 4). Specifically, for condors detected only in the Big Sur area during the exposure window, the mean lead concentration was 1.9 times higher than for condors that were also detected in southern California and 1.3 times higher in condors that were also detected at Pinnacles during their exposure windows (Supporting Information). This relationship was not evident among Big Sur condors detected at other sites during the post-ban period (Supporting Information)

Blood lead levels for condors in central California increased as reliance on food provision decreased during the exposure window (Tables 4 and 5 & Supporting Information). Big Sur condors that fed on proffered food for 7% of the window (i.e., lower quartile of risk factor) had a mean lead level that was 1.2 times higher than condors that fed on food provisions for 22% of the window (i.e., upper quartile of risk factor) (Supporting Information). Pinnacles condors that fed on food provisions for 3% of the exposure window (i.e., lower quartile of the risk factor) had a mean lead concentration that was 1.7 times higher than condors that fed on food provisions for 17% of the window (i.e., upper quartile of the risk factor) (Supporting Information).

Discussion

Our results show that variation in lead exposure in condors in California may be explained by increasing age and increasing independence from intensive management, as measured by decreased reliance on food subsidies, decreased detection in areas near release and food provisioning sites, and increased home range size. In addition, relative to the pre-ban period, condors during the post-ban period exhibited greater independence from intensive management. Decreased reliance on food provision and detection of condors near release and provisioning sites were associated with lead exposure independent of the effects of age. Older condors are more likely to have first access to carcasses because of age-based dominance hierarchies and therefore may be at greater risk of lead exposure than younger individuals (Hall et al. 2007). In addition, recently released individuals, especially in newly established flocks, usually remain close to the release location before they gradually expand their range, whereas older individuals with greater experience in the wild are wider ranging and less reliant on food provision (Hall et al. 2007). Taken together, our findings provide evidence that the risk of lead exposure is highest among condors that spend relatively more time away from managed sites, have relatively wider ranging movements, and have relatively more independent natural foraging behaviors and evidence that independence has increased in the population over time. These findings provide insight into the underlying processes likely to have contributed to the limited effectiveness of lead reduction efforts. Prevention of lead exposure may prove progressively more difficult as this population becomes increasingly wide ranging and less reliant on food provision, unless lead is eliminated from nonprovisioned food sources.

Lead exposure was highest at Pinnacles, where there was no evidence of reduced exposure during the post-ban period. In contrast, lead levels were lower during certain post-ban years in condors in southern California and Big Sur. Compared with condors at these 2 sites, condors at Pinnacles spent the greatest time away from release and provisioning sites and were the least reliant on food provision. Unlike the sites in southern California and Big Sur, which are largely surrounded by public land (Fire Resource Assessment Program 2011), Pinnacles is primarily surrounded by private land. In California, the majority of take involving feral pigs and nuisance wildlife (often because of property damage) and shooting of domestic animals occurs on private land (California Department of Fish and Wildlife 2001). Restrictions on lead ammunition for these shooting activities were not included in the 2008 regulations (California Fish and Game Commission 2008). Lead levels were lowest in condors in Big Sur and increased in magnitude when individuals were detected in southern California or Pinnacles in addition to the Big Sur area. Condor lead levels have been historically low in Big Sur relative to other sites, which is attributed in part to a preference for marine mammal carrion by many Big Sur condors (Sorenson & Burnett 2007). Among condors in southern California, individuals released at the Lion Canyon and Castle Crags locations had significantly higher lead levels than condors released or fledged from other locations. One possible explanation for higher lead exposure among these release cohorts, after adjusting for age, is greater dominance exerted by these individuals while foraging on natural food sources and potentially a heightened risk of spent lead ammunition ingestion. Dominant condors often gain first access to carcasses and could consume relatively more lead ammunition fragments, especially because they commonly initiate feeding around the bullet wound channel (Hall et al. 2007).

Elevated lead exposure in the condor population exhibited significant seasonal variation. Peak lead levels and outbreaks of lead exposure in central California occurred in the fall when hunter-shot deer carrion is most abundant in this area (Sorenson & Burnett 2007; California Fish and Game Commission 2008). In southern California, lead levels exhibited peaks in April through June and July and August. Temporal scan statistics revealed significant outbreaks of lead exposure in southern California in August to September and November to December, coincident with the multiple deer hunting seasons in that area (California Fish and Game Commission 2008). Similar to previous reports (Hall et al. 2007; Sorenson & Burnett 2007), lead exposure was also detected at other times of the year in California, indicating that lead exposure was not strictly limited to deer hunting. Feral pig and nongame animal hunting occur year-round in California, and take of feral pigs and nuisance wildlife to mitigate damage to private property, and euthanization of farm animals by gunshot provide year-round carrion for condors. October to May is a popular time for pig hunting in southern California because tracking is easiest during the wet season (Waithman 2001), which potentially explains the spring peak in lead exposure in southern California. Lead exposure occurring during the post-ban period exhibited similar seasonal variation and was likely the result of imperfect compliance, poaching, and activities not covered by the regulations, such as shooting of domestic animals and depredation. Lead ammunition in animals from nonfatal gunshot occurring prior to the regulations may have also exposed condors post-ban.

Investigations into sources of lead indicate that lead ammunition is the principal source of lead poisoning in California condors (Finkelstein et al. 2012). To date, lead paint has been documented as a source of poisoning for a few isolated cases and is the only nonammunition source of lead for which there is evidence of exposure in the population (Finkelstein et al. 2012). Metal in trash could also be a source of exposure to condors. Breeding condors, particularly individuals in southern California, have a propensity to ingest trash and feed it to their chicks

(Mee et al. 2007). We did not evaluate blood lead concentrations in chicks; however, there was no evidence of higher exposure in condors caring for young.

Although food provisioning has provided condors with an uncontaminated food base, it is not conducive for establishment of self-sustaining populations (Cade 2007). Regardless, condors are likely to continue to increase their range and become less reliant on provisions, and the natural progression of these behaviors will increase the probability of condors feeding on gun-shot carrion. Because condors engage in communal scavenging, the proportion of animals shot with lead-based ammunition versus nonlead alternatives will continue to greatly influence the risk of lead exposure in naturally foraging condors. Although outreach efforts have occurred within the condor range in California, there has not yet been any broad-scale non-lead ammunition provisioning programs, and efforts have focused primarily on hunters and not yet expanded to engage all shooters. Voluntary lead reduction efforts have also so far been insufficient to prevent lead poisoning in the condor population in Arizona and Utah (Austin et al. 2012). While hunter outreach programs have been successful in Arizona, with 80–90% participation by deer hunters, outreach programs in Utah are still in their infancy (Austin et al. 2012).

Our results suggest that condors that exhibit greater independence, as demonstrated by greater time spent away from release and provisioning sites and less reliance on food provision, have higher lead exposure than conspecifics that have not yet developed independence. A recovering self-sustaining condor population requires natural foraging; however, lead ammunition in the condor's natural food sources will select against this strategy and could preclude recovery. Large scale poisoning events are common among vultures that forage communally, many of which are reliant on ongoing management actions, including supplemental feeding, to reduce persistent threats. Our results highlight the challenges of recovering threatened vultures as populations become less reliant on continued management. Our multidisciplinary approach will be useful as a model for investigations in these intensively managed populations. As with other declining vultures, condors have adapted to a shifting food base over the past few centuries, and this species' future is critically linked to natural food sources that are devoid of contaminants

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Supporting Information

Descriptions of daily tracking methods (Appendix S1), blood lead data (Appendix S2), risk factor characterization (Appendix S3), home range size estimation (Appendix S4), GEE regression model development (Appendix S5), temporal cluster analysis (Appendix S6), results of the comparison of lead levels among sympatric scavenging bird species (Appendix S7), mean blood lead levels for key risk factors in the multivariable analyses (Appendix S8), and supplemental post-ban GEE model outputs (Appendices S9–S11) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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