



Urbanization's influence on the distribution of mange in a carnivore revealed with multistate occupancy models

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Abstract

Increasing urbanization and use of urban areas by synanthropic wildlife has increased human and domestic animal exposure to zoonotic diseases and exacerbated epizootics within wildlife populations. Consequently, there is a need to improve wildlife disease surveillance programs to rapidly detect outbreaks and refine inferences regarding spatiotemporal disease dynamics. Multistate occupancy models can address potential shortcomings in surveillance programs by accounting for imperfect detection and the misclassification of disease states. We used these models to explore the relationship between urbanization, slope, and the spatial distribution of sarcoptic mange in coyotes (*Canis latrans*) inhabiting Fort Irwin, California, USA. We deployed remote cameras across 180 sites within the desert surrounding the populated garrison and classified sites by mange presence or absence depending on whether a symptomatic or asymptomatic coyote was photographed. Coyotes selected flatter sites closer to the urban area with a high probability of use (0.845, 95% credible interval (CRI): 0.728, 0.944); site use decreased as the distance to urban areas increased (standardized $\hat{\beta} = -1.354$, 95% CRI $-2.423, -0.619$). The probability of correctly classifying mange presence at a site also decreased further from the urban area and was probably related to the severity of mange infection. Severely infected coyotes, which were more readily identified as symptomatic, resided closer to the urban area and were most likely dependent on urban resources for survival; urban resources probably contributed to sustaining the disease. Multistate occupancy models represent a flexible framework for estimating the occurrence and spatial extent of observable infectious diseases, which can improve wildlife disease surveillance programs.

Keywords *Canis latrans* · Coyote · Disease ecology · *Sarcoptes scabiei* · State misclassification

Introduction

Global urbanization and human encroachment into wildlife habitats have increased the potential transmission of zoonotic diseases (Daszak et al. 2000; Bradley and Altizer 2007) contributing to spillovers from wildlife populations to humans and our commensals (Patz et al. 2004; Allen et al.

2017). Anthropogenic transformation of the natural environment can also lead to insidious disruptions in the host–pathogen dynamic as revised selection regimes favor atypical fitness responses in the host, the pathogen or both (Patz et al. 2004). Urban habituation by *Pteropus* bats in Australia, which began roosting and feeding in urban environs after natural habitats were converted, increased the exposure of horses and humans to the deadly Hendra virus (Plowright et al. 2011). Access to food subsidies has caused wildlife to aggregate around clumped resources resulting in unusually dense wildlife populations promoting the horizontal transfer of pathogens. In North America, raccoons (*Procyon lotor*) had increased burdens of a lethal nematode, *Baylisascaris procyonis*, after they aggregated at experimentally provided food sources which mimicked garbage heaps (Wright and Gompper 2005). The European badger (*Meles meles*) has adapted to forage for earthworms in agricultural pastures where it has heightened the transmission of bovine tuberculosis to cattle (da Silva et al. 1993; Woodroffe et al. 2009).

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Landscape conversion may cause a decline in both natural shelters and prey or as the pathogen amplifies host morbidity, natural prey may become more difficult to capture. Moribund animals may no longer be able to survive in their natural habitat forcing a dependency on urban resources (Murray et al. 2015), influencing the spatial occurrence of a disease with infected hosts being more prevalent nearer to human-transformed environs.

Estimating the incidence and spatial distribution of a zoonotic pathogen are important for mitigating disease outbreaks. Yet, wildlife disease surveillance programs are often reactive instead of proactive and often do not account for imperfect detection and state misclassification, potentially underestimating the full extent of an infection due to false negatives (Adams et al. 2010). In many cases, the etiology of the disease and the diagnostic test needed to detect the pathogen (e.g., antibody or DNA/RNA based tests) may prolong the time between a disease outbreak and its detection, but some diseases exhibit symptoms that are identifiable to an observer with some degree of certainty. Skin diseases featuring lesions and/or hair loss, such as mange, which is found in numerous mammalian species (Bornstein et al. 2001), contagious ecthyma in musk ox (*Ovibos moschatus*; Vikøren et al. 2008) and bighorn sheep (*Ovis canadensis*; Wilson and McFarlane 2012), winter tick in moose (*Alces alces*; Jones et al. 2019), giraffe skin disease (Muneza et al. 2019), and infectious cancers such as Tasmanian devil (*Sarcophilus harrisii*) facial tumor disease (Preece et al. 2017) may be apparent during observations or from photographic surveys. Other diseases, such as white-nosed syndrome in bats are observable during certain seasons but are cryptic during other periods (Blehert et al. 2009; Huebschman et al. 2019). Changes in behavior or posture due to debilitating infections like chronic wasting disease in cervids (Williams and Young 1980) or rabies in mammals (Davis et al. 2019) could also be documented, although most likely with a greater degree of uncertainty. These observable symptoms could be identified in the field with remote cameras allowing for rapid detection of the disease and collection of large data sets.

It has been suggested that the injection of ecological methods into disease surveillance programs and associated modeling of zoonotic diseases may enhance our ability to rapidly respond to and mitigate disease outbreaks (McClintock et al. 2010; Preece et al. 2017). Occupancy models use repeated surveys to account for imperfect detection and incorporate covariates to explain detection and site occupancy (MacKenzie 2006). Recent developments also incorporate hierarchical levels of uncertainty, such as the use of diagnostic tests that differ in specificity and sensitivity (McClintock et al. 2010). Multistate occupancy models are an extension that provides a flexible framework to handle more than two conditions or host states and to estimate the probability of state misclassification (Nichols et al. 2007;

MacKenzie et al. 2009). Here we used multistate occupancy models to understand the effect urbanization can have on the occurrence and spatial distribution of an infectious disease. Using remote cameras at the National Training Center (NTC), Fort Irwin, California, USA, we collected images of desert-dwelling coyotes (*Canis latrans*) infected with sarcoptic mange, a contagious skin disease found amongst mammals and caused by the mite *Sarcoptes scabiei*.

Materials and methods

Host–pathogen complex

Sarcoptic mange is commonly associated with canids in both North America and Europe, including coyotes (Pence et al. 1983), red foxes (*V. vulpes*; Newman et al. 2002), kit foxes (*V. macrotis*; Cypher et al. 2017), and wolves (*C. lupus*; Almberg et al. 2012). The coyote population at the NTC represents an ideal study system for evaluating the influence of urban resources on disease dynamics because coyotes are prevalent in both urban and exurban regions; access to centralized resources (e.g., garbage or compost) can cause coyotes to aggregate, increasing the potential for contact between infected and susceptible individuals (Murray et al. 2016; Reddell 2018); and mange is identifiable from images of infected hosts. Urban resources can also reduce immune defense if they are nutrient poor or contain toxicants, such as anticoagulant rodenticides (Murray et al. 2016). Immuno-compromised hosts can acquire secondary infections by other parasites, such as *Echinococcus multilocularis*, which may further increase morbidity and/or mortality (Catalano et al. 2012). Individuals infected with mange also typically have suppressed immune systems, reduced reproductive rates, and decreased fat stores, which may compromise thermoregulation (Pence et al. 1983; Pence and Windberg 1994). Alternatively, easy access to urban resources may allow debilitated hosts to survive longer and enhance the spread of the disease (Råberg et al. 2009; Becker et al. 2015).

Sarcoptes scabiei burrows into the epidermis and consumes live cells and tissue fluid (Pence and Ueckermann 2002). Transmission of the disease generally occurs through direct contact with an infected host, as mite larvae and nymphs leave their epidermal burrows to inhabit exposed skin, indirect transmission is also possible as mites can survive off the host for a limited period of time (Bornstein et al. 2001). Visual symptoms of the disease include lesions, hyperkeratosis, and alopecia (Bornstein et al. 2001). Infected hosts are classified based on symptoms of worsening disease state: Class I—active lesions apparent on <5% of their body, primarily on the lower legs, ischium, and base of ears; Class II—lesions covering between 5 and 50% of an individual's

body; and Class III—lesions covering > 50% of the body (Pence et al. 1983).

Study area

The NTC is a military training facility encompassing 3055 km² and located in the Mojave Desert in southern California (Fig. 1). The garrison is 16.1 km² with an average population size of 8845 people (U.S. Census Bureau 2010). The average elevation of the garrison is 748 m and the surrounding land-cover is dominated by creosote (*Larrea tridentata*) and white bursage (*Ambrosia dumosa*). Military training exercises occur in the northern and eastern sections of the installation and have created disturbed landscapes with extensive road networks and areas practically devoid of vegetation. The western and southwestern sections of the installation are occupied by the NASA Goldstone Deep Space Communications Complex and a recovery area for the threatened desert tortoise (*Gopherus agassizii*), both of which are far less disturbed than the rest of the installation. Summers are hot and dry (mean daily highs 39–41 °C) and winters are cool (mean daily high of ~ 18 °C) (WRCC 2016).

Annual average precipitation is 9.72 cm, with 80% of the rainfall occurring between November and March and 20% during summer convection storms from July to September.

We partitioned the study area into three zones: garrison, exurban, and wildland-interface based on perceived resource use and interaction rates among coyotes (Fig. 1). Based on the radius of the largest home range for resident coyotes (assuming a circular home range) occupying an exurban environment (Grinder and Krausman 2001), we applied a 4.36-km buffer around the garrison to define the exurban zone, or the area surrounding the garrison where use of anthropogenic resources by coyotes was expected. We delineated the wildland-interface zone with a final 4.36-km buffer extending from the exurban zone; we expected coyotes in this zone to have reduced use of garrison resources and increased interactions with non-garrison using coyotes. Areas beyond this range were considered wildland and we expected coyotes within this area to have limited to no access to urban resources and a low probability of encountering an urban coyote.

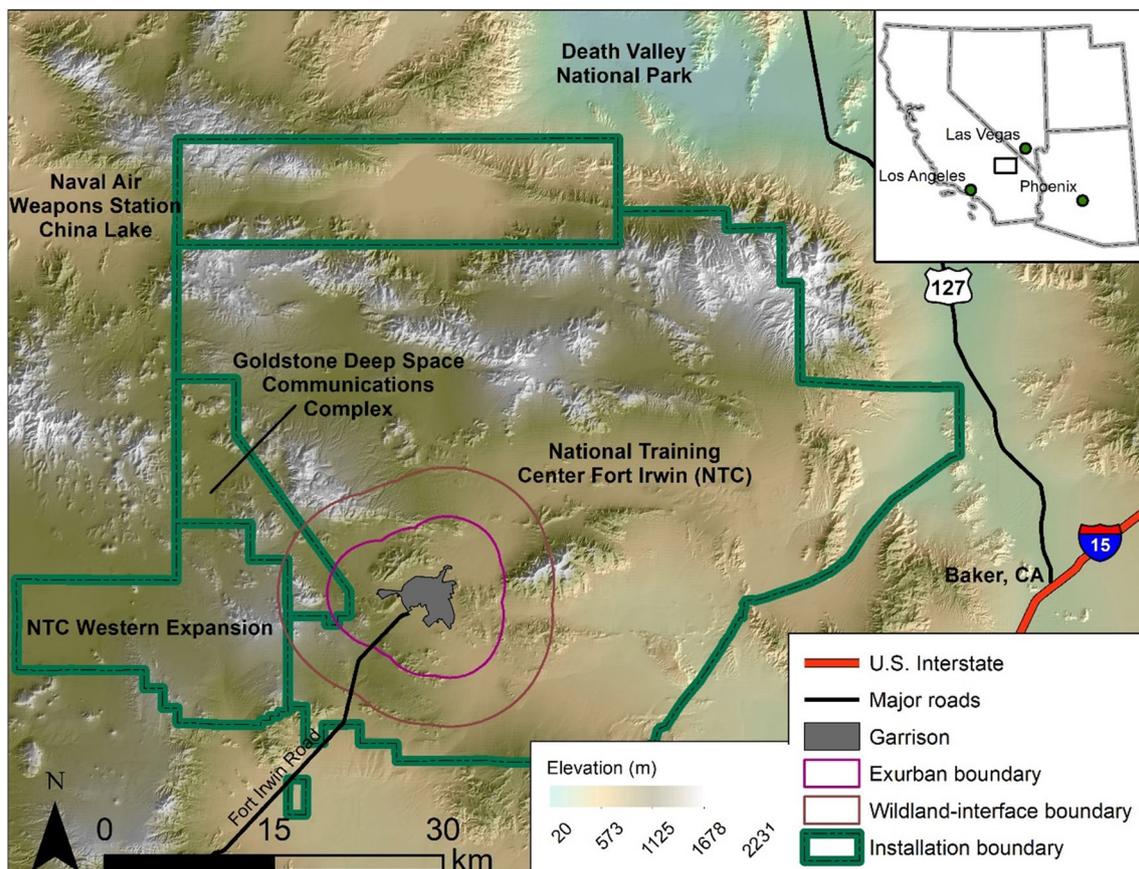


Fig. 1 The National Training Center, Fort Irwin, California, USA shown with exurban and wildland-interface zones. Elevation is shown as colored relief

Remote camera surveys

We randomly allocated cameras ($n = 60$) among the exurban and wildland-interface zones proportional to the size of each region, 36.7%, and 63.3% respectively, and secondarily distributed 48 cameras evenly between creosote flatlands (50.6%) and creosote hills (46.1%). We allocated the final 12 cameras to dry washes (3.3%), to ensure we had an adequate number of sample sites in this land-cover feature, which is often used by coyotes as a travel corridor in urban environs (Grinder and Krausman 2001; Reddell 2018). The density of cameras was similar in each zone. We did not set cameras within the garrison or live-fire/artillery ranges northeast of the garrison due to concerns regarding theft and personal safety, respectively (Fig. 1). With 60 cameras, we were only able to separate sites by at least 1.45 km or 33% of the mean home-range radius of an urban using coyote for each sampling session (Grinder and Krausman 2001). We set a single Reconyx PC800 Hyperfire Camera (Holmen, Wisconsin, USA) at each site mounted on a 1-m stake with a can of cat food staked 5 m in front of the camera (replenished every 10 days). Given that we were interested in assessing resource use and did not require coyotes to be continually present at a site for the duration of our study, our findings should be interpreted as use (MacKenzie 2006).

We were required to sample during periods of military leave to prevent potential disruption of military exercises. We conducted three sampling sessions: in December 2015, in June 2016, and in December 2016 for a total of 180 different sites surveyed. Each sampling session consisted of six,

5-day survey periods with each session considered closed to changes in occupancy. Encounter histories were developed for each site with a single detection denoting “use” of that site for the survey period (MacKenzie 2006).

Multistate occupancy models

We used single-season, multistate, occupancy models to determine the proportion of camera sites with evidence of mange. Here, we used a state-space representation to describe our model (Fig. 2). We first defined Z_i as a latent variable with three possible site states: unoccupied (0), occupied with uncertainty about mange presence (1), and occupied with mange (2). We modeled Z_i using a categorical distribution with probabilities given by

$$P(Z_i = k) = \begin{cases} 1 - \Psi, & \text{if } k = 0 \text{ (state 0)} \\ \Psi(1 - R), & \text{if } k = 1 \\ \Psi R, & \text{if } k = 2 \end{cases},$$

where ψ is the probability of occupancy, and R is the conditional probability that mange is present at a site given it is occupied. As the three true states are mutually exclusive, the above probabilities sum to one.

For the observation process, we defined Y_{it} as the observed state of site i at occasion t . Y_{it} takes a value of 0 if a coyote is undetected, 1 if a coyote is detected but mange is not observed, or 2 if an infected coyote is observed. We determined mange status based on observable hair loss,

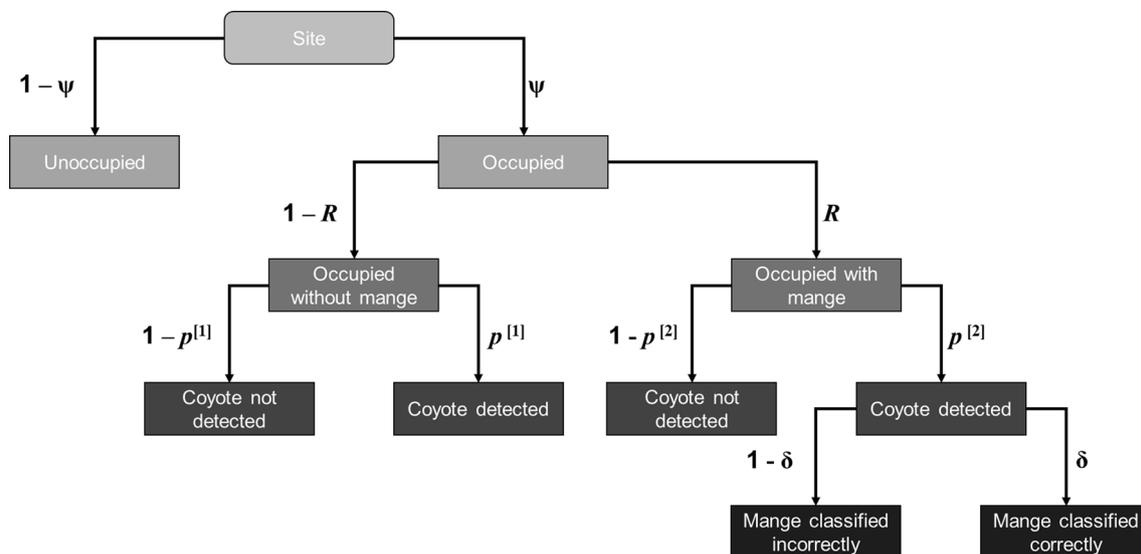


Fig. 2 Diagram of true site states and observable outcomes for multistate models where ψ is the probability of occupancy (use); R is the probability that mange is present at a site, given occupancy; $p^{[1]}$ is the probability of detecting a coyote given the true state of the site is 1

(mange absent); $p^{[2]}$ is the probability of detecting a coyote given the true state of the site is 2 (mange present); and δ is the probability of correctly classifying mange presence at a site given the true state of the site is 2

hyperkeratosis, and presence of lesions (Fig. 3a–c); only one of us (CDR) viewed the photos and recorded the site state to reduce observer bias. Because we could not reliably determine that individuals without apparent symptoms were not infected, we hereafter refer to individuals as asymptomatic if the presence of mange could not be discerned and symptomatic otherwise. Because asymptomatic coyotes could visit sites that were also visited by symptomatic coyotes, we classified the state of a site as the highest state observed during a survey. We defined a photographic event as a single visit by a coyote to a site, with a buffer of one hour delineating separate events by any individual, to obtain a count of how many individuals visited a site.

We also modeled Y_{it} conditional on Z_i (i.e., $Y_{it} | Z_i$) using a categorical distribution with probabilities given by the

following matrix: where $p^{[1]}$ is the detection probability of a coyote given the site is occupied without mange presence (state 1), $p^{[2]}$ is the detection probability of a coyote given the site is occupied with evidence of mange (state 2), and δ is the probability of classifying the site as infected given its true state is 2. For instance, $P(Y_{it} = 2 | Z_i = 2) = p^{[2]}\delta$. Note that the three probabilities in each row of the matrix sum to one.

True state (Z)	Observed state (Y)		
	0	1	2
0	1	0	0
1	$1-p^{[1]}$	$p^{[1]}$	0
2	$1-p^{[2]}$	$p^{[2]}(1-\delta)$	$p^{[2]}\delta$

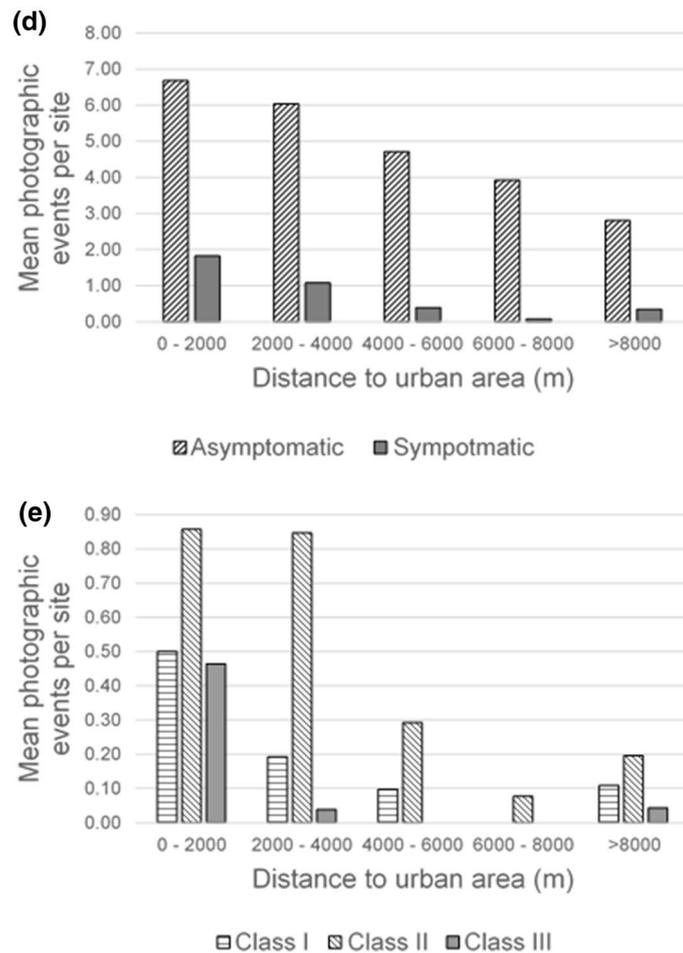
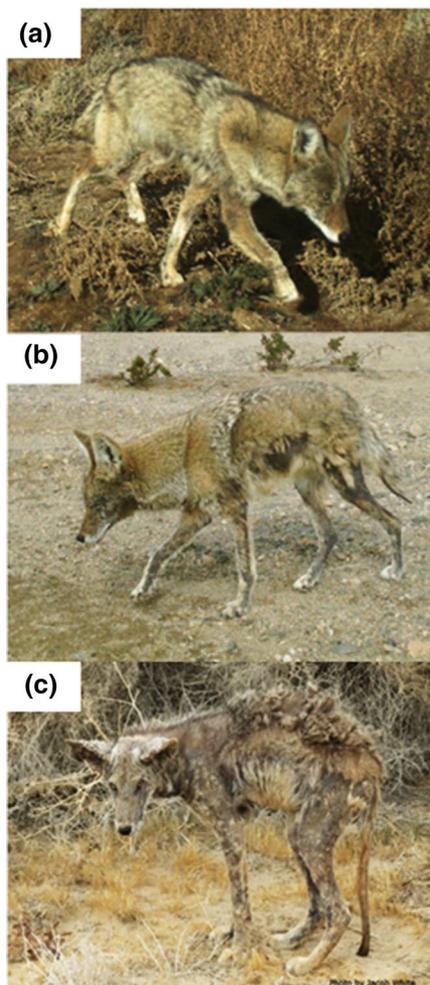


Fig. 3 Mange classes for symptomatic coyotes with **a** class I individuals exhibiting $\leq 5\%$ hair loss, **b** class II exhibiting 5–50% hair loss, and **c** class III exhibiting $> 50\%$ hair loss (photograph by Jacob

White) and average number of photographic events at a camera site based on distance (m) to the urban area for **d** asymptomatic vs. symptomatic coyotes and **e** mange classes among symptomatic coyotes

Modeling detection, classification, and occupancy probabilities

We used the generalized linear modeling framework with a logit link function to assess the effect of covariates (distance to urban areas, slope, and a trend over time) on the parameters associated with detection/classification ($p^{[1]}$, $p^{[2]}$, δ) and occupancy (ψ , R) probabilities. We calculated the distance (m) of each site to the edge of the garrison's urban areas and used this covariate to assess the effect of urban resources on ψ , R , $p^{[2]}$, and δ . We predicted that ψ and R would increase at sites closer to urban resources. If more severely infected coyotes (Class II/III) were more common in the urban area, we predicted that δ may also increase as distance to the urban edge decreased. Furthermore, if there are more symptomatic sites closer to the garrison, and a higher use of sites closer to the garrison by coyotes, we also predicted that $p^{[2]}$ should vary inversely with distance to the urban edge.

The terrain surrounding the garrison is variable with wide valleys intersected by desert mountain ranges with steep slopes. We predicted that ψ would decrease at sites with steeper slopes because coyotes are coursing predators and are more apt to forage in flat open terrain (Bleich 1999). Finally, the effectiveness of the bait may diminish as it putrefies, or coyotes may become habituated to the bait over time (Robinson et al. 2014). To account for this, we included survey as a discrete variable for trend over time and we predicted that $p^{[1]}$, $p^{[2]}$, and δ would decrease over time. Additional covariates were considered in a previous frequentist analysis, including season, distance to wash, elevation, and prey density, but their effects on detection and occupancy probabilities caused only minor improvements in model fit, so they were omitted from subsequent analyses (Reddell 2018).

We considered a total of 23 candidate models imposing different structures on the five primary parameters (Online Resource Appendix 1) and fitted these models in a Bayesian framework. Since we used a logit-link function to model each parameter as a function of covariates, we specified truncated normal prior distributions with mean 0 and precision 0.01 [$N(0, 0.01)$ T(-5, 5)] for all regression coefficients (β). Here, we standardized all continuous covariates by subtracting the mean and dividing by one standard deviation. For each model, we ran three independent Markov chain Monte Carlo (MCMC) simulations for 200,000 iterations, discarding the first 100,000 iterations. We kept every 100th sample to compute summaries (mean, standard deviation, and 95% credible intervals) of the posterior distribution of each parameter. We assessed convergence of the MCMC using the Brooks–Gelman–Rubin \hat{R} statistic (Brooks and Gelman 1998) and found no lack of convergence (All $\hat{R} < 1.1$). All fitted models were ranked using the deviance information

criterion (DIC; Spiegelhalter et al. 2002) and the model with the smallest DIC value was considered the most supported model. We also calculated model weights to quantify the relative strength of evidence for each model. For comparative purposes, we conducted model selection using the Gibbs variable selection approach (Hooten and Hobbs 2015; Online Resource Appendix 2). All analyses were performed using the JAGS software (Plummer 2003) called from R (R Core Team 2018) using the package jagsUI (Kellner 2018).

Results

We conducted a total of 1074 camera surveys over 179 sites; one site failed to collect data due to a camera malfunction. Asymptomatic coyotes were detected on 324 camera surveys at 121 sites, while symptomatic coyotes were detected on 76 camera surveys at 37 sites, with both asymptomatic and symptomatic coyotes detected at 31 sites, for a total of 400 coyote detections across 127 sites. We recorded a total of 819 photographic events, or total counts, of asymptomatic coyotes and 119 photographic events of symptomatic coyotes. We observed 31 class I events, 72 class II events, and 16 class III events. The mean number of events per camera site was generally higher nearer to the garrison and also higher for more severely infected coyotes (Fig. 3d, e).

The top ranked model based on DIC accounted for 99.98% of the model weight (Table 1). According to this model, the probability of occupancy (ψ) was strongly influenced by distance to urban areas and slope. As predicted, ψ decreased as the distance to urban areas (standardized $\hat{\beta} = -1.354$, 95% credible interval (CRI) $-2.423, -0.619$) and slope ($\hat{\beta} = -1.701$, 95% CRI $-2.645, -1.010$) increased (Fig. 4a, b). Contrary to our prediction, the probability of mange presence at an occupied site (R) was constant and its posterior mean was 0.519 (95% CRI 0.396, 0.645). However, the probability of correctly classifying mange status (δ) decreased with distance to urban areas ($\hat{\beta} = -0.708$, 95% CRI $-1.021, -0.414$; Fig. 4c). Contrary to our predictions, detection probabilities for asymptomatic sites ($p^{[1]}$) and symptomatic sites ($p^{[2]}$) increased over time and the estimated standardized effects of trend ($\hat{\beta}$) on $p^{[1]}$ and $p^{[2]}$ were 0.396 (95% CRI 0.080, 0.738) and 0.387 (95% CRI 0.102, 0.673), respectively (Fig. 4d). The estimates for $p^{[1]}$, $p^{[2]}$, and δ were 0.256 (95% CRI 0.163, 0.364), 0.701 (95% CRI 0.643, 0.757), and 0.205 (95% CRI 0.149, 0.282), respectively, when the trend covariate was set at its mean value; $p^{[2]}$ was also consistently higher than $p^{[1]}$. Predicted ψ was high with a posterior mean of 0.845 (95% CRI: 0.728, 0.944; Fig. 5a), while keeping both distance and slope covariates constant at their mean values, and sites closer to urban areas had a higher probability of being in state 2 (i.e., occupied with evidence of mange; Fig. 5b). Finally, the probability of

Table 1 Model selection results for the top five multistate occupancy models fitted to describe coyote occupancy and disease state

Model	Deviance	DIC	Δ DIC	w
$\psi(D+S), R(\cdot), p^{(1)}(T), p^{(2)}(T), \delta(D)$	1272.99	1454.54	0	0.9998
$\psi(D+S), R(D), p^{(1)}(T), p^{(2)}(T), \delta(D)$	1273.94	1471.27	16.73	0.0002
$\psi(D+S), R(\cdot), p^{(1)}(\cdot), p^{(2)}(\cdot), \delta(D)$	1292.80	1478.35	23.81	0
$\psi(D+S), R(\cdot), p^{(1)}(\cdot), p^{(2)}(D), \delta(D)$	1297.09	1483.87	29.33	0
$\psi(D+S), R(D), p^{(1)}(\cdot), p^{(2)}(\cdot), \delta(D)$	1293.61	1495.24	40.70	0

The Deviance is the information unexplained by a model, DIC is the Deviance Information Criterion, Δ DIC is the change in DIC, and w represents model weights. The parameters include ψ , the probability of occupancy, R the conditional probability that mange is present at a site given it is occupied, $p^{(1)}$ the detection probability of a coyote given the site is occupied without mange presence, $p^{(2)}$ the detection probability of a coyote given the site is occupied with evidence of mange, and δ the probability of classifying the site as infected given the site is occupied with evidence of mange. The standardized covariates used in the models are represented by D (distance to urban areas), S (slope), and T (trend). A “.” represents a constant parameter that does not depend on any covariate. The full model set and estimates of the regression coefficients from the top model are presented in Online Resource Appendix 1

detecting a coyote at a site where mange was classified as being present ($p^{(2)}\delta$) decreased with distance from the garrison (Fig. 5c) and sites with mange were clustered near the urban area (Fig. 5d). Like DIC, the Gibbs variable selection approach yielded nearly the same results (Online Resource Appendix 2). Both the posterior inclusion and model probabilities suggested strong evidence for the effects of distance to urban areas and slope on ψ , for the effect of distance to urban areas on δ , and $p^{(2)}$ also showed a clear trend with time.

Discussion

The coyote-mange complex is a model host-disease system for describing the spatial extent of an infectious disease with multistate occupancy models. We observed the disease state with some level of certainty using photographs taken with remote cameras and estimated several state parameters. We were also able to explore the relationships among different covariates, including the association between the urban area and the state parameters.

Many species of carnivores have adapted to exploit urban environs, especially when urban areas are juxtaposed to potentially prey poor habitats, as is often the case in arid regions, or where natural habitats have been disturbed or fragmented (Gehrt et al. 2010). At least three other canid

species that inhabit urban environs also have experienced mange outbreaks. The endangered San Joaquin kit fox (*V. m. mutica*) resides in a semi-natural landscape that is heavily impacted by agriculture and urbanization and a substantial population of kit foxes has colonized Bakersfield, California, where they have been impacted by mange (Cypher et al. 2017; Montecino-Latorre et al. 2019). Mange also occurs in red foxes in Great Britain where there is a weak association between its occurrence and the distance to the nearest city (Scott et al. 2020). Raccoon dogs (*Nyctereutes procyonoides*) in Tokyo, Japan experience a high occurrence probability of mange when associated with urban and suburban habitats (Saito and Sonoda 2017).

The main urban center on the NTC was clearly associated with the pattern of spatial use of sites by coyotes. The probability that a coyote visited a camera site was 0.986 at 500 m and only 0.602 at 8000 m; thus the odds of any coyote using a site based on the distance to the urban area was 70:1 at 500 m and 1.5:1 at 8000 m. Coyote selection for sites nearer to the garrison is consistent with our observations of them using anthropogenically provided resources, such as organic compost or garbage for food (Reddell 2018). Previous studies have also shown that coyotes visited compost piles more frequently than other urban natural areas (Murray et al. 2016). Water also may be a limiting resource for coyotes in arid environments and the presence of anthropogenic water sources may increase relative use of urban sites (Gese and Bekoff 2004; Kluever et al. 2016).

Coyotes can occupy highly urbanized environments, but they typically tend to select for moderate levels of urbanization in combination with natural or semi-natural habitats (Grinder and Krausman 2001; Grubbs et al. 2009; Murray et al. 2015; Ellington and Gehrt 2019). In these environments, urban coyotes often exhibit spatial and temporal avoidance of humans by residing in natural environments during the day and utilizing urbanized environments during the night (Gehrt and Riley 2010). Diet is also highly variable, with some urban coyotes relying primarily on natural prey items and others incorporating large amounts of anthropogenic subsidies (Newsome et al. 2015).

Coyotes also avoided using steeper slopes with the odds of them using flat terrain being 22:1 versus 1:10 for a 20% slope. Their use of flat terrain is consistent with their hunting of black-tailed jackrabbits (*Lepus californicus*), their primary prey in desert systems (Cypher et al. 2018). The Mojave Desert has relatively low prey densities compared to temperate regions (Hayden 1966; Nagy et al. 1976) and during years of below average rainfall the diets of non-urban coyotes were more diverse and included more anthropogenic food items (Cypher et al. 2018). Precipitation at our study site was below the historic average (9.72 cm) for both 2015 (6.78 cm) and 2016 (5.44 cm), which may have promoted greater use of anthropogenic subsidies (NCEI 2020). We

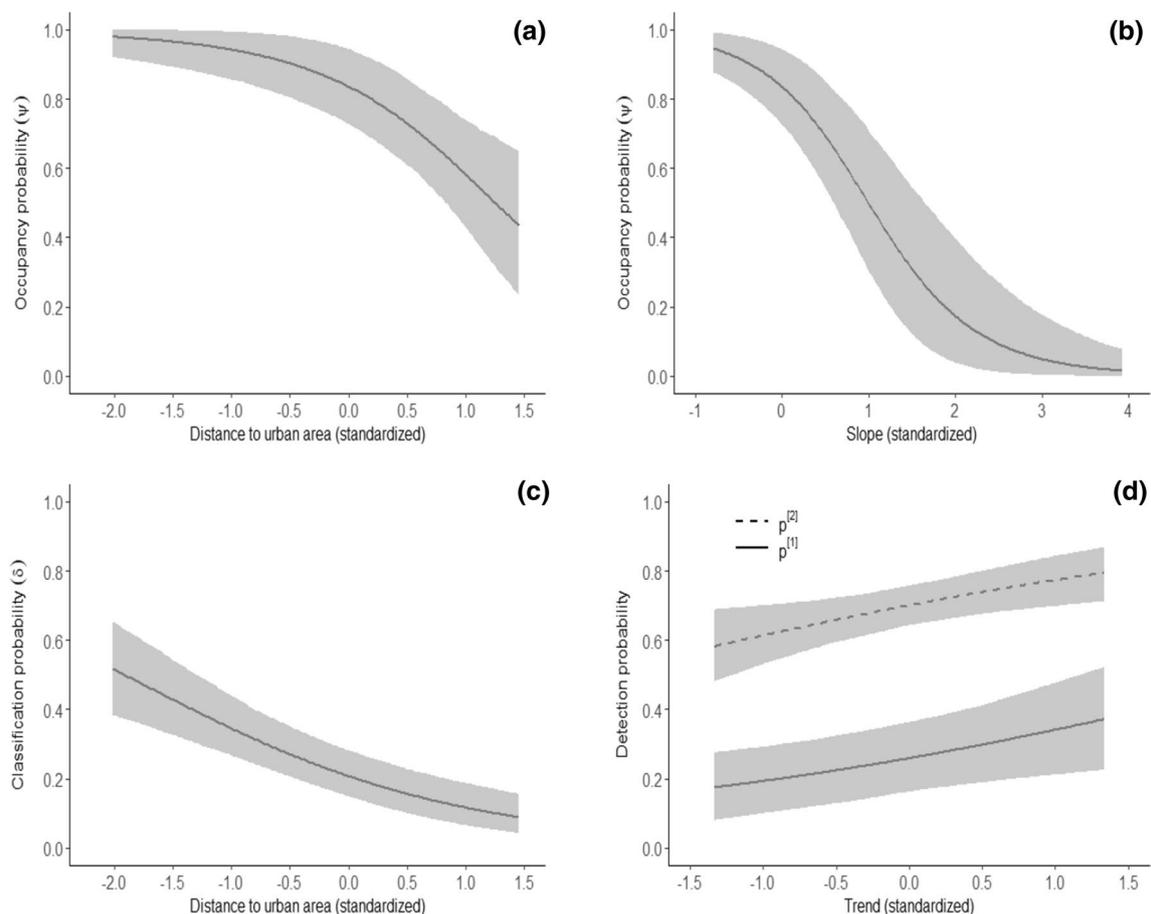


Fig. 4 Estimated relationships (95% credible intervals in gray) between **a** ψ and distance to urban area, **b** ψ and slope, **c** δ and distance to urban area, and **d** the temporal trend in $p^{[1]}$; the probability a

coyote is detected given the site is occupied without mange presence, and $p^{[2]}$ the probability a coyote is detected given the site is occupied with evidence of mange. All covariates are standardized

frequently observed coyotes feeding and resting at compost piles and witnessed symptomatic coyotes traveling through the most active areas of the garrison during daylight hours.

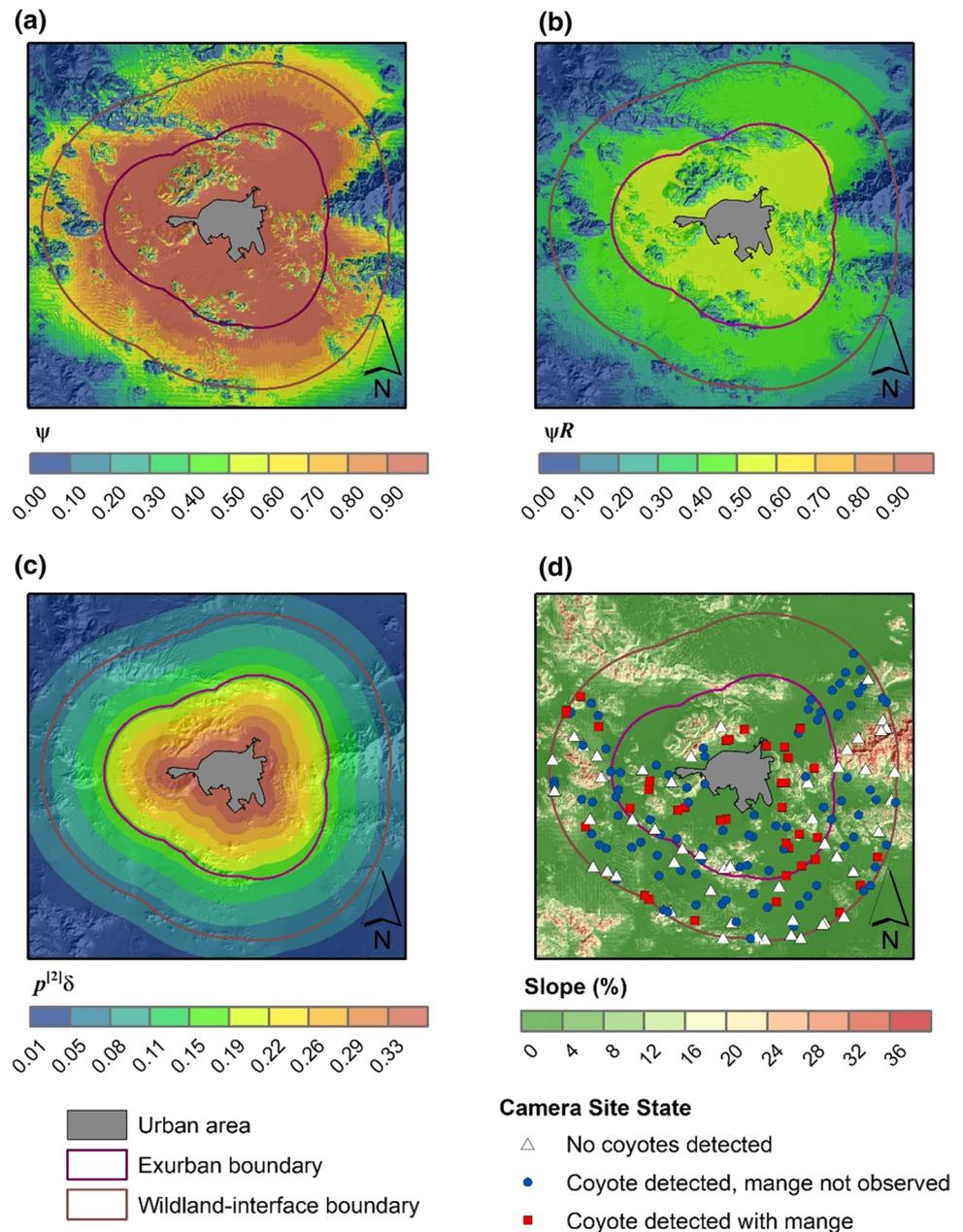
The conditional probabilities of mange presence and identification

The probability of mange presence at a site, R , was constant in our top model and did not vary with distance to the garrison. This was contrary to our prediction but may be related to the extent of our study area. We allocated cameras within a region that was only 8.72 km distant from the edge of the garrison, yet we simultaneously found that home ranges for severely infected coyotes that were considered to be transients in our study area or individuals that were not resident near the garrison but that were still recorded using urban subsidies, reached a maximum size of 435.7 km² (Reddell 2018). This yields a radius of 11.78 km for a hypothetical circular home range and is 2.7 times larger than the 4.36-km estimate we used to delineate our sampling area. Thus, our

study extent may not have been large enough to elucidate a possible relationship between distance to the urban edge and the occurrence of sarcoptic mange at a site or no relationship existed. A lack of a relationship between mange occurrence and the distance to the urban area may have occurred simply because coyotes, whether symptomatic or not, use sites closer to the urban area.

The probability that we correctly classified mange presence at a site given it was used by an infected individual, δ , increased at sites closer to the urban area suggesting that a relationship between urban environments and the spatial distribution of mange exists. There are two explanations for this trend in δ : (1) an increased number of infected individuals near the garrison provided more opportunities to photograph an infected individual and hence more opportunities to identify mange as being present at a site; or (2) individuals near the garrison exhibited more severe classes of infection (Class II or III) increasing our ability to recognize an infected animal and correctly identify mange as being present at a site. The mean number of photographic events for symptomatic

Fig. 5 Maps of the study area at the NTC Fort Irwin from 2015–2017 displaying **a** the probability of coyote occupancy (ψ), **b** the probability a site was occupied with mange present (ψR), **c** the probability of correctly classifying a site with mange present ($p^{21}\delta$), and **d** observed site states (white triangles: no coyotes detected; blue circles: coyote detected, mange not observed; red squares: coyote detected with mange observed) and slope (%)



coyotes and all three classes of infection decreased as the distance to urban areas increased, supporting both explanations (Fig. 3d and e). Those classes representing the highest severity of infection also had the highest mean number of photographic events < 4 km from the urban edge, which is within the distance we used to demarcate our exurban zone and define our study extent. These observations are supported by the spatial distribution of sites with mange present, which were clustered in the exurban zone (Fig. 5d). Further, the home range size of radio-collared coyotes we considered to be resident within the urban study area, that is, individuals that used the garrison to a substantial degree, was small. Seasonal estimates of home range size for resident urban

coyotes determined with the 95% minimum convex polygon averaged $22.7 \pm 3.4 \text{ km}^2$ ($n = 23$), which equates to a circular home range with a radius of 2.69 km (Reddell 2018). This indicates that coyotes that frequently used the garrison most likely occurred at higher density within the exurban zone than within the wildland-interface zone; estimates of resource selection by these coyotes further support their use of and potential dependence on urban resources (Reddell 2018).

Both symptomatic and asymptomatic coyotes used urban resources in our study, but individuals in the latter stages of infection may be more dependent on urban resources (Murray et al. 2015). Class III designated coyotes were shown to

have significantly reduced fat deposits compared to healthy individuals and Class II designated red foxes were shown to suffer from muscle catabolism as a result of undernourishment (Pence and Windberg 1994; Newman et al. 2002). The energetic cost of capturing natural prey may necessitate that debilitated individuals rely on anthropogenic subsidies, such as large compost piles, for survival, despite its nutritional quality (Murray et al. 2016). Concurrent with this study, we radio-collared and monitored 15 severely infected coyotes, and 10 of those individuals died, suggesting these individuals were in poor condition (Reddell 2018). Debilitated coyotes have also been recorded utilizing manmade structures for shelter, which is atypical for healthy individuals (Gehrt et al. 2009; Bateman and Fleming 2012). We observed severely infected coyotes, with extreme alopecia, using buildings and vehicles on the garrison, most likely as shelter from the harsh environmental conditions. Temperatures in the Mojave Desert can fall below freezing in winter and often exceed 40 °C throughout the summer creating lethal conditions for individuals lacking the ability to thermoregulate and potentially increasing their reliance on urban resources.

Detecting both symptomatic and asymptomatic coyotes

Both probabilities of detection, $p^{[1]}$ and $p^{[2]}$, increased during later surveys (Fig. 4d) and could be the result of a learned behavioral response by coyotes that became more habituated to the lure. We observed several instances of coyotes making repeated attempts to extract the lure (cat food) from its anchor. Model estimates revealed a striking difference in our ability to detect coyotes at sites of differing disease state, with the odds of detecting a coyote at a site without mange detected being 1:3 compared to a site with mange being 2.3:1, yielding an odds ratio of 6.9:1. In other words, we had seven times the odds of detecting a coyote at a site where mange was observed compared to a ‘mange-free’ site. We believe that this difference was a result of higher densities nearer to the urban center, resulting in ψ being higher near the garrison coupled with the fact that δ was also higher nearer to the garrison. The increased use of these sites by all coyotes and our increased probability of correctly classifying sites with mange present, due to an increased number of severely infected individuals being photographed or because severely infected individuals frequented our cameras sites, would offer more opportunities to photograph a coyote and thereby increase detection at sites where mange was also observed. The effect of distance to the urban area on ψ and δ may also be masking its effect on R and $p^{[2]}$, as the majority of our sites with mange were located within the exurban zone near the garrison (Fig. 5d).

Our ability to correctly classify an occupied site with mange, $p^{[2]}\delta$ (Fig. 5c), may have been compromised because our measure of occupancy is really a measure of use, coyotes may visit a site but they are not resident at a camera site (MacKenzie 2006) and because the same site could be visited by symptomatic and asymptomatic coyotes between surveys. Asymptomatic coyotes consist of truly uninfected individuals and those that are infected, but the symptoms were not observed (e.g., Class I). We had four times more asymptomatic encounters than symptomatic encounters and nearly seven times more asymptomatic photographic events compared to symptomatic photographic events. The increased number of asymptomatic encounters at sites where mange was observed would tend to reduce the estimate of δ and increase its uncertainty, which could be improved by using multiple cameras at a single site yielding different angles and multiple photographs of a single individual, potentially improving our ability to detect mange.

The utility of multistate models for wildlife disease surveillance

Multistate occupancy models could be applied to a variety of species susceptible to diseases that have readily observable symptoms. At least two other observable diseases, winter tick in moose calves (Jones et al. 2019) and Tasmanian devil facial tumor disease (Preece et al. 2017), have also caused widespread declines in the species affected. The prevalence and spatial extent of these diseases could have been easily assessed with a surveillance program similar to what we used here. Multistate models also have recently been used to account for imperfect detection in diagnostic testing by including additional states when the pathogen is present, such as the probability a sample contains an ambiguous result versus the probability a sample contains a positive result (Rodrigues et al. 2020).

We used single-season occupancy models which assume that the state of a site (unoccupied, occupied with mange or without mange) remains the same during the sampling session (i.e., geographic closure assumption); however, if the same sites were repeatedly sampled over different sampling sessions, multi-season, multistate dynamic occupancy models could be used (Royle and Kéry 2007; MacKenzie et al. 2009). These models enable estimation of state transition probabilities at repeatedly sampled sites, which would yield a greater understanding of temporal disease dynamics.

As urbanization continues, wildlife managers will need to address the increased risk of epizootics for wildlife communities and the potential for zoonoses to arise. Multistate occupancy models represent a generalizable and flexible framework that can account for the hierarchical levels of uncertainty characterizing the surveillance of

wildlife diseases, enabling a better view of spatiotemporal disease dynamics. This will improve our ability to mitigate disease outbreaks in wildlife populations and reduce exposure of humans and our commensals to zoonotic disease agents.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval For this type of study formal consent is not required because we only photographed animals and did not handle them. For additional work mentioned here (Reddell 2018), consent for capturing and handling animals was approved by the IACUC of NMSU (Protocol # 2015-001) and the California Department of Fish and Wildlife (Permit # 2330).

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