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Research Article

Lack of Observed Movement Response to Lead Exposure of California Condors

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ABSTRACT Lead poisoning is an important conservation concern for wildlife, and scavenging birds are especially at risk from consumption of carcasses of animals killed with lead ammunition. Because current methods to identify lead exposure require animal capture and blood collection, management would benefit from the development of a less costly and noninvasive behavioral test for illness in wild animals. We attempted to design such a test to identify lead exposure in California condors (*Gymnogyps californianus*) that we tracked with global positioning system (GPS) telemetry in southern California, USA, 2013–2016. We measured blood-lead concentrations in tracked birds and expected that flight behavior would be influenced by lead exposure; thus, we measured the effect of blood-lead concentrations on 2 different types of movement rates and on the proportion of time condors spent in flight. We found no effect of lead exposure on any of these 3 behavioral metrics. Our work suggests that the measurements we took of flight behaviors were not a useful tool in predicting lead exposure in the mildly to moderately exposed birds we studied. Wild birds are effective at hiding illness, especially condors who have a strong social hierarchy in which showing weakness is a disadvantage. However, focusing on behaviors other than flight, expanding the sample studied to include birds with a wider range of lead concentration values, or analyzing tissues such as feathers (rather than, or in addition to, blood) may be more useful for identification of lead exposure and other diseases that may limit wildlife populations.

KEY WORDS animal movement, blood-lead concentrations, California condor, flight behavior, *Gymnogyps californianus*, lead exposure, southern California.

Lead poisoning is an important conservation concern for wildlife (Fisher et al. 2006, Buechley and Şekercioğlu 2016). Scavenging birds are especially at risk of lead exposure from ingestion of lead-based ammunition in carcasses of animals killed by hunters (Church et al. 2006, Finkelstein et al. 2012, Behmke et al. 2017). Worldwide, ingested toxins, including lead, are the most significant extrinsic threat to avian scavengers and are the primary cause of decline of 88% of threatened or near-threatened vulture species (Buechley and Şekercioğlu 2016). Vultures are obligate scavengers and, because they forage communally, a single contaminated carcass can simultaneously poison many individuals (Ogada et al. 2012, Kelly et al. 2014). Consequently, in severe cases, small numbers of poisoned carcasses can result in population collapse (Green et al. 2004). Thus, for certain species, lead poisoning has the potential to change population trajectories (Finkelstein et al. 2012).

Identifying lead exposure in wild animals can be challenging. For birds that are acutely poisoned, visible signs may include emaciation, green biliverdin staining of vent feathers, or neurological impairment (Trainer and Hunt 1965, Beyer et al. 1988, Fisher et al. 2006, Fallon et al. 2017). However, such subjective tests are imprecise, and the standard method to assess lead exposure is through collection and testing of a blood sample (Church et al. 2006, Finkelstein et al. 2012, Kelly et al. 2014). These methods require capturing the animal, which can be invasive, costly, and time-consuming.

An alternative method to identify lead exposure and other diseases in wildlife would therefore be useful. A behavioral test based, for example, on remotely collected data would be less invasive and less costly than current methodologies.

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Developing such a test should be feasible because clinically exposed birds may exhibit a number of potential behaviors symptomatic of lead poisoning, including circling flight, excessive drinking, a reduced ability to fly, or seeking protective cover (Abel and Grossman 1992, U.S. Geological Survey [USGS] 1999). Such a test could be applied to wild animals that are remotely tracked through radio-telemetry. Behaviors associated with illness may be inferred from movement patterns in telemetry data (Ecke et al. 2017). Likewise, animals sick from disease other than lead exposure can exhibit behaviors that might be diagnosed from telemetry data (Halliday 1976, Wolfe et al. 1998, Köhler and Triebskorn 2013). These tests would be especially important for critically endangered, highly managed species (e.g., black-footed ferrets [*Mustela nigripes*], Florida panthers [*Puma concolor couguar*], whooping cranes [*Grus americana*], California condors [*Gymnogyps californianus*]) for which many individuals are tracked and disease or poisoning may be an important limiting factor in population recovery.

We attempted to design a behavioral test to identify lead exposure of California condors (condors). Lead poisoning is the leading cause of death of condors (Rideout et al. 2012). Acute exposure of condors to lead can result in neurological impairment, loss of appetite, reduced movements, and eventually death (Walters et al. 2008). Because of their small population size and risk status, condors are intensively managed throughout their range, and many birds are tracked with global positioning system (GPS) telemetry. We measured 3 flight behavioral parameters that can be characterized with GPS telemetry data from condors that we expected would be affected by illness: hourly distances traveled, speeds between telemetry points, and the proportion of locations in flight. The first 2 of these describe movements of condors, and the third provides information on the relative proportion of time these birds spend either resting or in flight. Our objective was to determine the extent to which measured flight behaviors of condors would be affected by variation in lead exposure. We predicted that exposed condors would travel shorter distances per hour, exhibit slower speeds between telemetry points, and spend less time in flight than would unexposed birds.

STUDY AREA

The condors we studied in southern California, USA, ranged over an area of approximately 15,600 km^2 from the coast north of Los Angeles across mountains to inland deserts (Fig. 1). Elevations in the study area start at sea level at the Pacific Ocean and rise to >3,000 m above sea level (ASL) in the Sierra Nevada. Land cover ranged from open grasslands and agricultural fields to coniferous and deciduous forests (USGS Gap Analysis Program 2011). Dominant vegetation species included blue and mixed oak (*Quercus douglasii* and *Quercus* spp.). Monthly temperatures during the study in the Tehachapi Mountains (an area consistently used by condors) ranged from a mean low of −2°C in December to a mean high of 31°C in July and August, and average annual precipitation was 47 cm (Weather Underground 2017).

METHODS

Condor Capture and Lead Measurements

Twice per year, biologists from the California Condor Recovery Program at the United States Fish and Wildlife Service (USFWS) trap condors, attach a telemetry unit to some of the birds, test them for lead, and release them at Hopper Mountain National Wildlife Refuge (NWR) in Ventura County and Bitter Creek NWR in Kern County (Fig. 1). Their goal is to capture and monitor the health of each bird in the southern California population at least once per year. These management efforts allow insight into the status and eventual fate of each individual condor in the population.

In the course of regular monitoring, USFWS biologists captured condors in baited, walk-in trapping pens. Condors remained in flight pens adjacent to the trapping pens, sometimes for several days, until biologists captured them with a handheld net and drew blood from the medial metatarsal vein. Biologists placed whole blood samples in collection tubes with di-potassium ethylenediaminetetraacetic acid (K_2-EDTA) additive and immediately analyzed samples with a field test kit (LeadCare®, ESA Biosciences, Chelmsford, MA, USA) to obtain the lead concentration value. If this value was >35 μg/dL (a conservative value that does not necessarily indicate clinical symptoms of lead poisoning), the team transported the bird to the Los Angeles Zoo for chelation treatment. Otherwise, biologists gave the bird a standard health evaluation, replaced the telemetry unit if non-functional, and released the bird at the capture site. A certified commercial laboratory (California Animal Health and Food Safety Laboratory, University of California, Davis) conducted more precise testing of lead concentrations in blood samples using graphite furnace atomic absorption spectrometry on a PinAAcle 900Z (PerkinElmer, Waltham, MA, USA). Laboratory staff quantitated lead in the sample by comparison with external calibration solutions and controlled the quality of the analytical run through the use of a method blank, a reporting limit check, and standard reference materials containing certified concentrations of lead (Kelly et al. 2014). The detection limit of blood-lead in this laboratory typically is 5 μg/dL; if a sample was below the detection limit, we considered the lead concentration value to be 0.

This study was carried out in accordance with the recommendations in the Guidelines to the Use of Wild Birds in Research of the Ornithological Council (Fair et al. 2010). Condor field program permits were reviewed and approved by the USFWS Permit Coordinator, California Condor Coordinator, and Region 8 Endangered Species Division. The use of GPS transmitters was authorized as a recovery action under section 10(a)(1)(A) with a permit issued to the Hopper Mountain NWR Complex (no. TE-108507 HMNWR-0). In addition, this work was authorized in the state of California under a separate Memorandum of Understanding between managers of the Hopper Mountain NWR Complex and the California Department of Fish and Wildlife under sections 650 and 670.7, Title 14, California Code of Regulations.

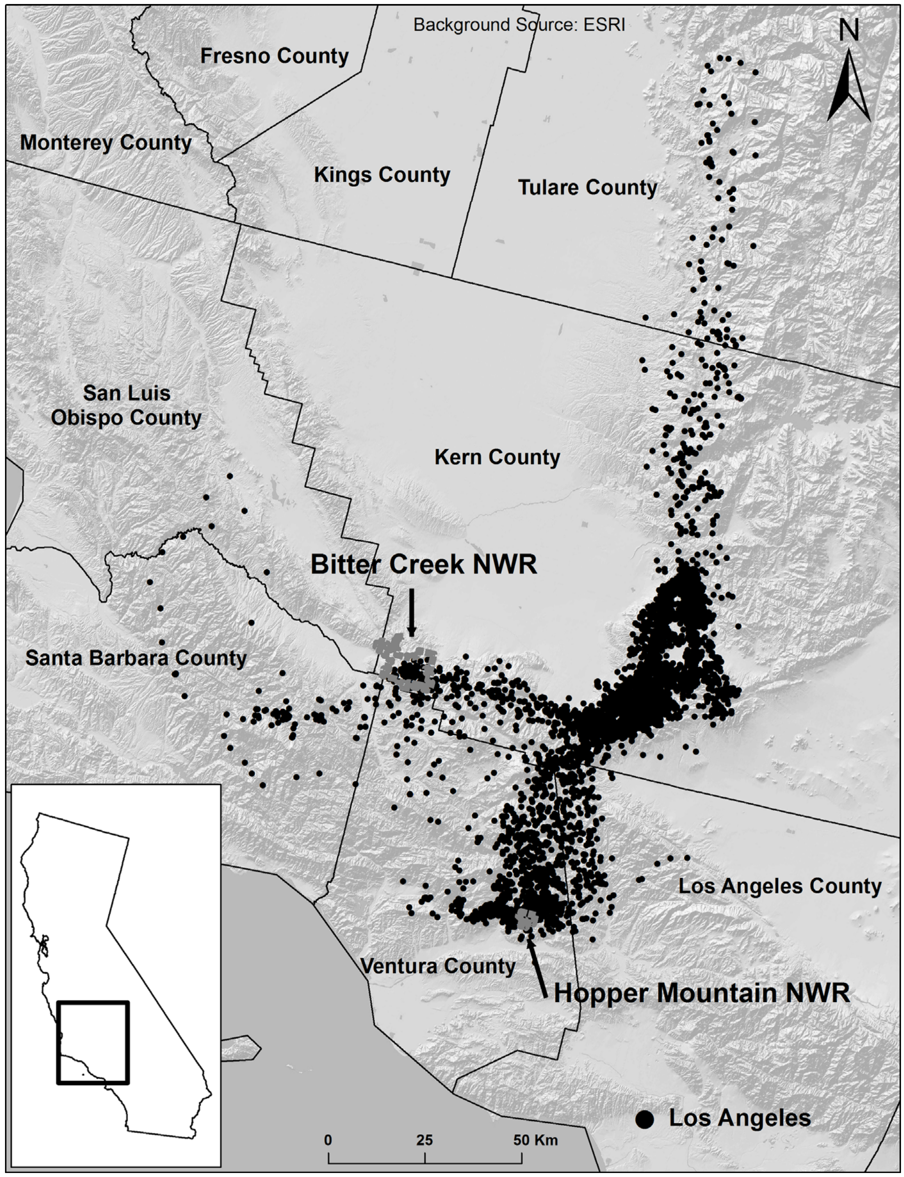

Figure 1. Global positioning system locations during the 1-week period from day 15–21 before blood collection of 31 California condors tracked in southern California, USA, December 2013–August 2016, and locations of Bitter Creek and Hopper Mountain National Wildlife Refuges (NWR).

Telemetry Data Collection and Processing

We tracked condors with solar-powered GPS-Global System for Mobile Communications (GPS-GSM) patagial telemetry units (Cellular Tracking Technologies [CTT], Rio Grande, NJ, USA or Microwave Telemetry [MTI], Columbia, MD, USA). The CTT telemetry units collected GPS data at 30-second or 15–30-minute intervals, whereas the MTI units collected data at intervals between 1 minutes and 2 hours. The GPS data included location, date, time, altitude, ground speed (knots), horizontal and vertical dilution of precision (HDOP and VDOP), and fix quality (2D or 3D). The CTT telemetry units collected altitude data as meters ASL, whereas the MTI units collected altitude data as meters above the ellipsoid.

We interpreted behavior in telemetry data collected from condors during December 2013 to August 2016. For analysis purposes, we sub-sampled higher-frequency GPS telemetry data from the CTT and MTI units to 15-minute intervals, and we removed GPS data collected at night (time between sunset and sunrise). For the MTI units, we converted altitude above ellipsoid to altitude ASL by associating each GPS location with a value representing a geoid undulation in a 2.5-minute grid (Pavlis et al. 2012). We then subtracted this value from altitude above ellipsoid to obtain altitude ASL.

We filtered the remaining telemetry data to remove GPS locations for which diagnostic or altitudinal data indicated errors. For example, we removed 2D fixes and locations with HDOP or VDOP $\geq$10 (D'Eon and Delparte 2005), and we removed fixes with altitudes ASL >4,000 m that were also inconsistent with neighboring data points. For example, if altitudes at points in a series were 1,500 m, 6,000 m, and 1,500 m, we interpreted the location with the larger altitude as indicative of a GPS error.

We used ArcGIS v.10.3 (Environmental Systems Research Institute, Redlands, CA, USA) to obtain the ground elevation ASL at each GPS location from an approximately 30-m resolution digital elevation model (USGS 2015). We then subtracted the ground elevation value from the altitude ASL of each location to calculate flight altitude above ground level (AGL). Finally, we removed fixes with altitudes AGL ≤ -50 m (Katzner et al. 2012).

Flight Behavioral Data

Because we had little prior knowledge of how lead exposure affects movements of condors (other than acutely poisoned birds greatly reduce their activity and thus would not be likely to fly to the trapping pen), we evaluated 3 different metrics of condor flight behavior that we expected could be indicative of lead exposure. These were hourly distances traveled by condors, movement speeds between points, and the proportion of GPS locations that indicated birds were in flight. We chose these 3 parameters because illness in birds causes reduced or erratic movements (USGS 1999) and because these 3 metrics measure movements and flight behaviors of condors. As a first step to calculate the first 2 of these metrics, we used the movement.pathmetrics tool in Geospatial Modelling Environment (Beyer 2015) to measure distances between each consecutive GPS location.

To calculate hourly distances traveled, we then summed the distance traveled between the points nearest to the start and end of each nominal hour (e.g., 0800–0900), limiting a defined hour to 45–80 minutes, and then standardized those distances to a 60-minute hour (Rus et al. 2017). Because the hourly distances had a varying number of locations within each hour (e.g., 15-min data had 5 locations/hr and 30-min data had 3 locations/hr), we determined that calculating speed between points would be important, as this is a more standardized distance metric. To do this, we calculated the linear distance between 2 consecutive points and divided that number by the time difference between those 2 points (Katzner et al. 2015). We assigned each of these measurements to the hour of the day in which the first GPS telemetry point occurred.

To compute the proportion of GPS locations in flight, we defined flight locations using published information on golden eagles (*Aquila chrysaetos*; Katzner et al. 2015) that we modified to account for condor behavior. We defined flight locations as those with either a recorded speed $\geq$3.5 knots or a recorded speed <3.5 knots that also had an altitude AGL $\geq$100 m. We then calculated the proportion of locations within a specified time period (defined below) that were in flight. Because of a known issue with estimation of flight speeds in the 30-second data from the CTT units (speeds were underestimated), we did not include in this analysis the sub-sampled 30-second data.

Lead Exposure Events and Movement Periods

We studied lead exposure events for the subset of condors for which we had blood-lead concentration values and telemetry data. We defined an event as the combination of the blood-lead measurement and the telemetry data collected prior to the blood draw. In these analyses, we used blood-lead concentration values from laboratory tests rather than those from field test kits. Because we did not know how long before capture that condors may have been exposed to lead, for each event we tested the degree to which blood-lead concentrations predicted movement over 6 periods of different durations and at different times before blood collection. The length and timing of these periods were 4 fixed time intervals of 2, 7, 14, and 30 days before blood collection and 2 1-week intervals, from day 15–21 and from day 31–37 prior to blood collection. We used these specific lengths and timings based on the half-life of lead in condor blood samples (14 days; Fry et al. 2009) and on deviations from that half-life that we deemed might reasonably capture the uncertainty caused by our lack of knowledge of the time of lead exposure.

Birds were in captivity from 0 to 11 days before blood collection occurred. If a bird was in captivity for $\geq$1 day before blood collection, then we counted those captive days as part of the period, but we did not consider movement data for those days. For example, if a bird was in captivity for 1 day before blood was collected, then the 2-day period only included data from the single day that the bird was free-ranging. Likewise, the 7-day period only included 6 days of data, the 14-day period only included 13 days of data, and the 30-day period only included 29 days of data. The 1-week periods from day 15–21 and day 31–37 would be unaffected. We also only included telemetry data on the day of capture if the unit collected $\geq$5 locations on that same day, in the time before the bird was captured. However, if a bird was captured and blood was collected on the same day, then we did not include telemetry data from the day of capture (i.e., periods always began the day before blood collection).

Statistical Analyses

We ran 3 sets of linear mixed-effects models using the lme4 package (Bates et al. 2015) in R (R Core Team 2016) to test for a behavioral response that was predicted by blood-lead concentrations. The response variables in each of the 3 model sets were hourly distances (averaged over each period), speeds between points (reported as distance/min), and proportion of locations in flight (within each period). We used a square root transformation of the hourly distance moved response variable and a log transformation of the speeds between points response variable to meet the distributional assumptions of our statistical tests (Zuur et al. 2007). The proportion of locations in flight response variable met distributional assumptions so no transformation was necessary.

For the model sets with hourly distances and proportion of locations in flight as the response variables, our predictors included as fixed effects the blood-lead measurement (μg/dL), age (in years), and a categorical variable for describing the period, as defined above. We included month and event number nested within individual bird as random effects in these models. All birds were of known age because they were either raised in captivity and released into the wild or they were wild-hatched at monitored nests.

For each of these 2 model sets, we first ran a global model as described above with all fixed effects, and we calculated 95% Wald confidence intervals for each coefficient. We then used

the dredge function in the MuMIn package in R (Barton 2016) to run all possible sub-model combinations (Doherty et al. 2012). We used Akaike's Information Criterion corrected for small sample size (AIC_c) to rank the models and identify the models with the most support in the data (sum of model weights [Σw_i] >0.9; Burnham and Anderson 2002, Anderson 2008).

Because the results of these 2 model sets did not show an effect of lead on flight behavior (see Results), we grouped the data by period and ran 12 additional models, 2 for each period. For these additional models, we did not include a fixed effect for period, and within each period, we tested for effects of lead exposure and age on our 2 response variables, hourly distances moved and proportion of locations in flight. For these models, we included month and individual bird as random effects, and we calculated confidence intervals and performed model selection as described above. For each period, we also used a likelihood ratio test (using the lmtest package in R; Zeileis and Hothorn 2002) to determine if 2 nested models within a model set differed from each other.

For the input dataset analyzed by models with speeds between points as the response variable, instead of calculating averages by period, our response variable was measured for every time interval between consecutive GPS points. Because each measurement can therefore be assigned to multiple periods, the different periods cannot be included in a single linear model. For this reason, we grouped the data by period and ran 6 separate full models, one for each period, and in each we included the blood-lead measurement and age as fixed effects. In this case, we included random effects for month, hour, and event number nested within individual bird. We calculated confidence intervals and used model selection and likelihood ratio tests as described above.

RESULTS

Our analyses included data from 67 events from 31 condors (16 F and 15 M, ranging in age from 1 to 36 yr at time of blood collection). We considered 79,835 GPS locations ($\bar{x} \pm SD = 1{,}192 \pm 430$ locations/event). Our models considered data from 23 to 67 events/period and from 1,288 to 61,586 measurements of speeds between points/period (Table 1). Blood-lead concentration values ranged from 0 (below the limit of detection) to 180 μg/dL.

We calculated distances moved by condors over 21,567 hours in the 67 events (321 ± 103 hr/event). Average hourly distances moved per event ranged from 5.7 km to 7.4 km over the 6 periods (Table 1). Our global model suggested little to no predictive value for any of the fixed effects we used to predict distances traveled by condors (Table 2), and the confidence intervals for coefficients all overlapped zero. Model selection suggested that only 2 models had support in the data (54% and 41% model weights). Both of these included the period identifier and the top model also included age (Table 3). Again, neither of these models suggested any predictive value for the fixed effects (i.e., the confidence intervals for the coefficients overlapped zero). Models with the blood-lead measurement did not have support in the data.

For the 6 models we ran that evaluated data by period, either the null model or the age only model was the top model, and these 2 models had 90–95% of all model weights. The age model was different from the null model (based on a likelihood ratio test) only in the day 15–21 period when it was the top model, and the age coefficient did not overlap zero. During this period, older birds traveled longer distances. The blood-lead measurement did not predict hourly distances in any of the 6 periods.

Speeds between points ranged from 0 m/minute to 1,481 m/minute over the 6 periods (Table 1). For each of the 6 models we ran, the global model suggested no predictive value for any of the fixed effects we used to describe speeds between points (Table 4), and the confidence intervals for each coefficient overlapped zero. In each of the 6 model sets, the null model had ≥95% of all model weights (Table 3), and the likelihood ratio test indicated that the null model was different from the second model. The blood-lead measurement did not predict speeds between points in any of the 6 periods.

Of the 79,835 GPS locations, 26,943 (34%) met our definition of flight locations (402 ± 169 locations/event). The average proportion of locations in flight in any period ranged from 0.34 to 0.40, although, for any one event within a period, from 1% to 95% of recorded locations indicated that the bird was in flight (Table 1). The global model suggested no predictive value for any of the fixed effects we used to predict the proportion of locations in flight (Table 2), the

Table 1. Behavioral metrics evaluated to test for movement response during 67 lead exposure events for 31 California condors tracked in southern California, USA, December 2013–August 2016. Data for each period include sample sizes (*n*), means ± standard deviations, and ranges for the 3 response variables used in models to investigate flight behavior: hourly distances, speeds between points, and the proportion of locations in flight.

	Hourly distances (km)					Speeds between points (m/min)					Proportion of locations in flight				
Period	*n* condors	*n* events	$\bar{x}$	SD	Range	*n* condors	*n* measurements	$\bar{x}$	SD	Range	*n* condors	*n* events	$\bar{x}$	SD	Range
2-day	17	24	5.7	4.9	0.3–17.3	17	1,288	102.7	200.8	0–1,481	17	23	0.38	0.19	0.06–0.76
7-day	29	60	7.4	4.9	0.5–31.3	29	8,961	115.1	203.7	0–1,481	29	59	0.40	0.17	0.03–0.80
14-day	31	67	6.4	3.2	0.2–16.8	31	25,185	109.9	199.2	0–1,481	31	66	0.36	0.14	0.01–0.88
30-day	31	66	6.5	2.9	0.3–18.1	31	61,586	108.8	200.8	0–1,481	31	65	0.36	0.12	0.02–0.87
Day 15–21	30	65	6.1	2.8	0.4–13.5	31	16,211	104.9	199.2	0–1,342	31	65	0.34	0.12	0.02–0.68
Day 31–37	31	65	6.6	2.9	1.3–12.7	31	15,922	112.1	207.5	0–1,380	31	65	0.36	0.14	0.09–0.95

Table 2. Beta coefficients and standard errors from the global linear mixed-effects models describing factors influencing average hourly distances traveled and the proportion of locations in flight by 31 California condors tracked in southern California, USA, December 2013–August 2016, during 67 lead exposure events. The reference variable for period is the 14-day period.

	Hourly distances		Proportion of locations in flight	
Parameter	**Beta**	**SE**	**Beta**	**SE**
Intercept	70.90	5.30	0.34	0.04
Lead	0.01	0.06	0.00	0.00
Age	0.58	0.32	0.00	0.00
2-day period	−6.99	3.61	0.00	0.02
7-day period	3.62	2.57	0.03	0.02
30-day period	1.37	2.56	−0.01	0.02
Day 15–21 period	−0.50	2.59	−0.03	0.02
Day 31–37 period	1.98	2.80	0.00	0.02

confidence intervals almost always overlapped zero, and the null model contained 100% of weights in the model set (Table 3). For each of the 6 models we ran that included data only for each of the 6 periods, the confidence intervals for each coefficient overlapped zero, the null model had 100% of all model weights in each model set, and the likelihood ratio test indicated that the null model was different from the second model. The blood-lead measurement did not predict the proportion of locations in flight in any of the 6 periods.

DISCUSSION

The behavioral and physiological consequences to birds of lead exposure are poorly known, and wildlife managers would benefit from the development of behavioral tests for illness in wild animals. These tests would be beneficial whether lead exposure is clinical, thus resulting in treatment, or subclinical. We attempted to use high-resolution telemetry data to design a behavioral test to aid in the diagnosis of lead exposure of condors. However, the metrics we measured did not vary in ways that allowed us to detect a behavioral response by condors to lead exposure. We discuss below 3 possible categories of explanations for our results based on the biology of birds, especially obligate-soaring birds, the sample of condors we used in this study, and the specific parameters we measured to infer lead exposure.

Table 3. Top model in Akaike's Information Criterion corrected for small sample size (AIC_c) model selection in each of 8 model sets describing factors influencing flight behavior of 31 California condors tracked in southern California, USA, December 2013–August 2016, during 67 lead exposure events. Model results include 1 model set for hourly distances, 1 model set for the proportion of locations in flight, and 6 model sets for speeds between points. Model refers to the response variable for the model, effects refers to the fixed effects in each top model, K refers to the number of parameters (including intercepts) in a model plus 1 for the residual error term, and w_i is the weight of evidence in favor of each model.

Model	Effects	K	w_i
Hourly distances	Age + period	11	0.54
Proportion of locations in flight	Intercept only	5	1.00
Speeds between points			
2-day	Intercept only	6	0.95
7-day	Intercept only	6	0.97
14-day	Intercept only	6	0.98
30-day	Intercept only	6	0.95
Day 15–21	Intercept only	6	0.98
Day 31–37	Intercept only	6	0.98

Bird Biology

Animals that are sick may be subject to an increased risk of predation or a loss in social status (Hart 1988). A variety of social contexts can modulate the expression of behaviors indicative of sickness (e.g., birds may behave as if they are not sick to defend their territories, to gain access to mates, or to maintain their social ranking [Lopes 2014]). Because strong selection is present to suppress external signs of illness, mildly or moderately sick birds may not show changes in movement patterns that could be detected in telemetry data. Thus, with the exception of extremely sick birds, identifying illness in condors by analyzing their behaviors may be difficult.

Because condors are an obligate-soaring species, perhaps flight is so critical to them that sick condors do not substantially alter their flight patterns until they are near death. Evidence from other work indicates that sick birds may travel over long distances (Dusek et al. 2014, van Dijk et al. 2015). Rather than flight performance declining at a gradient with increasing blood-lead concentrations, response to lead exposure instead may follow a threshold-type response such that, when some critical blood-lead concentration is reached, the bird ceases all routine flight activity. Anecdotal observations from USFWS-led condor monitoring suggest that this does occur; biologists previously have found very sick birds based on observing that they did not fly or leave a given area for an extended period of time. If such a threshold-based response influences movement of these birds, then we would be unlikely to detect a response with our tests (unless the bird was acutely poisoned).

Sample of Condors

The sample of birds we used in this study may not have been fully representative of the full range of lead exposure that condors experience. Our sample was limited to birds that were able to fly into the trapping pens and that were equipped with working telemetry units. Further, the highest blood-lead concentration we recorded in our sample birds was 180 μg/dL; lead concentrations in living condors have been recorded as high as 800 μg/dL (authors' personal observations). We are uncertain at which blood-lead concentration value condors begin to show clinical symptoms from lead exposure. If our sample had included birds with higher blood-lead concentration values, those birds may have been affected clinically and we may have detected a movement response to lead exposure. Finally, although condors are sensitive to diseases such as lead poisoning, they may be less so than are golden eagles, a non-obligate soaring species that have shown a negative flight response to increasing blood-lead concentrations (Ecke et al. 2017).

Parameters Measured to Infer Lead Exposure

The behavioral and biological parameters we measured may not have been appropriate to test for a response to lead exposure. Other metrics besides the flight behaviors we measured may be more valuable to study and should be

Table 4. Beta coefficients and standard errors from the 6 global linear mixed-effects models (1 model per period) describing factors influencing speeds between points by 31 California condors tracked in southern California, USA, December 2013–August 2016, during 67 lead exposure events.

	2-day		7-day		14-day		30-day		Day 15–21		Day 31–37	
Parameter	**Beta**	**SE**	**Beta**	**SE**	**Beta**	**SE**	**Beta**	**SE**	**Beta**	**SE**	**Beta**	**SE**
Intercept	2.56	0.55	1.90	0.42	1.94	0.35	1.80	0.33	1.83	0.38	1.98	0.34
Lead	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Age	−0.03	0.04	0.02	0.01	0.01	0.01	0.02	0.01	0.01	0.01	0.01	0.01

considered in future efforts when comparing healthy and lead-exposed birds. Possible metrics to consider may include the altitude at which birds fly, the timing of arrival to and departure from roost sites, the duration of time on the ground, or the timing of arrival at a carcass. A condor with severe lead exposure may be more aggressive than typical (as may be the case for lead-exposed humans; Needleman et al. 1996, Nevin 2007, Mielke and Zahran 2012) and thus the first to feed on a carcass, or it may behave subordinately to others, regardless of its social status, and thus the last one to feed on a carcass.

Our measurement technique (i.e., data collected at 15–30-min intervals) may have been too coarse to detect a response to lead exposure. Although some of the telemetry data we collected were at 30-second intervals, the number of birds from which we collected those data was so small that we were compelled to analyze all of our data at less frequent intervals. Because birds are so effective at concealing illness, possibly only more intensive data collection (e.g., shorter intervals between fixes or use of accelerometry data) would allow the detection of behavioral changes in the parameters we considered. However, such finer-scale data may not be necessary because others have found a response with coarser data. For example, in the golden eagle study (Ecke et al. 2017), the negative response to lead exposure was measured with telemetry data collected at 15-minute intervals.

We also did not know the date or severity of each bird's exposure to lead. The lead concentration values we used in our study were only a snapshot in time and likely did not indicate the severity of lead exposure. Blood-lead concentrations are dynamic and influenced by the nature of the exposure. Therefore, they may be of clinical concern shortly after a severe exposure to lead, in a situation where lead concentrations in the bird are increasing. Alternatively, blood-lead concentrations can be of clinical concern some time after an exposure of intermediate severity to lead, in a situation where lead concentrations in the bird are peaking. Finally, blood-lead concentrations can be of clinical concern a longer time after a severe exposure to lead, in a situation where lead concentrations in the bird are decreasing. Thus, because elevated blood-lead concentrations are so dynamic and can be indicative of so many different internal states and exposure routes, our analyses may have been confounded so thoroughly that the broad-scale data and statistical tools we used were unable to detect effects of lead exposure on movement.

The effects of lead exposure are individual-dependent and likely influenced by the bird's history of such exposure (Finkelstein et al. 2010). In particular, birds with a history of lead exposure or acute lead poisoning may show a stronger response to a non-severe lead exposure event than would a bird with less historical exposure to lead. Although we attempted to account for this by including age as one of the fixed effects in our models, age is indicative of potential, not actual, exposure to lead. Future studies should therefore also consider known past exposure events when evaluating current behavioral responses to illness.

Finally, sampling tissues other than blood or multiple tissues may be indicative of diverse exposure events and histories. Different tissues within a single bird may have widely varying lead concentrations, indicating that lead is unequally distributed throughout the bodies of organisms (Behmke et al. 2017). This may be due largely to variations in uptake and half-life of lead in tissues. Thus, measuring lead exposure by sampling any one tissue may not be sufficient to determine the degree of lead exposure and intoxication. That said, sampling feathers may provide more precise linkages to lead exposure, allowing tracking of the trajectory of lead concentrations (whether they are increasing, peaking, or decreasing) over the feather growth period (at $\sim$5-day resolution; Finkelstein et al. 2010). That finer-grained resolution may therefore be more closely associated with movement patterns than are blood-lead concentrations.

MANAGEMENT IMPLICATIONS

Our work represents one of the first attempts to identify lead exposure in condors through behavioral analyses. Lead poisoning is critical to many wildlife species, and consequently, developing a behavioral test is an important goal for wildlife management. As such, reporting the inability to detect a response in movement behavior to lead exposure is useful because it reduces the pool of potential metrics that may be considered in future evaluations of behavioral tests. Future study of this issue should consider using a more representative sample of condors, testing other tissues for lead concentrations (rather than, or in addition to, blood), or focusing on behaviors less fundamental to condor survival than flight.

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