



Anthropogenic subsidies influence resource use during a mange epizootic in a desert coyote population

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Abstract

Colonization of urban areas by synanthropic wildlife introduces novel and complex alterations to established ecological processes, including the emergence and spread of infectious diseases. Aggregation at urban resources can increase disease transfer, with wide-ranging species potentially infecting outlying populations. The garrison at the National Training Center, Fort Irwin, California, USA, was recently colonized by mange-infected coyotes (*Canis latrans*) that also use the surrounding Mojave Desert. This situation provided an ideal opportunity to examine the effects of urban resources on disease dynamics. We evaluated seasonal space use and determined the influence of anthropogenic subsidies, water sources, and prey density on urban resource selection. We found no difference in home range size between healthy and infected individuals, but infected residents had considerably more spatial overlap with one another than healthy residents. All coyotes selected for anthropogenic subsidies during all seasons, while infected coyotes seasonally selected for urban water sources, and healthy coyotes seasonally selected for urban areas with greater densities of natural prey. These results suggest that while all coyotes were selecting for anthropogenic subsidies, infected resident coyotes demonstrated a greater tolerance for other conspecifics, which could be facilitating the horizontal transfer of sarcoptic mange to non-resident coyotes. Conversely, healthy coyotes also selected for natural prey and healthy residents exhibited a lack of spatial overlap with other coyotes suggesting they were not reliant on anthropogenic subsidies and were maintaining territories. Understanding the association between urban wildlife, zoonotic diseases, and urban resources can be critical in determining effective responses for mitigating future epizootics.

Keywords *Canis latrans* · Disease dynamics · Human–wildlife conflict · Mixed effects · Urbanization

Introduction

Urbanization can degrade and fragment natural habitat endangering native species (McKinney 2002, 2006). However, some native species can exploit urban environments to their benefit. Urban areas may relax competition or decrease predation risk, provide subsidized food resources in the form of human garbage, alternative prey, or intentional feeding, and offer shelter in the form of buildings, bridges, and other structures (Gosselink et al. 2003; Oro et al. 2013). Native species able to adapt to urban areas often exhibit increased fecundity, survivorship, and higher population densities than conspecifics residing outside of urban areas (Fedriani et al. 2001; Oro et al. 2013; Newsome et al. 2014).

Anthropogenic food subsidies are often reliably abundant and can be localized over small areas, such as landfills or compost piles (Oro et al. 2013), which can be beneficial to urban-adapted species, but may also be detrimental if they facilitate disease transmission (Becker et al. 2015). Increased

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densities and reduced territoriality due to abundant and clumped resources can lead to individuals aggregating at resources, increasing contact rates, and pathogen transmission (Johnson et al. 2002; Wright and Gompper 2005; Newsome et al. 2013). Abundant resources may prevent malnourishment and promote immune defense, but resources lacking in protein or other nutrients can decrease immune defense and promote infection (Bradley and Altizer 2007; Becker et al. 2015). Anthropogenic subsidies may also contain toxicants, such as mycotoxins in compost or anticoagulant rodenticides in natural prey, which can depress immune defense (Riley et al. 2007; Murray et al. 2016). Far-ranging species may transmit pathogens to outlying exurban populations or sympatric species that do not occur in urban areas (Bradley and Altizer 2007).

The coyote (*Canis latrans*) is one of the larger carnivores inhabiting metropolitan areas across North America (White and Gehrt 2009; Poessel et al. 2013). Similar to other canids, coyote social groups are characterized by a mated pair or less often, larger familial packs that establish and defend a territory against other conspecifics (Gese and Bekoff 2004). Transient coyotes also occur, are unaffiliated with a social group, and travel alone over large areas that generally overlap multiple territories (Gese and Bekoff 2004). Such behavioral plasticity most likely enables coyotes to exploit urban resources, with abundant and centralized resources reducing territoriality, resulting in increased group size and higher densities (Johnson et al. 2002; Gese and Bekoff 2004; Hidalgo-Mihart et al. 2004; Gehrt and Riley 2010). Urban coyotes can become nuisance animals when they raid garbage cans or prey upon domestic animals, and they can spread diseases to pets (e.g., tuberculosis, canine distemper, or canine parvovirus; Gese et al. 1997; Grinder and Krausman 2001a) or harbor zoonotic pathogens fatal to people (e.g., rabies virus or *Echinococcus multilocularis*; Catalano et al. 2012). The potential for human–coyote conflict may be exacerbated when diseases, such as sarcoptic mange, debilitate coyotes to the point where they become more reliant on anthropogenic food subsidies and are more active during daylight hours (Murray et al. 2015, 2016).

Sarcoptic mange is a contagious skin disease caused by parasitic mites (*Sarcoptes scabiei*), that burrow into the epidermis and consume live cells or tissue fluid (Bornstein et al. 2001). *Sarcoptes scabiei* can be transmitted through direct contact with an infected host or indirectly when mites have become dislodged from a host, although survival off-host is dependent on environmental conditions (Arlian et al. 1989; Bornstein et al. 2001). Hosts that exhibit a hypersensitivity reaction to the mites generally develop lesions that are intensely pruritic, followed by extensive hyperkeratosis, and alopecia, which can be classified into sequential states as the infection develops: class

0—no active lesions apparent; class I—active lesions on <5% of the body surface, primarily on the lower legs, ischium, and base of ears; class II—an infection covering 5 to 50% of the body; class III—infections with >50% of the body covered; and class IV—individuals that exhibited signs of recovery through hair regrowth around lesions (Pence et al. 1983; Bornstein et al. 2001). Initial symptoms commonly begin manifesting from 10 to 30 days post-exposure, while the development of more severe symptoms (class II/III) can manifest from 2 to 11 months, based on individual (Pence et al. 1983; Pence and Windberg 1994; Bornstein et al. 2001). Moreover, individuals in the latter stages of the infection often have decreased fat stores, reduced reproductive rates, and may exhibit changes in behavior including listlessness and a reduced wariness of humans (Trainer and Hale 1969; Pence et al. 1983; Pence and Windberg 1994; Niedringhaus et al. 2019). Although some individuals can recover and partially regrow hair (3–20%), severe cases often result in mortality due to reduced ability to capture prey, inability to thermoregulate due to hair loss, or infections (Pence and Ueckermann 2002; Chronert et al. 2007; Wilson 2012).

Understanding how diseases influence the space and resource use of urban wildlife is critical in reducing pathogen transmission and mitigating the impacts of epizootics on wildlife populations and public health. We studied a coyote population on the National Training Center (NTC), Fort Irwin, California, USA, a military base in the Mojave Desert, to explore how coyotes utilized urban resources during a sarcoptic mange epizootic. Since 2008, coyotes at the NTC have become bolder, approaching residents of the installation's garrison for food during the day, foraging on garbage, and sheltering in anthropogenic structures (L. M. Aker and C. A. Everly, Ft. Irwin, NTC, *pers. comm*). Prevalence of sarcoptic mange in the coyote population also incited public health concerns (L. M. Aker and C. A. Everly, Ft. Irwin, NTC *pers. comm*). Our objectives were to: (1) compare seasonal home range size and spatial overlap among coyotes that differed in infection status; and (2) determine which urban resources were primarily driving use of urban areas by coyotes. We predicted that infected individuals would demonstrate a greater reliance on urban areas by having smaller home ranges and a greater spatial overlap among other infected individuals, due to the highly concentrated nature of urban resources, while selecting primarily for anthropogenic subsidies, as these resources would be readily available for coyotes suffering from the debilitating effects of sarcoptic mange. Conversely, we predicted that healthy individuals would exhibit less dependence on urban areas by maintaining larger home ranges with less spatial overlap among all other groupings of coyotes, and primarily selecting for urban areas containing abundant natural prey.

Materials and methods

Study area

The NTC is located approximately 60 km northeast of the city of Barstow in the Mojave Desert of San Bernardino County, California, USA (Fig. 1). The NTC is 3055 km² with an 18.3 km² garrison and a population of 8096 residents (United States Census Bureau 2020). Areas north and east of the garrison are heavily disturbed due to military training exercises and off-road activity. A recovery area for the threatened desert tortoise (*Gopherus agassizii*) and the NASA Goldstone Deep Space Communications Complex are located to the west and northwest of the garrison and

are generally free of military disturbance. The elevation is 748 m above sea level for the garrison, with elevations ranging from 230 m at the southern edge of Death Valley National Park to 1875 m in the Avawatz Mountains, with a mean elevation of 898 m \pm 241 (SD) for the entire installation. Vegetation types in the natural areas are dominated by creosote bush (*Larrea tridentata*) and white bursage (*Ambrosia dumosa*; 87% of the natural area), with smaller patches of saltbush scrub (*Atriplex* spp.; 6%), blackbush scrub (*Coleogyne ramosissima*; 4%), dry washes (2%), and playas (1%). Temperatures ranged from average daily highs of 39 °C in summer and average lows of 6 °C in winter, with an average annual precipitation of 9.5 cm \pm 3.8 (WRCC 2016).

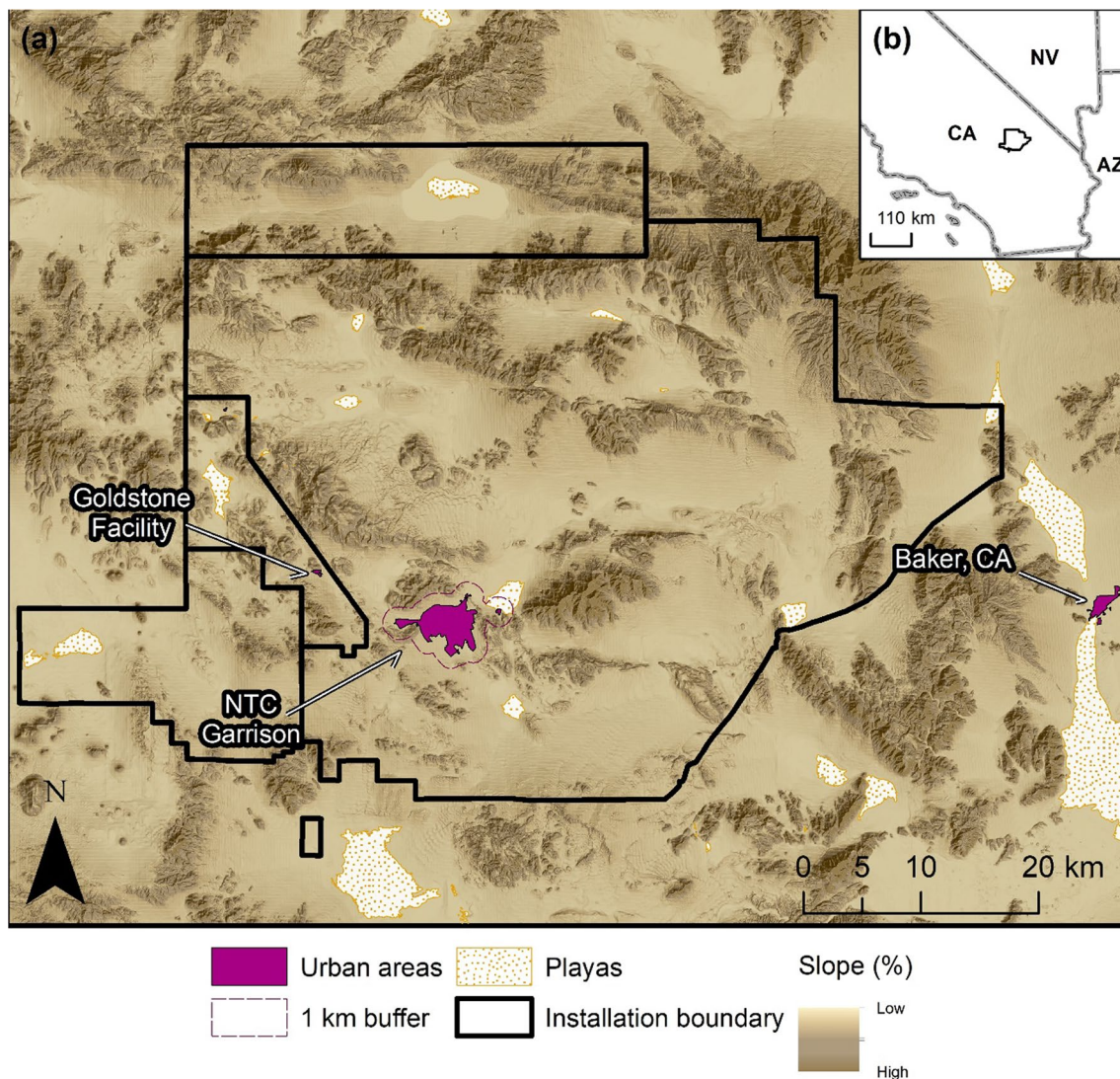


Fig. 1 **a** Project study area, National Training Center (NTC) Fort Irwin, California, containing all nearby urban areas, the one-kilometer buffer used for the resource analysis, all nearby playas, the NTC

boundary, and slope (%) from 2015 to 2017, and **b** an inset displaying the location of the NTC within the state of California

Capture and telemetry

We captured coyotes using large cage traps (Humane Way Live Animal Traps, Kent, Washington, USA) and Collarum neck snares (Wildlife Control Supplies, LLC, East Granby, Connecticut, USA) intermittently from May 2015 to January 2017. We generally trapped year-round when weather permitted ($< 27^{\circ}\text{C}$ for Collarum neck snares) and checked traps every 6 h. We immobilized coyotes using ketamine hydrochloride (5 mg/kg) and medetomidine hydrochloride (50 $\mu\text{g/kg}$; Orion Corporation, Espoo, Finland) or with Telazol[®] (tiletamine hydrochloride and zolazepam hydrochloride; Zoetis, Inc., Kalamazoo, Michigan, USA; 6 mg/kg) and Midazolam (1 mg/kg; Akron, Inc. Lake Forest, Illinois, USA) injected intramuscularly. After processing, we administered antisedan hydrochloride (200–250 $\mu\text{g/kg}$, Orion Corporation, Espoo, Finland) intramuscularly as an antagonist to the medetomidine when applicable. Animals were sexed, weighed, and aged by tooth wear (Gier 1957). We fitted individuals with either a GPS store-on-board collar (model TGW-4400-3, Telonics Inc., Mesa, USA) or a standard VHF collar (Advanced Telemetry Systems Inc., Isanti, Minnesota, USA), both with Telonics CR-2a programmable collar releases set to activate at the conclusion of the study. Coyotes were only collared if the collar weight was $< 7\%$ of the animal's body weight, with 5 kg being the threshold for affixing a VHF collar, and 9 kg for GPS collars (Sikes and Gannon 2011). Some individuals were not collared due to their poor physical condition or, in one case near the end of the study, not having a serviceable collar available. We marked coyotes with a unique pair of ear tags (National Band and Tag Company, New Port, USA) and collected hair, vibrissae, tissue (skin) snipped from the top of the pinna with dissecting scissors, fecal, and blood samples. We classified coyotes with sarcoptic mange following the classifications outlined by Pence et al. (1983) stated earlier in the Introduction. We also collected skin samples for PCR analysis by the California Department of Fish and Wildlife, Wildlife Investigations Laboratory in Rancho Cordova and the California Animal Health and Food Safety Laboratory in Davis, CA, to confirm the presence of sarcoptic mange. All trapping and handling followed acceptable methods (Sikes and Gannon 2011) and were approved by the New Mexico State University Institutional Animal Care and Use Committee (Protocol #2015-001) and the California Department of Fish and Wildlife (SC-002330).

We tracked coyotes using triangulation and homing techniques with a handheld 3-element Yagi antenna. Locations consisted of ≥ 3 compass bearings with intersecting angles between 20° and 160° collected in < 15 min to mitigate for animal movement. We estimated locations using Locate III (Truro Computing, Nova Scotia, Canada), and only locations with error ellipses < 0.25 ha and an azimuth standard

deviation $< 6^{\circ}$ were retained (White and Garrott 1990). We used sequential tracking and partitioned the 24-h cycle (Laundré and Keller 1984; Gese et al. 1990) into 6, 4-h blocks, with the intent to continuously track individuals over an 8–12-h timespan. We programmed GPS collars to collect Quick Fix Pseudoranging locations to maximize battery life. We set GPS fix interval at 1 h from 0600 to 1759 and 2 locations per hour from 1800 to 0559, for a total of 36 locations per 24-h cycle.

Space use

We calculated the size and location of home ranges with 95% minimum convex polygons (MCP) using the Home Range Tools 2.0 extension (Rodgers et al. 2015) for ArcGIS 10.3.1 (ESRI 2015). We also estimated home range size using 99% dynamic Brownian Bridge Movement Models (Kranstauber et al. 2012); however, we were unable to include individuals fitted with VHF collars, given the relatively small sample of relocations (Online Resource Appendix 1). Given that home range sizes were not significantly different for GPS collared individuals between the two methods, we opted only to present the MCP results (Online Resource Appendix 1). Additionally, MCP home ranges allowed us to compare estimates with previous studies, as it is a historically common technique used to estimate home range size. Many individuals were only monitored for a single season because of high mortality rates within the infected population and because we continued to capture new individuals throughout the duration of the study. We generated seasonal home ranges to account for this high turnover rate, classifying May to October as the dry season and November to April as the wet season (Larson et al. 2020). Our data revealed two types of space use patterns by collared coyotes: relatively small and stable home ranges and those with much larger home ranges (Online Resource Fig. 1.1). We classified individuals as “resident” if they maintained a stable home range within a particular area and “non-resident” if they exhibited wide-ranging movements across the study area without exhibiting any fidelity to a specific area, similar to transient individuals (Gese et al. 1990).

To compare home range size among healthy and mange-infected animals, we classified mange status as a binary factor: coyotes exhibiting mange class 0 or I were considered healthy, and coyotes exhibiting mange class II or III were considered infected. Individuals exhibiting mange class I generally did not exhibit the poor body conditions typical of coyotes designated as class II or III, and generally did not suffer from mortalities attributed to illness or disease during the study, suggesting that their behavior may be similar to class 0 coyotes, hence our dichotomous classification (Wilson 2012; Reddell 2018). Individuals were rarely recaptured,

so we were only able to observe individuals opportunistically during tracking sessions or after an individual's mortality and subsequent recovery to monitor changes in infection states. Given the lack of mortalities attributed to illness or disease for class I coyotes, compared to class II or III coyotes, we believe this dichotomous classification best represents the influence severe cases of sarcoptic mange can have on coyote behavior at the NTC during our study.

We constructed observation–area curves for individuals fitted with VHF collars to determine the number of locations necessary for estimates of seasonal home range size to asymptote using the “hrBootstrap” function from the R package move (R Development Core Team 2014; Kranstauber and Smolla 2016). We calculated a second seasonal home range if a resident transitioned to a new distinct area during a single season, or if a non-resident developed a stable home range, given we had collected sufficient relocations. We used a linear mixed model using restricted maximum likelihood estimation (REML) in an unbalanced repeated measures design to compare home range estimates using SAS 9.4 (SAS Institute Inc., Cary, NC, USA). We assessed normality using the Shapiro–Wilk test and subsequently log-transformed home range size estimates to obtain a normal distribution. We incorporated coyote ID as a random effect, season as the within-subject fixed effect, residency status, mange status, and collar type as between-subject fixed effects, and interactions between mange status, collar type, and residency status.

To assess the potential for pathogen transmission through contact between individuals and determine if coyotes were aggregating within and around the garrison, we evaluated spatial overlap in relation to residency and mange status with the utilization distribution overlap index (UDOI; Fieberg and Kochanny 2005), calculated with the adehabitatHR package in R (Calenge 2006). Unlike similar indices constrained between 0 and 1, UDOI can be > 1 if the utilization distributions have a high degree of overlap but are not uniformly distributed and is a superior performing index for measuring potential contact rates between individuals (Fieberg and Kochanny 2005; Robert et al. 2012). We assessed the differences in spatial overlap by comparing the composite mean UDOI of healthy and infected residents to all residency and mange status combinations.

Resource selection

We developed resource selection functions using mixed-effects logistic regression binomial models using the lme4 package in program R (Gillies et al. 2006; Bates et al. 2015). We defined use as all observed locations and determined availability by randomly generating twice the number of locations for each animal within a 1-km buffer around the garrison, using ArcGIS 10.3.1 (ESRI 2015), which served

as the binomial response variable (Design II; Manly et al. 2002). We restricted the extent of our resource analysis to this 1-km buffer around the garrison as larger spatial extents resulted in Spearman's rank correlation coefficients of $|r| > 0.60$ among urban covariates. Given the restricted spatial extent of the resource analysis and to avoid overfitting our resource selection models, we did not include residency status as a variable in the resource analysis. We developed separate model sets for each season (2015 Wet Season, 2016 Dry Season, and 2016 Wet Season), with “0” representing random available locations, and “1” representing observed or use locations. Individual coyotes were treated as a random effect, while mange was treated as a binary factor with healthy status as the reference level.

To determine the drivers of resource use in the urban area, we examined three resource covariates that should be more abundant and centralized within the garrison compared to the non-urban areas. We used satellite images to digitize anthropogenic food subsidies (compost piles and food service buildings) and water sources (standing water treatment ponds, water fill-up stations, and other sites with reliable sources of fresh water; ESRI 2015) on the garrison as coyotes readily exploited these food sources (Murray et al. 2015) and water may be a limiting factor in arid regions, particularly for individuals debilitated by mange (Gese and Bekoff 2004). These food and water sources were visited in the field to confirm their authenticity. We then calculated the distance from used and available locations to anthropogenic food subsidies and the nearest anthropogenic water sources (ESRI 2015). Finally, we conducted distance sampling to estimate lagomorph density, as the presence of urban resources (e.g., grass, anthropogenic water) may also attract natural prey to the garrison (Buckland et al. 2001; Online Resource Appendix 2). We used lagomorph density as a proxy for overall natural prey density, as rodent biomass and lagomorph density were highly correlated in another desert biome (Robinson et al. 2014).

We assessed collinearity among the covariates using Spearman's rank correlation and standardized continuous covariates by subtracting the mean and dividing by 2 SDs (Gelman 2008). We evaluated model support using Akaike's Information Criterion corrected for small sample size (AIC_C), using the MuMIn package in R (Bartoni 2022), and selected the top model with lowest AIC_C value of each model set (Burnham and Anderson 2002; Gillies et al. 2006). We used the effects package in R (Fox 2003) to generate effect displays for the predictors in the top model. We calculated variance inflation factors for covariates in top-ranked models to further assess multicollinearity, reassessing and potentially excluding models with VIF scores > 5 (Menard 2002). We used k -fold cross-validation to test model predictive performance, with Spearman's rank correlation coefficient as a test statistic, 5 partitions (k), 30 bins, and 10 repetitions (Boyce et al. 2002).

Results

Space use

We captured 41 coyotes (25 males, 16 females), with 26 individuals exhibiting signs of sarcoptic mange between May 2015 and January 2017; we only had 3 individuals recaptured soon after their initial capture (Online Resource Table 3.1). We recorded 18 mortalities from our study sample, with 12 causes of mortality being unknown but occurring in individuals exhibiting mange class II or III at the time of capture. We fitted 36 (15 GPS, 21 VHF) individuals with transmitters: 20 (8 VHF, 12 GPS; 12 healthy and 8 infected) yielded a sufficient number of locations for seasonal home range estimation and resource selection analysis. While we were unable to reliably recapture or resight individuals to determine transitions from one mange state to another, we did note that three individuals (coyotes 101, 102, and 103) appeared to be in better condition during a latter point of the study.

We calculated a total of 41 seasonal home ranges, with data collected from the 20 individuals with a suitable number of relocations, (2015 Wet Season, $n = 11$; 2016 Dry Season, $n = 15$; 2016 Wet Season, $n = 15$), with one individual having two separate home ranges calculated in the 2016 Wet Season (Online Resource Table 3.2 & Table 3.3). Home range sizes did not vary by season ($n = 41$; $F_{2,22} = 0.67$, $P = 0.521$). Differences in the size of home ranges suggested that there were resident and non-resident coyotes using the garrison with the home ranges of residents being much smaller than those of non-residents, average 95% MCP home ranges were $22.7 \pm 3.4 \text{ km}^2$ ($n = 23$) and $343.3 \pm 80.9 \text{ km}^2$ ($n = 18$), respectively ($F_{1,16.3} = 49.63$, $P < 0.001$). Home range sizes did not differ by mange status ($F_{1,15.6} = 0.31$, $P = 0.585$) or as an interaction with residency status ($F_{1,15.1} = 0.85$, $P = 0.371$). Home range size differed between collar types ($F_{1,14.9} = 10.60$, $P = 0.005$), but multiple comparison tests revealed that only non-resident home ranges differed between collar types ($t_{17.4} = 3.08$, $P = 0.007$), whereas collar type did not influence the size of resident home ranges ($t_{16} = 1.01$, $P = 0.330$). Given that Wilcoxon rank-sum exact test found home range sizes for VHF and GPS residents (VHF = $22.2 \pm 4.5 \text{ km}^2$, GPS = $24.4 \pm 5.4 \text{ km}^2$) were significantly smaller than mean VHF non-resident home range size (VHF = $78.5 \pm 18.5 \text{ km}^2$; $W = 17$, $P = 0.003$), we elected to use residency status as a binary covariate in the subsequent analysis.

The utilization distribution overlap index (UDOI) among healthy residents was < 0.30 across all seasons, was more variable between healthy and infected resident dyads (range 0.15 to 0.59), and greatest among infected

individuals (range 0.59 to 1.50; Fig. 2a). Overlap among healthy residents and healthy/infected non-residents was 0.07 to 0.31 across all seasons, whereas overlap among infected residents and healthy/infected non-residents was low in the 2015 Wet Season (0.09/0.05) but increased to levels approaching and exceeding 1.0 in later seasons (Fig. 2b).

Resource selection

The full global model held 100% of the model weight for all seasonal model sets (Table 1). The relative probability of a coyote using a site decreased with increasing distance to anthropogenic subsidies for healthy and infected coyotes during all seasons. (Table 2, Fig. 3; Online Resource Table 3.4). The relative probability of use increased with increasing distance to water for healthy coyotes in all seasons and for infected coyotes in the 2015 Wet Season. We observed a negative trend for infected coyotes in the 2016 Dry Season and 2016 Wet Season (Table 2; Online Resource Appendix 3). The relative probability of use increased with increasing prey density for healthy coyotes in the 2015 Wet Season and 2016 Dry Season, while a negative association was observed in the 2016 Wet Season and in all seasons for infected coyotes (Table 2; Online Resource Appendix 3). Predictive performances for the top models from k -fold cross-validation estimated ρ values were 0.79 in the 2015 Wet Season, 0.95 in the 2016 Dry Season, and 0.77 in the 2016 Wet Season.

While the association with anthropogenic subsidies followed similar trends for healthy and infected individuals across all seasons, the magnitude of association was significantly different in all cases (Table 2, Fig. 3). The strength of the association between an infected resident's selection of a site and the site's proximity to anthropogenic subsidies increased in the later seasons, with an odds ratios > 1 indicating a stronger selection for a site compared to healthy coyotes. The odds ratios of an infected coyote selecting a site at a distance of 0 m from anthropogenic subsidies over a healthy coyote were 0.54 (CI 0.46–0.63) in the 2015 Wet season, 1.33 (CI 1.15–1.52) in the 2016 Dry Season, and 1.52 (CI 1.18–1.98) in the 2016 Wet Season, whereas when they selected sites at a distance of 3000 m from anthropogenic subsidies, the odds ratios were 13.01 (CI 8.62–19.42) in the 2015 Wet Season, 0.30 (CI 0.25–0.35) in the 2016 Dry Season, and 0.15 (CI 0.11–0.21) in the 2016 Wet Season.

Discussion

Our goal was to examine whether infections due to sarcoptic mange influenced space and resource use of a desert coyote population that had access to an urban

Fig. 2 Utilization distribution overlap index (UDOI) averages and standard errors between different coyote (*Canis latrans*) groups: **a** spatial overlap between healthy or infected residents, and **b** spatial overlap between healthy or infected residents and non-residents

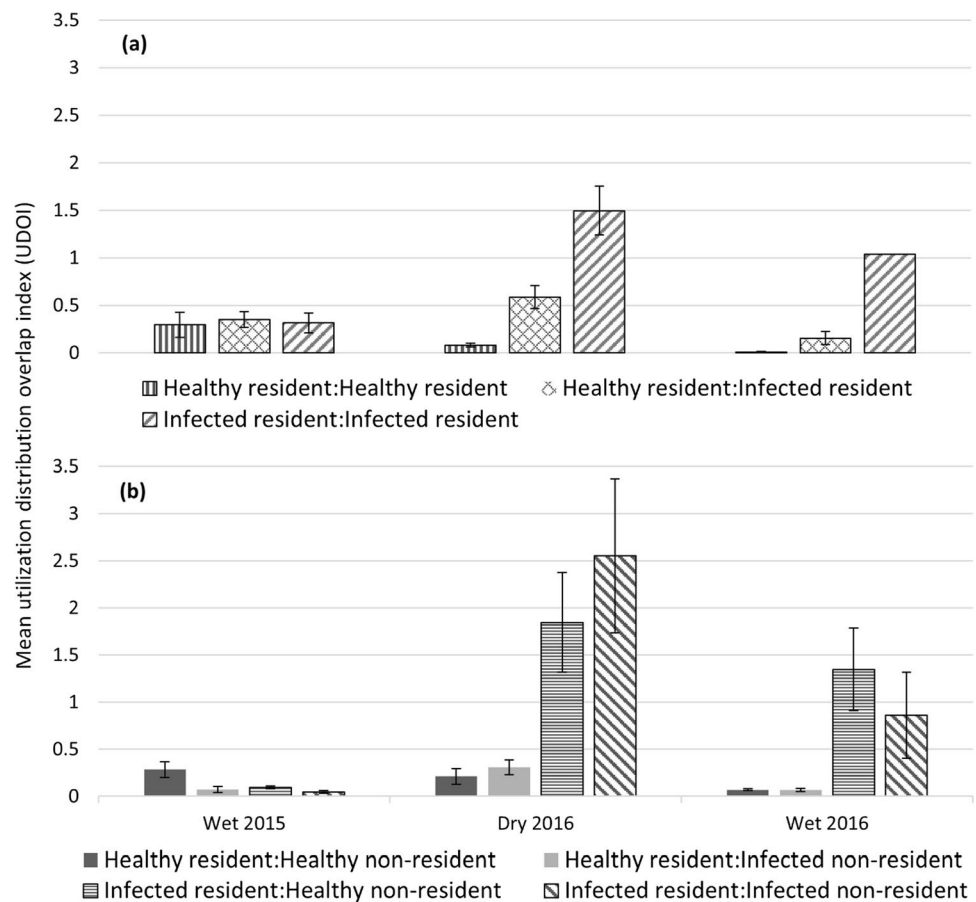


Table 1 Subset of the top two most supported mixed-effects logistic regression models describing urban area resource use for all coyotes at the NTC Fort Irwin from 2015 to 2017

Season	Model	<i>K</i>	AIC _c	ΔAIC _c	<i>w_i</i>	Deviance	<i>ρ</i>
Wet 2015	Mange + anthro + water + prey + mange × anthro + mange × water + mange × prey	9	15,565.65	0.00	1.00	15,547.64	0.79
	mange + anthro + water + mange × anthro + mange × water	7	15,659.84	94.19	0.00	15,645.83	0.87
Dry 2016	Mange + anthro + water + prey + mange × anthro + mange × water + mange × prey	9	73,669.21	0.00	1.00	73,651.21	0.95
	Mange + anthro + prey + mange × anthro + mange × prey	7	75,772.58	2,103.37	0.00	75,758.58	0.90
Wet 2016	Mange + anthro + water + prey + mange × anthro + mange × water + mange × prey	9	42,636.46	0.00	1.00	42,618.45	0.77
	Mange + anthro + water + mange × anthro + mange × water	7	42,931.19	294.74	0.00	42,917.19	0.77

We present the number of parameters (*K*), akaike's information criterion adjusted for small sample size (AIC_c), ΔAIC_c, AIC_c weights (*w_i*), absolute deviance ($-2 \times \log\text{-likelihood}$), and *k*-fold cross validation *ρ* values

environment. Contrary to our predictions, home range size did not vary between healthy and infected individuals, as has been observed by others (Murray et al. 2015); rather, we observed two different spatial patterns with some coyotes occupying small home ranges centered on the urban environment and others having home ranges encompassing large tracts of natural habitat that also overlapped the urban environment (Online Resource Appendix 3). We found infected residents of the garrison exhibited greater spatial overlap with other infected residents and

non-resident coyotes than healthy residents. Finally, we found that healthy and infected coyotes selected for anthropogenic resources during all seasons, while infected coyotes selected for urban water sources during the 2016 Dry Season and 2016 Wet Season, and healthy coyotes selected for urban areas containing higher densities of natural prey during the 2015 Wet Season and 2016 Dry Season.

Generally, coyotes at the NTC had relatively large home ranges compared to other urban populations. Studies of resident coyotes in other western cities ranged from 11 to 23

Table 2 Estimates of beta coefficients, standard errors, and 95% confidence intervals for variables in the most supported urban models describing seasonal resource selection for all coyotes at the NTC Fort Irwin from 2015 to 2017

		β	SE	95% Confidence interval		z value	P
				LL	UL		
Wet 2015	Intercept	− 1.26	0.06	− 1.38	− 1.14	− 20.61	< 0.001
	Mange	0.47	0.07	0.33	0.61	6.79	< 0.001
	Anthro ^a	− 3.36	0.12	− 3.60	− 3.13	− 28.06	< 0.001
	Water ^a	0.83	0.10	0.64	1.02	8.58	< 0.001
	Prey	0.56	0.06	0.44	0.69	8.78	< 0.001
	Mange × anthro ^a	1.67	0.13	1.40	1.93	12.51	< 0.001
	Mange × water ^a	− 0.29	0.11	− 0.51	− 0.08	− 2.69	0.01
	Mange × prey	− 0.84	0.09	− 1.01	− 0.67	− 9.69	< 0.001
Dry 2016	Intercept	− 0.79	0.05	− 0.88	− 0.70	− 16.76	< 0.001
	Mange	− 0.27	0.07	− 0.40	− 0.14	− 4.14	< 0.001
	Anthro ^a	− 1.14	0.03	− 1.20	− 1.08	− 38.15	< 0.001
	Water ^a	0.58	0.03	0.52	0.63	19.91	< 0.001
	Prey	1.55	0.04	1.47	1.62	41.15	< 0.001
	Mange × anthro ^a	− 0.77	0.05	− 0.86	− 0.68	− 17.01	< 0.001
	Mange × water ^a	− 1.84	0.04	− 1.92	− 1.75	− 42.20	< 0.001
	Mange × prey	− 2.17	0.08	− 2.33	− 2.01	− 26.78	< 0.001
Wet 2016	Intercept	− 0.78	0.06	− 0.89	− 0.67	− 13.97	< 0.001
	Mange	− 0.43	0.13	− 0.68	− 0.17	− 3.32	< 0.001
	Anthro ^a	− 1.21	0.03	− 1.27	− 1.14	− 37.92	< 0.001
	Water ^a	0.55	0.03	0.49	0.61	17.83	< 0.001
	Prey	− 0.17	0.03	− 0.23	− 0.11	− 5.46	< 0.001
	Mange × anthro ^a	− 1.17	0.08	− 1.33	− 1.02	− 14.98	< 0.001
	Mange × water ^a	− 1.52	0.07	− 1.66	− 1.38	− 21.57	< 0.001
	Mange × prey	− 0.86	0.08	− 1.02	− 0.71	− 10.79	< 0.001

^aDistance (m) to resources

km², with our resident urban coyotes being on the upper end of that range (Grinder and Krausman 2001b; Grubbs and Krausman 2009; Poessel et al. 2016). Our seasonal home range estimates for non-residents were also large, with non-resident individuals fitted with GPS collars averaging 475.7 ± 67.17 SE km² and reaching a maximum size of 898 km², while other studies in western cities estimated non-resident home range sizes from 63 to 746 km² (Grinder and Krausman 2001b; Grubbs and Krausman 2009; Poessel et al. 2016). We found that infection status did not influence the size of coyote home ranges, which was also observed for rural coyotes at Wind Cave National Park, South Dakota (Chronert et al. 2007), but infected coyotes had home ranges 3.9 times larger than healthy individuals in Edmonton, Alberta (Murray et al. 2015). Diseased coyotes in Edmonton may have been forced to utilize more developed habitats over urban natural areas, resulting in larger home range sizes similar to non-resident coyotes (Murray et al. 2015). Indeed, increased home range sizes for coyotes have been associated with urban development in other highly urbanized environments containing fragmented patches of natural land-cover (Gehrt et al. 2009). Coyotes at the NTC were not constrained

by access to natural land cover, as they could traverse the extent of the garrison within an hour and easily depart urban areas during periods of high human activity. This consistent access to natural cover may have allowed some infected coyotes to utilize anthropogenic resources while maintaining a relatively small and stable home range similar to healthy residents. However, infected coyotes also included individuals with home ranges similar in size to healthy non-resident coyotes, which may suggest that for some infected individuals, short-term use of the anthropogenic subsidies was tolerated, but extended use of the area was not (Newsome et al. 2013).

The high spatial overlap of infected coyotes, whether among other infected residents or non-residents, along with high selection for anthropogenic subsidies, suggests infected individuals were aggregating at these resources, which could promote horizontal transfer of the mite (Bradley and Altizer 2007; Becker et al. 2015). Anthropogenic subsidies may be fostering amicable intraspecific interactions and direct contact as resource enrichment can lead to group formation and increased sociality (Macdonald 1983). Abundant resources have been linked to increases in coyote

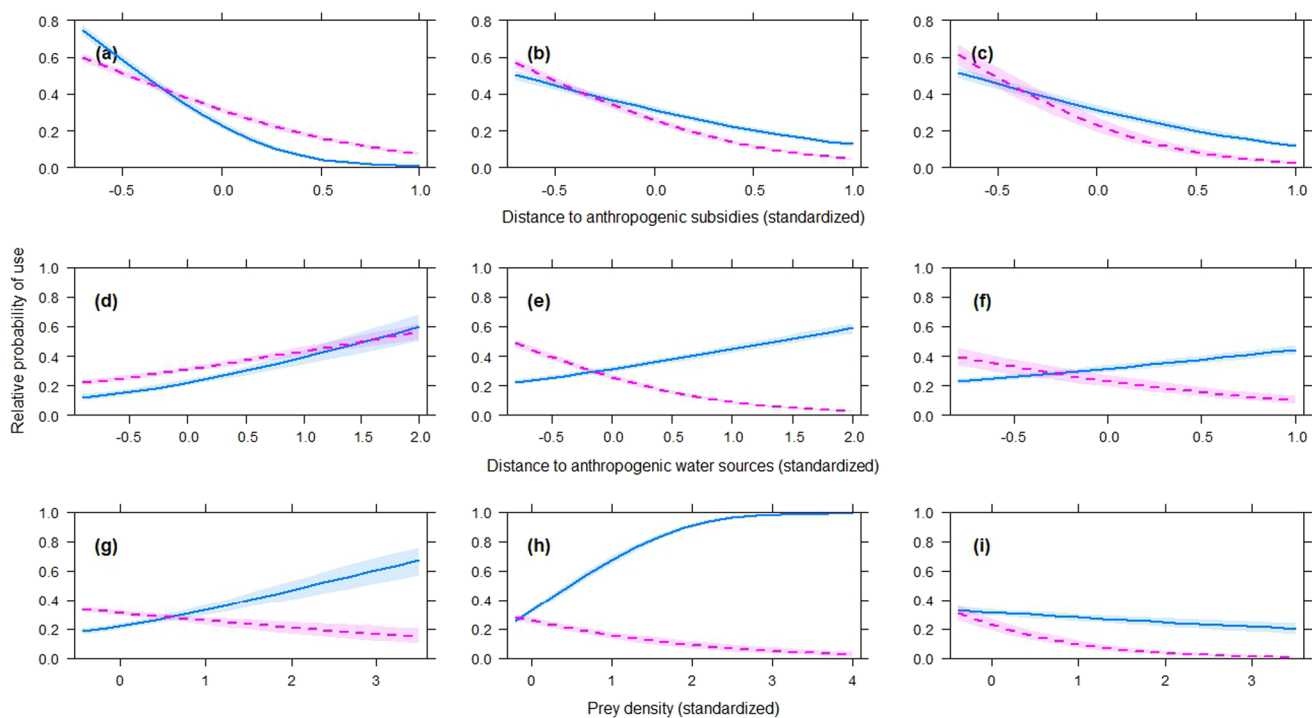


Fig. 3 Interaction plots with 95% CIs of mange status \times distance to anthropogenic subsidies in standardized meters, **a** 2015 wet season, **b** 2016 dry season, **c** 2016 wet season; distance to water in standardized meters, **d** 2015 wet season, **e** 2016 dry season, **f** 2016 wet season; and

standardized prey density, **g** 2015 wet season, **h** 2016 dry season, and **i** 2016 wet season, with blue representing healthy coyotes and pink indicating infected coyotes for the top resource selection models at the NTC Fort Irwin from 2015 to 2017

group size (Hidalgo-Mihart et al. 2004) and increased social tolerance of conspecifics among dingoes (*Canis lupus dingo*; Newsome et al. 2013). We observed as many as 9 coyotes around the compost piles in the garrison, while the largest group observed outside the urban area was only 4 individuals. Conversely, while healthy coyotes selected for anthropogenic subsidies, healthy residents did not exhibit extensive spatial overlap with other coyotes. This suggests that these individuals may have been maintaining territorial boundaries and excluding other coyotes from their home ranges, or perhaps limiting their time around anthropogenic subsidies and potentially reducing exposure to coyotes infected with sarcoptic mange. The lack of overlap with infected coyotes, but the use of anthropogenic resources may suggest that use of these resources could be related to residency status, with healthy residents being less reliant on such resources (Reddell 2018). These results imply that while all coyotes utilized anthropogenic subsidies, the potential for the horizontal transmission of sarcoptic mange may vary depending on an individual's residency status, suggesting an avenue through which intraspecific interactions may spread disease to outlying wildland populations.

The strong selection for anthropogenic subsidies by coyotes may also be a detriment to their overall health and ability to resist the infection, with some of these food subsidies

possibly introducing other avenues for disease transmission. Anthropogenic subsidies have been documented to have variable effects on wildlife, with host immunity increasing or decreasing depending on the nutritional value of the subsidy and physiology of the host (Becker et al. 2015). Urban coyotes in Edmonton, Alberta, were found to consume a greater amount of anthropogenic subsidies and were associated with poorer body condition and greater immune stress when compared to rural coyotes (Sugden et al. 2020). Healthy coyotes exhibited selection for both anthropogenic subsidies and natural prey sources, suggesting they had some flexibility in their diet, while infected coyotes appeared far more reliant on anthropogenic subsidies. Moreover, while coyotes were observed eating garbage and getting handouts from residents, they were most frequently observed feeding on unsecured compost piles located at the garrison's landfill. Similarly, healthy and infected coyotes in Edmonton, Alberta, were attracted to unsecured compost piles, which were protein poor and generally contained high concentrations of mycotoxins (Murray et al. 2015, 2016). Additionally, we observed individuals resting on the larger compost piles throughout the day, which may have provided warmth during colder periods, especially for infected individuals with compromised thermoregulatory abilities due to hair loss (Cross et al. 2016). Consistent use of these piles as bed

sites may also contribute to indirect transmission of the mite, as mites may detach from an infected coyote and survive within these piles until they are utilized by another coyote (Arlian et al. 1989).

The difference between healthy and infected coyotes in regard to their selection for urban water sources suggests that infected individuals may be reliant on these resources, particularly during the dry season. Healthy individuals consistently selected areas farther from water sources, suggesting a lack of dependence on urban water sources. Coyotes in the Sonoran Desert were able to meet their water requirements from preformed and metabolic water obtained from their prey without the need of free water (Golightly and Ohmart 1984). Similarly, Kluever and Gese (2016) found that while anthropogenic water sources may influence a coyote's relative use of an area, they were not requisite for coyote occupation in the Great Basin Desert. Conversely, in 2 of the 3 models, infected coyotes exhibited a positive association with urban water sources, with a stronger relationship exhibited during the dry season when evaporative water loss would be at its greatest due to the extreme heat (Golightly and Ohmart 1984). This suggests that anthropogenic food subsidies may be a poor source of hydration compared to natural food items or that infected coyotes were experiencing greater water loss than healthy individuals, possibly due to the hair loss resulting from the infection.

Healthy coyotes' use of urban areas with increasing prey densities during the 2015 Wet Season and 2016 Dry Season suggests that natural prey can act as a driver of urban use for healthy coyotes, particularly during periods of elevated prey densities, such as the 2016 Dry Season (Online Resource Appendix 2). This increase in prey density was likely influenced by young of the year entering the population and the clustering of lagomorphs around urban water sources and green vegetation (Hayden 1966). During the dry season, we observed clusters of 5 to 12 lagomorphs in areas containing urban grasses (e.g., golf course, residential lawns, etc.) while only observing a maximum of 4 lagomorphs together during the wet seasons. Healthy coyotes may have been attracted to urban areas containing high concentrations of lagomorphs, particularly during the dry season, but utilized non-urban areas or resources when lagomorphs were more dispersed in the wet seasons. The negative association between healthy coyotes and prey density in the 2016 Wet Season may have resulted from lower prey abundance due to below-average precipitation during 2015 (6.78 cm) and 2016 (5.44 cm) (Windberg et al. 1997; Cypher et al. 2018). This area received above-average precipitation during the 2016 Wet Season, exceeding the historical annual average by the end of January 2017 (9.83 cm). This triggered extensive green-up in the surrounding area and may have increased the abundance of prey in outlying non-urban areas, thereby reducing the reliance of healthy coyotes on

urban resources during the 2016 Wet Season. The lack of association between areas with increased prey densities and infected residents further supports the idea that these individuals were reliant on anthropogenic subsidies as their primary food source.

While we believe combining class 0 and 1 coyotes is appropriate given they would likely be more behavioral similar than individuals that are debilitated by more severe infections, we do acknowledge that the transitional state of the infection introduces an additional variable of uncertainty into our results. The progression of sarcoptic mange varies by individual and the level of debilitation brought on by the infection that would engender a marked change in behavior compared to an uninfected coyote is not clear for coyotes designated as class II (Pence et al. 1983; Pence and Windberg 1994; Wilson 2012). Therefore, it is possible that some individuals identified as class I may have transitioned to a more severe state, while it is also possible that individuals identified as class II may have recovered or did not suffer from a level of debilitation that would alter their behavior during our study. Future studies examining the transitioning of infection states using mark re-sight methods with dedicated observers or remote cameras (Murray et al. 2016; Brewster et al. 2017) would be ideal for reducing this uncertainty and assessing how these transitions alter space use and resource selection at a finer scale.

Conclusions

Our results revealed that anthropogenic subsidies can act as drivers of urban use for coyotes, and because residents infected with sarcoptic mange have home ranges that overlap non-resident individuals, aggregation around these subsidies may increase transmission rates to susceptible hosts. Yet, healthy coyotes may limit their exposure to infected individuals by defending territories and using natural prey that may not be available to moribund individuals infected with mange. To mitigate the spread of mange, resource managers may consider implementing measures to prevent access to key anthropogenic resources for all coyotes. For example, reducing access to compost piles and water sources by infected individuals may result in higher mortality, which could help curb transmission of the disease, and reducing access to these resources for healthy coyotes may lower their potential exposure to infected individuals. As more natural habitats are altered through human development and urbanization, natural resource managers and public health officials may benefit from a greater understanding of how wildlife utilize urban resources to minimize the impact of epizootics on wildlife populations and limit the impact of potential zoonoses on public health.

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Declarations

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

Ethical approval Capturing and handling was approved by the IACUC of NMSU (Protocol # 2015-001) and the California Department of Fish and Wildlife (Permit # 2330).

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