Desert Tortoise Predator-Prey Dynamics in the Boulder City Conservation Easement

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Desert Tortoise Predator-Prey Dynamics Final Report

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Cover Figure: Photos of a Mojave desert tortoise (*Gopherus agassizii*), black-tailed jackrabbit (*Lepus californicus*), and coyote (*Canis latrans*) overlaid on a satellite image of the Boulder City Conservation Easement, Clark County, Nevada. Figure created by Gabrielle Berry, U.S. Geological Survey (USGS). Photos taken by a USGS camera trap on October 15, 2022, Berry on April 14, 2022, and a USGS camera trap on December 24, 2020, respectively, all within Clark County.

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EXECUTIVE SUMMARY

From February 2018 through December 2021, the U.S. Geological Survey's Western Ecological Research Center conducted an ecological study of predator and prey interactions in the Boulder City Conservation Easement (BCCE) in Clark County, Nevada. This study was prompted by questions about the predator-prey relationship between coyotes (*Canis latrans*) and black-tailed jackrabbits (*Lepus californicus*) and how they may affect variability in predation rates on Mojave desert tortoises (*Gopherus agassizi*). Fluctuations in the abundance of prey species have been linked with predation pressure on desert tortoises (Esque et al. 2010), however, key aspects about the underpinnings of hypothesized interactions were not quantified. For example, drought conditions were hypothesized to have triggered declines in jackrabbit populations but rabbit densities were not quantified. The overall project objective was to investigate the ecology of coyotes in relation to their presumed primary prey, the black-tailed jackrabbit and quantify their interactions. Specific project objectives and goals included:

- 1. Determine variability in the demographics of coyotes and black-tailed jackrabbit populations in the BCCE.
- 2. Determine the movements, home range, and habitat use patterns of coyotes and black-tailed jackrabbits in the BCCE.
- 3. Determine the health status and mortality rates of coyotes and black-tailed jackrabbits in the BCCE.
- 4. Develop reliable and cost-effective methods of estimating density of coyotes and black-tailed jackrabbits.
- 5. Analyze black-tailed jackrabbit abundance and predator densities and movement data to inform management of the BCCE.

Project activities included:

- **Spotlight transect surveys** Forty-two monthly nocturnal surveys were completed to evaluate prey species abundance and distributions 11 surveys in 2018, 12 surveys in 2019, 9 surveys in 2020, and 10 surveys in 2021. A total of 9 species or species groups (i.e., rodents) were observed.
- **Camera traps** Grid cameras (n = 40) placed at random locations in the BCCE detected a total of 41 species of mammals, birds, and reptiles. Cameras (n = 60) strategically placed in travel corridors and washes in the BCCE and surrounding areas detected a total of 63 species.
- Jackrabbits captures 185 jackrabbits were trapped and marked, with GPS collars yielding >95,000 data points. The primary cause of mortality was predation. No evidence for die-offs related to disease, either RHDV2 or other illnesses often associated with jackrabbits (e.g., tularemia, Rocky Mountain spotted fever), were observed. Two social status categories were identified that were previously unidentified for black-tailed jackrabbits residents versus transients. The social status of rabbits and their movements on the landscape may provide new insights to rabbit habitat use and reproductive ecology.
- **Coyotes captures** Twenty-one coyotes were trapped and marked, with GPS collars yielding >60,000 data points. Coyote survival was high, with hunting and vehicle collisions as the primary causes of mortality. To date, coyotes were generally unresponsive to fluctuations in jackrabbit densities. They may have a lag time in their

response, or anthropogenic subsidies may be contributing to their resistance to prey availability fluctuations.

INTRODUCTION

Clark County, Nevada strives to protect and manage Mojave desert tortoises (*Gopherus agassizii*) and their habitats in the Boulder City Conservation Easement (BCCE) through the Clark County Multiple Species Habitat Conservation Plan (Clark County 2000; Clark County 2021). Mojave desert tortoises are a federally Threatened species and recovery efforts are being implemented in Clark County, Nevada. The Desert Conservation Program (DCP) of the Clark County Department of Air Quality maintains compliance with the Endangered Species Act through a Federal permit for activities under the CCMSHCP in Clark County 2015). As part of the MSHCP tortoises are removed from harm's way in development areas, and some of those tortoises were translocated to suitable habitats in the BCCE (Nussear et al. 2009), and subsequently monitored by Clark County using radio-telemetry.

This project was designed to gain a better understanding of the dynamics and community interdependencies between the desert tortoise's primary predators – coyotes (*Canis latrans*) – and the coyote's primary prey – black-tailed jackrabbits (*Lepus californicus*). Using that information, the goal is to inform a strategy to mitigate future translocations from being severely impacted by coyote predation on desert tortoises.

Previous tortoise monitoring indicates that since the translocation of tortoises into the BCCE, the rates of mortality on the translocated and native populations of the Mojave Desert tortoises in the BCCE have increased and this has caused concern for tortoises. High levels of mortality occurring sporadically within the range of the Mojave desert have caused concern elsewhere in the American southwest. Although the exact causes for mortalities are difficult to determine without eye-witness accounts or unusually fine capture resolution, previous research indicates that coyote (*Canis latrans*) predation on desert tortoises can be widespread and locally intensive across the Mojave Desert (Esque et al. 2010). In the conclusion of that study, intensive coyote predation on tortoises was likely the result of a widespread decline in black-tailed jackrabbit (*Lepus californicus*) populations related to drought conditions. As a result of the decline in their primary prey item of jackrabbits, coyotes were thought to have switched from their preferred prey of jackrabbits to desert tortoises. Furthermore, it was hypothesized that coyote populations in proximity to human populations do not decline as readily with the loss of rabbits in wildlands because of food and water subsidies provided at the urban interface (Esque et al. 2010).

There are at least two alternative hypotheses to the prey-switching hypothesis. First, that fluctuations in lagomorph populations often result in subsequent changes in coyote populations (Clark 1972, Stoddart et al. 2001). A second alternative is that the life history strategy of desert tortoises is to survive through drought; however, under severe drought conditions, desert tortoises also succumb to drought, exacerbated by infections by *Mycoplasma* bacteria that cause Upper Respiratory Tract Disease (URTDS; Sandmeier et al. 2009). Furthermore, kill sites can be difficult to distinguish from scavenging activity by carnivores, particularly in multi-carnivore systems, if visual examinations are relied upon without companion species-typing of carnivore salivary DNA swabbed from prey carcasses, or if mortalities are not promptly investigated (Blejwas et al. 2006, Kilgo et al. 2012). In addition to coyotes, American badgers (*Taxidea taxus*) and mountain lions (*Puma concolor*) are also known to prey on adult tortoises in the Mojave Desert (Emblidge 2012, Greger and Medica 2009), but mountain lions, coyotes, kit foxes

(*Vulpes macrotis*), bobcats (*Lynx rufus*), and badgers all have been documented engaging in scavenging of prey species killed by conspecifics or other ultimate causes (Bauer et al. 2005, Platt et al. 2010, Rogers et al. 2014, Frehner et al. 2017, Beasley et al. 2019). Furthermore, spotted skunks, ringtails (*Bassariscus astutus*), and ground squirrels (*Ammospermophilus leucurus, nd Xerospermophilus tereticaudus*, respectively) and other rodents have been observed at sites baited with meat and are also likely tortoise scavengers. All of those carnivorous species reside in and around the BCCE (this report) and therefore could potentially prey on or scavenge tortoises killed by other causes. While there is an abundance of speculation about the causative agents of tortoise mortality, most of the discussion regarding causation is speculative and anecdotal; yet, there are no doubt losses of desert tortoises in the BCCE and that some level of coyote predation occurs (Terry Christopher – unpublished data; Esque et al 2010).

Recently, concern has increased regarding the rates and causes of presumed coyote predation on a translocated population of the Mojave Desert tortoise in the BCCE. The Clark County Desert Conservation Program is currently working on projects investigating the presence of subsidized predators (coyotes and ravens [*Corvus corax*]) on the BCCE to determine what effect they may be having on the tortoise population in the area. However, very little research has been done in the Mojave Desert to study the demographics, distribution, movement patterns, and habitat use and ecology of coyotes in concert with their primary prey species, black-tailed jackrabbits.

This project expands investigations of predator and prey relationships toward further understanding the results derived from this broader predator distribution investigation of the greater BCCE. The project provides data-driven insights into predator and prey population dynamics, habitat use, and health that are relevant to an ecologically based program directed toward the successful management of the BCCE as a sustainable habitat reserve. Additionally, as translocated desert tortoises in the BCCE are already intensively monitored, this presents a unique opportunity to evaluate the interactions of a monitored population of translocated desert tortoises in the context of a concurrent study of coyote and jackrabbit interactions via a camera trap network, marked animals, and Global Positioning System (GPS) / Very High Frequency (VHF) collared coyotes and black-tailed jackrabbits. Monitoring of predator and prey populations should improve the ability to make informed management decisions regarding desert tortoise translocations in the broader ecological context of predator-prey interactions in the BCCE, southern Nevada, and contribute to desert tortoise conservation in the greater Mojave Desert.

The primary goal of this project was to gain a better understanding of the population dynamics and community interdependencies of one of the desert tortoise's primary predators, coyotes, and to develop a strategy to mitigate future translocations from being severely impacted by coyote predation. To accomplish this goal, we implemented a study with the following 5 objectives: 1) estimate demographic variability of coyotes and jackrabbits; 2) estimate the home range size and habitat use patterns of coyotes and jackrabbits; 3) determine the health status and estimate survival and cause-specific mortality rates of coyotes and jackrabbits; 4) evaluate reliability of methods for estimating population density that are cost effective; and 5) synthesize jackrabbit and coyote demographics and spatial ecology.

METHODS

Study Area

The study area encompasses the entire BCCE, a large land parcel within the city limits of the municipality of Boulder City, and managed by Clark County, NV, as part of its Multispecies Habitat Conservation Plan (Figure 1). We defined our study area for analysis purposes as a 95% Kernel Density Estimation of all coyote GPS points, plus a five km buffer. The area is bounded to the north by a power utility easement and Interstate Highway 11, to the east by the Eldorado Mountains, to the south by BLM lands and the Highland Range, and to the west by solar plants, the Highland Range, and the McCullough Mountains. The BCCE is roughly bisected by US Highway 95 and contains two other paved roads: the Nelson Road and a service road to providing access to extensive solar fields also occupying a considerable amount of lands adjacent to the easement. Graded service roads accompany major power transmission lines and a system of dirt access roads exist that are marked as "open", while other roads are marked "closed". A considerable amount of unauthorized off-highway vehicle use occurs within the study area as social trails.



Figure 1. Map depicting the study area including the Boulder City Conservation Easement and a buffer, near Boulder City, Nevada.

There are four primary habitat types available to coyotes and jackrabbits in the BCCE. Upland habitats are the predominant landform occurring from the upper bajada (outwash plain) to the valley bottoms and excluding major washes. Interconnected dendritic or major washes occur among the upland habitat types. With heavy rain, there is overland flow that runs across both habitat types. One large wash system drains from east to west in the northern one-half of the BCCE; a second major wash drains from south to north in the southern half of the BCCE; and there is a third major watercourse draining McCullough Pass from the west toward the Eldorado Dry Lake. There are a few rocky outcrops within the BCCE, and rocky hills and mountainous terrain surround the BCCE. Effluent from the Boulder City Utilities Department creates a manmade habitat that is used by coyotes and jackrabbits. Coyotes and jackrabbits use a fifth habitat type – the urban/wildland interphase– this habitat type is outside the BCCE proper but has a large influence on the coyotes, and this habitat is important to this study.

Vegetation within the BCCE is primarily a creosote bush and white bursage (Larrea tridentata and Ambrosia Dumosa; respectively) shrubland association with upland habitats of the bajadas and rocky hills. The BCCE also encompasses some of the rocky hill areas on the eastern, southern, and western boundaries. Vegetation on the rocky hills is similar to the flatter areas with minor variation, including greater shrub diversity. A variety of other perennial shrubs (e.g., Mormon tea - Ephedra nevadensis, turpentine bush - Thamnosma montana, desert trumpet -Eriogonum inflatum, range ratany - Krameria erecta, spiny hopsage - Gravia spinosa, bladder sage - Salazaria mexicana, wild buckwheat - Eriogonum fasciculatum, tarbush - Ericameria cooperi) and cacti (e.g., staghorn cholla - Cylindropuntia acanthocarpa, beaver tail prickly pear -Opuntia basilaris, hedgehog cactus - Echinocereus englemannii, pineapple cactus - Escobaria chlorantha, and fishhook pincushion cactus - Mammilaria tetrancistra) are present. A large, isolated patch of teddy bear cholla (Cylindropuntia bigelovii) occurs near the western boundary of the BCCE, and scattered Joshua trees (Yucca Jaegeriana) at higher elevations. There are also robust populations of native winter annuals (e.g., Chaenactis fremontii, Phacelia fremontii, *Cryptantha* spp., *Eriogonum* spp., *Erodium texanum*, *Chorizanthe rigidus*, *C. thurberi*, Chylismia brevipes) and summer annual (Pectis papposa, Kallstromia sp., Bouteloua spp., *Portulaca* sp., *Boerhavia* spp.) plant species that are expressed when precipitation is sufficient for growth.

Invasive species that are of concern in the BCCE include red brome (*Bromus rubens*), Sahara mustard (*Brassica tournefortii*), russian thistle (*Salsola* spp.), and tamarisk (*Tamarix ramosissima*). Major wash systems are lined intermittently with small trees and shrubs (1-3 m tall) of catclaw acacia (*Senegalia greggii*), desert almond (*Prunus fasciculatum*), cheesebush (*Ambrosia salsola*), and desert broom (*Baccharis* spp.). Where the washes drain from rocky hills, in the east, south, and west, desert willow trees (*Chilopsis linearis*) up to 4 m tall exist. The wash system drains toward Eldorado Dry Lake to the west with very fine silt and clay accumulations on the western edge of the North section of the BCCE. One unique habitat type is the thicket of mostly invasive plants that creates a dense corridor at the effluent for the Boulder City Municipal Sewage Treatment plant. Besides many invasive species, there are a few cottonwood (*Populus fremontii*) trees there.

The Eldorado Mountains are of volcanic origin and most of the bedrock is basalt. The Highland Range is also mostly volcanic with rhyolites with some tufa layers. The McCullough Mountains, in the vicinity of McCullough Pass, are igneous and mostly granitic with volcanic intrusions, and there are some metamorphic outcrops of mica schist. Soil textures range in a

gradient from undifferentiated bedrock and boulders or talus on the mountains and hills to the finest silts and clays in the valley bottom. Soils in the valley are well-mixed igneous and metamorphic layers and many areas have well-developed caliche layers that provide good substrate for caliche caves, which may also provide shelter/cover for wildlife. Soils in the valley bottom are highly friable with a high density of mesopredator burrow complexes that are visible in an aerial view. Eldorado Valley is a closed valley with the terminus of Eldorado Dry Lake.

Capture and monitoring

Coyotes

Coyotes were baited to capture sites where we set foothold traps (Minnesota Brand, MB-550-RJ). Bait sites were established in areas that indicated regular coyote use and were often in washes. Bait sites were also selected to minimize interactions with the public and the probability of encountering domestic pets and other non-target species. Foothold traps have been used extensively to capture coyotes safely and successfully (*reviewed by* Schemnitz et al. 2009 and Shivik et al. 2010). Bait sites were pre-baited for 1-3 weeks before trapping was initiated. After some early trapping activities, we refrained from placing cameras at the prospective trap sites because the coyotes were disturbed by their presence, as indicated by coyotes staring into the camera as they were photographed. Sites were baited with salvaged roadkill deer (NDOW scientific collection permit #39800) and commercially raised chicken. Following repeated coyote use and dominance of bait sites, traps were placed and opened at last light of the day.

Lead personnel involved in the handling and immobilization of coyotes attended and completed training by a licensed veterinarian, Dr. Mark Johnson of Global Wildlife Resources LLC. ACUC approval for all aspects of the field study involving animal handling was obtained and all field procedures follow American Society of Mammalogists guidelines for field studies (Sikes et al. 2016). When a covote was captured, we immobilized the captured individual as quickly as possible to minimize stress. Coyotes were immobilized using a recommended dosage of 2 mg/kg of Ketamine and 0.07 mg/kg of Medetomidine. Immobilization drugs were administered by hand injecting the solution of Ketamine and Medetomidine into a caudal muscle after using a "Y" pole to restrict the animal's movements. Following administration, we waited 15 minutes for the drugs to take effect. Once the animals were fully anesthetized, coyotes were removed from the traps, restrained, and placed on ground sheets. Coyotes were then processed by fitting a VHF/GPS collar (Lotek, Litetrack Iridium 250 or Lotek, Litetrack Iridium 360), placing numbered vinyl ear tags, as well as recording the sex, weight, morphometric measurements, and age class of the coyote. Age was estimated by using tooth wear as an indicator (Gipson et al. 2000; Figure 2). Coyote safety under anesthesia was maintained by frequently taking body temperature readings. Any abnormally high temperature reading was mitigated by treating the animal with cold water and increasing ventilation. Abnormally low temperature readings were mitigated by wrapping the animal in a thick blanket. After processing the animal, the anesthetizing agent was reversed with 0.35mg/kg of the Medetomidine antagonist Atipamezole. Coyotes were then released promptly at the site of capture and observed postrelease to ensure the effects of immobilizing drugs had dissipated. Total handling time for covotes was thirty minutes to one hour.



Figure 2. Chart of progressive wear on coyote incisors in 2-year increments used to age live animals in the field (Gipson et al. 2000).

<u>Coyote VHF/GPS collars</u> - VHF/GPS collars attached to the coyotes were one of two similar models, either Lotek Litetrack Iridium 250 or 360. Only adult and sub-adult coyotes >8kg total weight were fitted with GPS collars. The deployed VHF/GPS collars were programmed to collect a location fix every 3 hours, except during the first five days of each month, during which they collected fixes at 1-hour intervals. Captured coyotes received unique ear tags to permanently identify them in the event of recapture or collar drop-off. All collars placed on coyotes were equipped with an electronic release mechanism to facilitate release or "dropping" of collars without further capture and handling. This release mechanism allows for a timed release at or near the conclusion of field work, prior to GPS battery depletion.

<u>Coyote health status</u> - We evaluated coyote health status during capture events by searching captured individuals for parasites, recording their weight, and assigning a body condition score based on their muscle mass and fat stores. Body condition scores were assigned as a value of one through five, with one corresponding to an emaciated animal in very poor health, and five being an obese animal with large fat reserves.

Black-tailed jackrabbits

Black-tailed jackrabbits were captured using two different types of box traps (Tomahawk Model#109 15×15×42 inches, and Comstock Custom Cages 12×15×30 inches), each of which employ different triggering mechanisms. Comstock traps use trigger wires that lie between the trap entrance and the bait, and the wires must be moved to trigger the trap. Tomahawk traps use a treadle pan placed between the trap entrance and the bait, and the pan must be stepped on to trigger the trap. Traps were set in washes, at lagomorph dust bath sites, and in other areas with

heavy jackrabbit use indicated by sign, such as scat accumulations. Box traps have been successfully used to capture jackrabbits (Smith 1990, Balph 1971, Rusch 1965, Tiemeier 1965, Lechleitner 1958) as well as other hare species globally (Schai-Braun et al. 2012, Bisi et al. 2011).

Trap sites were pre-baited for 5-10 days before trapping was initiated. Traps were typically baited with apples, though other bait sources, such as hay and carrots, were also tried in the BCCE. Traps were opened in late afternoon or early evening and remained open until each trap was checked, at which point all traps were deactivated by wiring the trap doors open. This was done so that animals could still enter the traps and access bait but would no longer be captured after entering a trap. Initially, we checked traps near sunrise, allowing an entire night for traps to be open and set for rabbit captures. However, we observed that trapped jackrabbits exhibited substantial agitation and stress in the early morning sun. After evaluating this observation, we changed methods so that traps were checked starting at 1 am, while it was still dark. The countenance and physical condition of trapped jackrabbits considerably improved when processing occurred at night. Considering the increase in jackrabbit welfare by shortening trap check times, we further modified methods by attaching trap transmitters to jackrabbit traps. These transmitters signaled when a trap was triggered and allowed personnel to arrive at a trap just a few minutes after an animal had been captured.

When a jackrabbit was captured, we immediately covered the trap with a blanket to calm the captured animal. Jackrabbits were removed from the box traps by placing a hand on the scruff of the neck with ears laid flat along the back, and a second hand grasping the animal just in front of the pelvis. This allowed the animal to be lifted from the box trap without injury (Tiemeier 1965). Upon removal from traps, jackrabbits were restrained in a cloth bag or pillowcase to facilitate marking procedures, sample collections, and measurements (Altemus 2016). We placed a hood on the jackrabbit that incorporated a modified sock with attached ear plugs, which was placed over the jackrabbits' face to limit visual and auditory stimuli. After placing the hood, we began by fitting the animal with a GPS collar and placing numbered vinyl ear tags. Following that, we recorded the sex, weight, and age class of the jackrabbit. Finally, when necessary, we collected parasites and blood samples. Total handling time for the jackrabbits was ideally <15 minutes from covering the trap with a blanket to releasing the animal.

<u>Black-tailed Jackrabbit VHF/GPS collars</u> - Collars on jackrabbits have been used frequently as a method to study populations (Smith et al. 2002, Smith 1990, Stoddart 1970, Knowlton et al. 1968, Harrison 2019). If collar materials are not unduly stiff, they do not appear to have adverse effects on jackrabbit health or behavior (Wywialowski and Knowlton 1983). We used three varieties of tracking devices on jackrabbits. Only adult and sub-adult jackrabbits >1750g total weight had GPS collars attached. Short-term collars were built using Holohil VHF collars in combination with IgotU GPS loggers and weighed 55g (Johnston et al. 2014). We deployed up to 25 of these short-term collars programmed to obtain GPS location fixes every 0.5 hr for up to 6 weeks to obtain fine scale measurements of habitat use and movements within 24hour periods. Long-term collars were made by Sirtrack (model# Litetrack RF30) or Telonics (model# TGW-4000-4). In 2019, we deployed 10 Litetrack RF30 collars (35g total weight) programmed to obtain GPS location fixes every three hours for up to 12 months. In 2020 and 2021, we deployed 10 Telonics 4000-4 collars (55g total weight) programed to obtain GPS location fixes every four hours for up to 12 months to observe movements of individual jackrabbits over multiple seasons. All collars placed on jackrabbits were equipped with a mechanism to facilitate release or "dropping" of collar to avoid further capture and handling. An electronic timed release to drop the collar was unavailable due to weight and technological constraints, so the rabbit collars were equipped with a release mechanism made of cotton panels or latex tubing. These materials gradually deteriorate, resulting in the release of the collar during the course of the study (Collins et al. 2014, Garshelis and McLaughlin 1998). All trapping and handling methods were reviewed and approved by U.S. Geological Survey IACUC and conformed with recommendations in Sikes et al. (2016).

Jackrabbits were tracked and monitored using traditional radio telemetry once every 7-10 days. Rabbits were tracked to remotely download data from the UHF-equipped Sirtrack long-term collars in 2019. They were also tracked to quickly find any collars that had dropped due to deterioration of drop off devices or to identify causes of any observed mortalities, data which were used for survival analyses.

<u>Data collection on captured black-tailed jackrabbits</u> - Black-tailed jackrabbits that we captured also received uniquely numbered color-coded ear tags to permanently identify them in the event of re-encounter (McGregor and Jones 2016). Ear tags have been used in many studies to mark jackrabbits (Lechleitner 1958, Tiemeier 1965), and there have been no reported incidents of undue distress by the jackrabbits regarding the tags. Most studies report minimal tag loss over time.

We aged jackrabbits based on several criteria, including weight. Animals <1.8 kg were considered sub-adults based on published values of black-tailed jackrabbit growth and development (Haskell and Reynolds 1947), the presence of well-developed reproductive organs (large, dark, prominent testes or evidence of lactation), and to a lesser degree on our own observations gained through our handling experiences. We observed that sub-adults and juveniles had "short" faces with a faint white dot on their forehead, a generally lighter and smoother coat, and finely furred, largely unblemished ears. We relied heavily on the presence of reproductive activity, in conjunction with animal weight, and our observations of sub-adult jackrabbit appearance.

<u>Black-tailed jackrabbit health status</u> - We evaluated black-tailed jackrabbit health status during capture events by searching them for parasites and recording their weight. Body condition scores were not assigned for jackrabbits due to the difficulty in deciphering the small differences between those jackrabbits in poor condition and those in good condition.

Home range size

Coyotes

We subset the coyote tracking location data by individual, sex, season, and year to estimate sex-specific seasonal home range sizes across years. Two seasons were specified, summer (May 1–October 31) and winter (November 1–April 30), based on long-term climate data recorded by the Boulder City, NV monitoring station (Western Regional Climate Center 2022). These season delineations reflected considerable temperature and vegetation changes in the study area and coincide with the typical coyote non-breeding (summer) and breeding (winter) seasons, between which coyote movements and home range sizes are expected to differ (Laundré and Keller 1984, Gese et al. 1988). Additionally, coyote populations are typically comprised of two primary behavioral classes, residents and transients (Gese et al. 1988). The classification of residency and transiency, if not accounted for, can bias estimates of population-scale demographics and habitat use/selection (Kamler et al. 2005, Hinton et al. 2015, Murphy et al.

2018). Therefore, we further subset the coyote data by residency status based on empirical variograms of the autocorrelation structure of the location data, which allowed us to identify residents versus transients (Fleming et al. 2014a, 2015; Averill-Murray et al. 2020; Karelus et al. 2021; Figure 3).



Figure 3. Variogram examples of the autocorrelation structure in GPS collar location data from a resident coyote and a transient coyote in our study. Residency is evident when the semi-variance plateaus across time, indicating an individual had an established home range, whereas transiency exists when the semi-variance increases across time, often linearly, indicating an individual did not have an established range.

We first calculated empirical variograms that estimated semi-variance as a function of time lag to visualize the autocorrelation structure of the location data for each individual within each season (Fleming et al. 2014a,b; 2015). The GPS collar fix rate intervals varied within each month, such that fixes were obtained every 1 hour during the first 5 days of each month and fixes were obtained every 3 hours during the remainder of each month; therefore, we specified corresponding lag bin widths that were aggregated in the variogram calculations to account for this irregular sampling (Fleming et al. 2018). We then fit isotropic and anisotropic versions of the following continuous-time movement models via perturbative hybrid residual maximum likelihood, using starting values from the calculated variograms (Fleming et al. 2015): Ornstein-Uhlenbeck (OU; Uhlenbeck and Ornstein 1930), Integrated Ornstein-Uhlenbeck (IOU; Gurarie and Ovaskainen 2011), and Ornstein-Uhlenbeck-Foraging (OUF; Fleming et al. 2014b). We performed model selection using Akaike's Information Criterion corrected for small sample size (AIC_c) to identify the 'best' movement model (Burnham and Anderson 2002). From the topranked movement model (i.e., $\Delta AIC_c = 0.00$), we estimated home range sizes with 95% optimally Weighted (to account for the aforementioned irregular sampling [Fleming et al. 2018]) Area-Corrected autocorrelated Kernel Density Estimated utilization distributions (wAKDE_c; Fleming et al. 2015, Fleming and Calabrese 2017). We fit all movement models and estimated 95% wAKDE_c home ranges using the *ctmm* package in the R statistical computing environment (Calabrese et al. 2016, R Core Team 2022).

Black-tailed jackrabbits

Individual jackrabbits were outfitted with collars that had 3 different fix rates: Short-term collars with 1-hr fix intervals, long-term collars with 3-hr fix intervals, and long-term collars with 4-hr fix intervals. In contrast to the coyote collars, those differing fix rates were not applied uniformly to all jackrabbits or across time. Therefore, to prevent bias in home range size estimates that could be caused by uneven sampling (fix rates) among individuals, we thinned the

location data for all short-term collars to 3–4-hr fix intervals. Because of short monitoring durations and small effective sample sizes (total number of times an individual crossed the extent of its home range; Fleming et al. 2019), we could not estimate annual home range sizes for most jackrabbits and therefore estimated seasonal home range sizes only.

We employed the same general analytical approach for estimating jackrabbit home range sizes as we did for estimating coyote home range sizes, using continuous-time movement models and AKDE_c. However, there were two notable differences: 1) we did not specify differing lag bin widths when calculating variograms for jackrabbits because we thinned the location data to 3–4-hr fix intervals for all individuals; and 2) we did not weight the AKDE_c estimation for jackrabbits because the sampling was not irregular following said data thinning. Similar to the coyote home range size estimation, we fit isotropic and anisotropic versions of continuous-time movement models via perturbative hybrid residual maximum likelihood estimation, using starting values from the calculated variograms (Fleming et al. 2015). We performed model selection based on AIC_c (Burnham and Anderson 2002), and, from the top-ranked model for each individual (i.e., $\Delta AIC_c = 0.00$), we estimated home range sizes with 95% AKDE_c (Fleming et al. 2015, Fleming and Calabrese 2017). We fit all movement models and estimated 95% AKDE_c home ranges using the R package *ctmm* (Calabrese et al. 2016).

Factors influencing home range size

To test if home range sizes varied at the population level by demographic and ecological factors, we fit generalized linear mixed effects models to the coyote $wAKDE_c$ -estimated 95% home range sizes and generalized linear models to the jackrabbit $AKDE_c$ -estimated 95% home range sizes. Negative-binomial error distributions were specified because the estimated home range sizes exhibited overdispersion (Booth et al. 2003). In all coyote models, we specified random intercepts for individual to account for within-individual clustering of the data caused by multiple home range sizes being estimated for most individuals (Booth et al. 2003, Harrison et al. 2018). In contrast, few jackrabbits had multiple home range sizes estimated, so random intercepts for individuals were excluded from the jackrabbit models. In both the coyote and jackrabbit models, we also included random intercepts for year to account for the potential dependency of home ranges within a given year. We fit models that included three-way interactions among season, sex, and residency status or two-way interactions between sex and residency status. We fit all models using R package *glmmTMB* (Brooks et al., 2017).

Habitat selection

Location data processing

For both species, we developed resource selection functions to estimate habitat selection within the home range (i.e., third-order selection [Johnson 1980]) in a use versus availability design (Boyce et al., 2002, Manly et al. 2002, Duchesne et al. 2010, Northrup et al. 2013). We first subset the data for each species by season (the same summer vs. winter delineations used in the home range analyses described above) and year to allow us to estimate season-specific habitat selection within each year. Next, we removed locations from the datasets if they were outside the boundary of the study area. We then filtered the coyote locations by satellite fix status and position dilution of precision (PDOP), removing all locations that were obtained with <3D satellite fixes and PDOP > 4. Collectively, the removal of locations based on the study area boundary, satellite fix status, and PDOP resulted in a 23% reduction of location sample sizes for coyotes. Constraints in GPS technology available to deploy on jackrabbits restricted our ability

to filter jackrabbit locations in the same fashion. When technology allowed, we filtered jackrabbit locations to remove locations that were obtained with <3D satellite fixes. To delineate habitat availability areas for each individual, we constructed minimum convex polygons (MCP) around each individual's season-specific locations within a given year using the R package *adehabitatHR* (Calenge 2006). Within each MCP, we generated 1 random available location for every known used location via the R package *sp* (Pebesma and Bivand 2005, Bivand et al. 2013); in other words, if an individual had 1,000 known used locations within a season within a year, then 1,000 random available locations were generated within that individual's MCP for the season within the year.

Habitat covariates

We hypothesized that 8 covariates may be important for predicting habitat selection of both coyotes and jackrabbits. Surface texture (ATI) was the difference in mean daytime and night-time surface temperatures for 2001-2010 (Inman et al. 2014, Nowicki et al. 2019). The "vector ruggedness measure local" covariate (VRML) depicted topographic ruggedness using Shuttle Radar Topography Mission data and a modified version of the vector ruggedness measure (Sappington et al. 2007, Dilts et al. In Prep). The terrestrial development index (TDI) quantified the level of development (urban, agriculture, energy and mineral extraction and transmission, and transportation, Carr et al. 2017). Elevation (meters), slope (degrees), and topographic position index (TPI) - a steady-state wetness index expressed as a function of slope and upstream contributing area - were calculated using a 30-m² digital elevation model (National Elevation Dataset, https://apps.nationalmap.gov/downloader). The normalized difference vegetation index covariate (NDVIamp), incorporating plant canopy data from the moderateresolution imaging spectroradiometer (MODIS) satellite (https://modis.ornl.gov/globalsubset), represented the 16-day average maximum NDVI minus the average minimum NDVI, which captured fine-scale spatiotemporal variation in vegetation productivity (Julien and Sobrino 2008). We created a distance from water (dWater) covariate by first geolocating each natural spring and anthropogenic guzzler within the study area on foot. We then combined those locations with publicly available data on water sources in the study area (e.g., Lake Mead) and calculated the distance (meters) of the centroid of each raster cell from all water sources. Prior to data extraction, we cropped the rasters for all covariates to the study area boundary and standardized the resolution of all rasters to 250 m for coyotes and 90 m for jackrabbits, which reflected discrepancies in home range sizes and therefore use areas of the two species.

Exploratory analyses

For each used and available location, we extracted values of said covariates using the R package *raster* (Hijmans and van Etten 2012), after which we standardized and centered the extracted values of all covariates. Prior to analysis, we investigated correlation among covariates to prevent the consequences of multicollinearity in our models (Zuur et al. 2010). Using the R package psych (Revelle 2022), we calculated pairwise Pearson correlation coefficients among all covariates for each season within each year. We conservatively excluded covariates from the same model if $-0.50 \le r \ge 0.50$; although most previous habitat selection studies used absolute r > 0.60 or r > 0.70 as cutoffs, we chose 0.50 because recent research has demonstrated that even weak-to-moderate pairwise correlation between two predictors can cause significant multicollinearity effects in regression models (Vatcheva et al. 2016, Kim 2019). Based on our exploratory correlation analyses, we excluded elevation and slope from all models because of high correlation with the TPI and ATI covariates; we note that both TPI and ATI used elevation

and slope in their calculations. Additionally, because of high correlation between TPI and ATI, we excluded those two covariates from the same models to prevent multicollinearity effects.

Model fitting, selection, and validation

We fit species-specific, season \times year-specific generalized linear mixed effects logit models to estimate the probability of use as a function of biological, ecological, and geographical covariates (Duchesne et al. 2010, Northrup et al. 2013). Within each model, we specified random intercepts for individuals and included a fixed effects interaction between the categorical variables sex and residency status, as well as a singular fixed effect for the distance to water covariate. This base model structure from which all other models were constructed represented: 1) explicit accounting for the autocorrelation (i.e., dependency) among locations for a given individual; 2) potential differences in habitat selection between residents and transients of each sex (Hinton et al., 2015); and 3) likely considerable importance of surface water proximity in shaping habitat selection in the desert environment of the study area. We fit a suite of 24 a priori habitat selection models using the R package glmmTMB (Brooks et al. 2017) and specified binomial error distributions in each model to compare used versus available locations. We used AIC_c for model selection and considered all models $\leq 2 \Delta AIC_c$ of the top-ranked model as competing (Burnham and Anderson 2002). We evaluated competing models for uninformative parameters and, if detected, removed models that contained the offending covariates from consideration (Arnold 2010, Grueber et al. 2011). We conducted model validation of the topranked, most parsimonious model for each season within each year using k-fold cross-validation implemented via the R package IndRSA (Bastille-Rousseau and Wittemyer 2019); we specified 10 folds for cross-validation (Hinton et al. 2015). We evaluated predictive performance using area under the curve procedures (AUC; Pierce and Ferrier 2000, Boyce et al. 2002, Johnson et al. 2006), which we implemented with the R package pROC (Robin et al. 2011). For each species within each year, we produced season-specific rasters of the predicted probability of use for the entire study area using the R package raster.

Survival and cause-specific mortality

We fit Cox proportional hazards models adjusted for staggered entry and right-censoring and produced Kaplan-Meier survival curves from the fitted Cox models to estimate annual survival probabilities (Therneau and Grambsch 2000, Murray and Patterson 2006). For coyotes, we fit all plausible models that included singular or additive combinations of sex, age (years), residency status, and year; residency status was obtained from results of the home range analyses described previously. Because the coyote radio-collar monitoring data were severely skewed towards winter (~70% of survival data), we did not include a main effect for season and instead specified seasons as the strata. We clustered the survival monitoring data by individual coyote in the Cox models because most individuals were monitored for >1 year and >1 age (i.e., temporally correlated observations).

The fates of some jackrabbits were uncertain because it was difficult to determine in the field whether some individuals remained alive or died after radio-collar failure/drop-off. Therefore, we created two survival datasets for jackrabbits, an optimistic dataset in which the uncertain fates were right-censored and the animal was assumed alive (AA), and a pessimistic dataset in which the uncertain fates were considered mortalities of unknown cause (assumed dead [AD]; Heisey and Fuller 1985, Pollock et al. 1989, Laufenberg et al. 2016). In each Cox model for jackrabbits, we clustered the data by individual and specified seasons as the strata. We fit all plausible models that included singular or additive combinations of sex, age class (adult vs.

subadult), residency status, and year; residency status was obtained from results of the home range analyses above.

We fit Cox proportional hazards models using the *survival* package in R (Therneau 2021) and used AIC_c for model selection, producing mean annual survival probability estimates from the top-ranked model for each species. We also estimated cause-specific mortality probabilities for each species that appropriately accounted for competing risks via nonparametric cumulative incidence functions implemented in the *cmprsk* package in R (Heisey and Patterson 2006, Gray 2020).

Cameras traps

Camera-traps have been used effectively to survey carnivore (*reviewed by* Kays and Slauson 2008, Meek and Fleming 2014, Rovero and Spitale 2016) and lagomorph populations (Lindsey et al. 2014). We deployed camera-traps throughout the study area in a variety of habitat types to observe and record data for the estimation of abundance, population density, and distributions of black-tailed jackrabbits and coyotes. Our primary camera-trap placements were located within two strata: Randomly placed cameras were located in the uplands for Random Encounter Model (REM) density estimation, whereas we also strategically placed cameras in washes to attempt to enhance detection rates and to observe animal movements along their natural thoroughfares. One of our camera survey objectives was to determine the costs and benefits of these and other methods for future consideration.

Random camera sites to estimate coyote and jackrabbit densities were selected using a set of random points within a 500-m grid pattern generated by GIS software (ArcMap 10, ESRI Redlands, CA). These sites were selected to overlap the areas surveyed with the spotlight line transects wherever possible. Cameras (Bushnell #119876) were placed in metal lock boxes 30 cm above the ground to record coyote and black-tailed jackrabbit activity at each site (Figure 4). Random cameras were programmed to take photos whenever movement was detected, with a minimum interval of one minute. Two grids, each consisting of 20 trail cameras, were placed in the BCCE, one in the north, and one in the south (Figure 5). Each grid contained five sites, with each site containing four cameras. Each site was separated from all other sites by at least 1 km, and each camera was separated from all other cameras by at least 500 m.

Digital trail cameras (Bushnell #119876C, and Moultrie M-40) were also strategically deployed in wildlife travel corridors (e.g., washes). Locations at the confluence of washes throughout the BCCE were selected as prospective camera sites. Cameras were programmed to take photos whenever motion was detected, with a minimum interval between subsequent photographs of 30 seconds. This shorter interval between subsequent photographs in wash camera settings (compared to the cameras placed at random grid site locations) was intended to increase detections of predators traversing the washes, thereby providing a better understanding of the frequency, group size, and composition of coyotes travelling together. Cameras were checked and data downloaded every 3-6 months, based on availability of field personnel and how data-intensive the sites were, e.g., sites that routinely acquired more images required more frequent visitation than sites with lower data acquisition rates.

Cameras in the grids and washes were checked seasonally to detect changes in species abundance and distribution. All photographic images were named using date and time the image was taken. Photographs were then visually sorted to species present and number of individuals observed in the photo following methods described in Harris et al. (2010) and Sanderson and Harris (2014). Preliminary analyses were performed using a suite of camera trapping software (e.g., Data Analyze, Data Organize, and others from the Cameratrapsweet program package) to manage camera trap data (Harris et al. 2010; additional information on software used is available at www.smallcats.org). Although cameras were placed to monitor black-tailed jackrabbits and coyotes, other species were routinely observed and recorded.

<u>Camera-traps placed at tortoise carcasses</u> - Camera traps were placed at eight desert tortoise mortality sites to investigate predator use of desert tortoise carcasses in the BCCE. USGS were notified of tortoise mortalities by the Great Basin Institute following the death of one of their BCCE monitored tortoises. Tortoise carcass sites were monitored for a period of up to three months. We used the cameras to catalogue the abundance of every species which used tortoise carcasses, and to confirm visitation of carcasses by GPS-monitored coyotes.



Figure 4. Example of a randomly placed grid camera in the BCCE during 2018. The lock box was necessary in this highly visited area to prevent theft. The T-post is driven into the ground with a sledge and the lockbox was attached with U-bolts.



Figure 5. Map of randomly placed grid cameras and strategically placed wash cameras in operation between 2018 and 2021, Boulder City Conservation Easement, Boulder City, Nevada.

Population density, size, and growth

We considered all individual coyotes and jackrabbits in photographic detections at camera-traps as unmarked regardless of their mark status (i.e., whether they had GPS-collars, ear tags, or not) and used random encounter models (REM) to estimate species-specific population densities (Rowcliffe et al. 2008, Caravaggi et al. 2016). To separate unique detections from likely successive detections of the same individuals, we used a 30-minute discrimination threshold between camera-trap photographs for coyotes and a 10-minute discrimination threshold between camera-trap photographs for jackrabbits. The REM model requires users to specify three camera-trap-specific model parameters, the radial detection distance (d), the zone of detection (θ), and operation time (days). We obtained measurements from a single camera-trap, from which we calculated d and θ , and we applied those calculated values to all deployed camera-traps. In contrast, the operation times that we specified were specific parameter, movement velocity (v; km traveled per day), which we estimated from the GPS-collar monitoring data via the OUF continuous-time movement models that were used in the home range size analysis previously described (Fleming et al. 2014b).

Prior to REM model fitting, we subset the camera-trap detection data by season and year for each species. We also calculated within-year, season-specific mean movement velocities for each species. Collectively, this approach allowed us to produce season-specific density estimates within each year, as we hypothesized that, for jackrabbits in particular, population sizes and therefore densities would exhibit seasonal and annual fluctuations (Woodbury 1955, Bronson and Tiemeier 1959, Keith 1983). Additionally, we further subset our camera-trap data by placement and fit separate REM models to produce density estimates from data obtained from only randomly placed camera-traps, only strategically placed camera-traps (e.g., in washes and other locations the species were more likely to use), and both randomly and strategically placed camera-traps combined. The resulting estimates from said subsetting allowed us to investigate the potential consequences of violating a primary assumption of REM - that animals move independently of camera-traps - which requires areas to be sampled completely at random (Rowcliffe et al. 2008). We fit REM models via bootstrapping using the R package remBoot (Caravaggi et al. 2017) and produced 95% confidence intervals around point estimates using 1,000 bootstrap iterations. We derived population growth rates (λ) across the entire camera-trap monitoring period using the exponential growth equation described by Gotelli (2008).

We fit post-hoc generalized linear mixed models, which included random intercepts for individuals and Gamma error distributions, to investigate temporal variation in movement velocities for each species, using the R package *glmmTMB*. We also fit post-hoc simple linear models with Gaussian error distributions to investigate whether density of either species was influenced by drought (Bronson and Tiemeier 1959, Jedrzejewski et al. 2018, Murphy et al. 2022). These simple linear models included a fixed effects interaction between seasonal mean monthly precipitation levels and camera placement type. We also calculated Pearson correlation coefficients between density and precipitation; we used Pearson rather than Spearman correlation because we expected the relationship to be linear instead of monotonic (Schober et al. 2018).

Spotlight line transect surveys

Spotlight line transect surveys have been used for decades to provide an index of relative abundance of lagomorphs (Smith and Nydegger 1985). Spotlight line transect surveys followed a design used to monitor jackrabbits recently in the Desert Renewable Energy Conservation Plan

(BLM 2016) area in the Mojave Desert of southern California (Longshore et al. 2017). Spotlight transect routes were selected to overlap with the placement of our random grid camera arrays, and to maintain long, straight sections of road that were at least two km from other survey routes. When possible, these routes were placed on adjacent roads to increase the efficiency of night surveys (i.e., reduce travel time lost when travelling between routes). Routes consisted of two 10-km transects in the northern half of the BCCE and one 7-km transect in the southern half of the BCCE. Spotlight surveys began 30 minutes after sunset. Starting points on the surveys were rotated among routes so that surveys were not run in the same order every night or month to reduce sampling bias. Two observers using a light bar placed on top of the vehicle and handheld LED spotlights from the passenger windows of the vehicles surveyed the routes at 8-10 km/hr. All wildlife observations were recorded along the route. When species were encountered, we recorded the GPS coordinates, perpendicular distance from the survey line to the first point the animal was observed, time, species, and ancillary notes. From February to May of 2018, all surveys consisted of a single survey night each month. From June 2018 onward, three consecutive nights were surveyed to investigate variability in the survey method. All surveys were conducted within 5 days of the full moon, to limit variation in animal activity patterns potentially associated with different moon phases. Spotlight surveys were not carried out during the onset of the COVID-19 outbreak in April, May, or June of 2020, but were continued in July of 2020 as procedures were adopted to keep personnel safe and reduce associated risks.

RESULTS

Coyote capture and monitoring

We captured and outfitted a total of 21 coyotes (11M:10F) with collars. Fifteen individuals (10M:5F) were monitored during 2020, and 20 individuals (10M:10F) were monitored during 2021. Fourteen individuals (9M:5F) were monitored during both years. A total of 30,577 and 32,461 locations were obtained during 2020 and 2021, respectively. The mean number of locations obtained per individual during 2020 and 2021 was $1,972 \pm 718$ and $1,623 \pm 548$, respectively.

<u>Coyote health status</u> - All coyotes were thoroughly checked for parasites during capture events. No parasites of any kind were detected on any coyotes. Mean weights of coyotes were 11.7 ± 1.3 kg and 9.7 ± 1.3 kg for males and females, respectively (Figure 6). Average body condition score for males was 3 ± 0.7 and for females was 2.5 ± 0.9 . Mean coyote age at time of capture was 4.50 ± 1.97 .



Figure 6. Mean coyote weights and body condition scores in the Boulder City Conservation Easement in 2019 and 2020. Error bars indicate one standard error from the mean.

Black-tailed jackrabbit capture and monitoring

A total of 82 jackrabbits (38M:26F:18U) that were captured and outfitted with collars had sufficient monitoring data for statistical analyses (67% of all captured jackrabbits, N =122). Thirty-four (14M:11F:9U), 51 (21M:20F:10U), and 42 (22M:11F:9U) individuals were monitored during 2019, 2020, and 2021, respectively. Three subadults (1M:1F:1U) and 31 adults (13M:10F:8U) were monitored in 2019; 11 subadults (4M:6F:1U) and 40 adults (17M:14F:9U) were monitored in 2020; and 9 subadults (4M:3F:2U) and 33 adults (18M:8F:7U) were monitored in 2021. After thinning the short-term collar data to 3–4-hour fix intervals, a total of 13,792, 12,962, and 5,885 locations were obtained during 2019, 2020, and 2021, respectively. The mean number of locations obtained per individual during 2019, 2020, and 2021 was 406 \pm 134, 255 \pm 72, and 140 \pm 37, respectively.

<u>Black-tailed Jackrabbit health status</u> - We aged captured jackrabbits to track trends in population level health. The greatest number of subadult jackrabbits was found in 2020 (Figure 7). We weighed captured jackrabbits to track trends in nutritional condition over time, however, there was little difference in the weights across time (Figure 8). No attempt was made to assign body condition scores to captured jackrabbits. We captured 201 jackrabbits that were examined for parasites. Fifteen were carrying ticks, three were infected with bot flies, and one had lice (Figure 9).



Figure 7. Percentage of the marked sample of black-tailed jackrabbit that is subadult the Boulder City Conservation Easement during 2019 through 2021. Error bars are one standard error from the mean.



Figure 8. Average weight of adult black-tailed jackrabbits in the Boulder City Conservation Easement by year. Error bars are one standard error from the mean.





Home range size

Coyotes

We estimated a total of 60 seasonal 95% wAKDE_c home range sizes for 20 individual coyotes; 36 (19M:17F) were winter home range sizes and 24 (14M:10F) were summer home range sizes. Small sample size prevented estimating seasonal home range sizes for one female coyote and one male coyote. Variograms indicated that 11 (5M:6F) and 13 (9M:4F) coyotes exhibited seasonal residency and seasonal transiency, respectively, during at least one season. The anisotropic OUF model was the top-ranked model for 87% (n = 52) of seasonal coyote home range sizes for resident males and transient males during winter were 35 km² (95% CI = 29–43) and 751 km² (95% CI = 357–1,276), respectively (Figure 10A). Mean home range sizes for resident females during winter were 26 km² (95% CI = 19–34) and 117 km² (95% CI = 71–179), respectively. Mean home range sizes for resident males and transient females and transient males during summer were 37 km² (95% CI = 23–51) and 425 km² (95% CI = 281–641), respectively. Mean home range sizes for resident females during summer were 23 km² (95% CI = 14–28) and 373 km² (95% CI = 145–788), respectively.

Small sample size prevented estimating annual home range sizes for one female and one male coyote. We estimated a total of 21 annual 95% wAKDE_c home range sizes for 19 individual coyotes (10M:9F). Five (2M:3F) and 14 (8M:6F)



Figure 10. Predicted conditional effects of A) seasonal and B) annual coyote home range sizes by sex and residency status, from negative-binomial mixed effects models.

individuals exhibited annual residency and annual transiency, respectively, during the study. The anisotropic OUF model was the top-ranked model for 86% (n = 18) of annual coyote home ranges. Annual coyote 95% home range size estimates ranged from 24 km² to 1,684 km². Mean annual home range sizes for resident males and transient males were 31 km² (95% CI = 26–38) and 471 km² (95% CI = 197–960), respectively (Figure 10B). Mean annual home range sizes for resident females were 29 km² (95% CI = 24–32) and 265 km² (95% CI = 110–612), respectively.

Black-tailed jackrabbits

Small sample size prevented estimating winter home range sizes for 11 adult (7M:2F:2U) and 2 subadult (1M:0F:1U) jackrabbits, and summer home range sizes for 14 adult (0M:6F:8U) and 3 subadult (0M:2F:1U) jackrabbits. We estimated a total of 98 seasonal 95% AKDE_c home range sizes for 90 (45M:30F:15U) individual jackrabbits; 52 (27M:17F:8U) were winter home ranges and 46 (22M:17F:7U) were summer home ranges. Variograms indicated that 26 (28.9%) jackrabbits (14M:8F:4U), 22 of which were adults, exhibited transiency during winter, whereas 24 jackrabbits (12M:9F:3U), 22 of which were adults, exhibited residency during summer. The anisotropic OU model was the top-ranked model for 62% (n = 32) of winter jackrabbit home ranges, followed by the anisotropic OUF model (n = 20). Approximately 46% (n = 24) of winter

jackrabbit home ranges were linear or elongated, and 54% (n = 28) were approximately circular (Fig. X). Winter jackrabbit 95% home range size estimates ranged from 3 ha to 2,490 ha. Mean home range sizes for resident and transient males during winter were 69 ha (95% CI = 28–103) and 306 ha (95% CI = 86–447), respectively (Figures 11A, and B). Mean home range sizes for resident and transient females during winter were 50 ha (95% CI = 32–69) and 637 ha (95% CI = 37–1,090), respectively.

The anisotropic OUF model was the top-ranked model for 50% (n = 23) of summer jackrabbit home ranges, followed by the anisotropic OU model (n = 21). Approximately 52% (n = 24) of summer jackrabbit home ranges were linear or elongated (Figure 12), and 48% (n = 22) were approximately circular. Summer jackrabbit 95% home range size estimates ranged from 6 ha to 2,586 ha. Mean home range sizes for resident and transient males during summer were 33 ha (95% CI = 19–45) and 584 ha (95% CI = 108–989). Mean home range sizes for resident and transient females during summer were 38 ha (95% CI = 22–53) and 966 ha (95% CI = 416–1,709), respectively.



Figure 11A and B. Predicted conditional effects of seasonal jackrabbit home range sizes by sex and residency status, from negative-binomial mixed effects models



Figure 12. Example of a non-circular jackrabbit home range in the BCCE. Red dots denote GPS-collar locations and black lines denote the 95% range with confidence intervals.

Population-level variation in home range size

<u>Coyote home ranges</u> - A negative-binomial mixed effects model indicated that seasonal coyote home range sizes, for all coyotes combined, were invariant to the sample size of locations ($\beta = 0.11$; p = 0.25). A separate negative-binomial mixed effects model indicated that coyote seasonal home range sizes differed substantially between residents and transients ($\beta = 1.83$; p < 0.0001) and estimated that transient coyotes had seasonal home ranges that were, on average, $3.71 \times$ larger than resident coyote home ranges. Although residents of both sexes had similar seasonal home range sizes, and ranges did not substantially differ between seasons for residents or transients when sexes were analyzed together combined, transient male coyotes had, on average, $2.92 \times$ larger seasonal range sizes than transient female coyotes (p = 0.002; Figure 10A).

A negative-binomial mixed effects model indicated that annual coyote home range sizes were invariant to the sample size of locations ($\beta = 0.54$; p = 0.11). A separate negative-binomial mixed effects model indicated that annual home range sizes did not differ between sexes ($\beta =$ 0.08; p = 0.93) but substantially differed between resident and transient coyotes of each sex ($\beta =$ 2.22; p = 0.03). This model indicated that regardless of sex, transient coyotes had annual home ranges that were, on average, 5.31× larger than resident coyote home ranges (p = 0.004; Fig. XB).

<u>Jackrabbit home ranges</u> - A negative-binomial mixed effects model indicated that seasonal jackrabbit home range sizes were positively related to the sample size of locations ($\beta = 0.49$; p = 0.03). Accounting for the effect of location sample size, a separate negative-binomial mixed effects model indicated that seasonal jackrabbit home range sizes substantially differed between residents and transients ($\beta = 3.13$; p < 0.0001) but did not differ between seasons ($\beta = 0.26$; p = 0.58) or sexes ($\beta = -0.15$; p = 0.74). This model indicated that transient jackrabbits had seasonal home ranges that were, on average, 11.89× larger than resident jackrabbit home ranges during both seasons (Fig. X).

Habitat selection

Coyotes

For winter 2020, the top-ranked model received 98% of the weight relative to the other 23 considered models (Supplementary Table S1). This model indicated that the probability of coyote use declined with increasing distance from water sources ($\beta = -0.33$, p < 0.0001), increasing TPI ($\beta = -0.29$, p < 0.0001), increasing TDI ($\beta = -0.07$, p = 0.002), and increasing VRML ($\beta = -0.18$, p < 0.0001), but use increased with increasing NDVI amplitude ($\beta = 0.28$, p < 0.0001). Coyote probability of use for all of those covariates during winter 2020 did not differ between sexes or between residents and transients (Figure 13A-E). The k-folds cross-validation indicated that this model had adequate predictive capacity, with a mean Spearman rank correlation among folds of r = 0.73; model predictive performance was moderate (AUC = 0.63).



Figure 13. Predicted probability of coyote use during winter 2020 (Nov. 2019–Apr. 2020), based on A) distance from water, B) topographic position index, C) terrestrial development index, D) vector ruggedness measure local, and E) normalized difference vegetation index amplitude, from the top-ranked habitat selection model.

For summer 2020, the top-ranked model received 100% of the weight relative to the other 23 considered models (Supplementary Table S2). This model indicated that the probability of coyote use declined with increasing distance from water sources ($\beta = -0.53$, p < 0.0001),

increasing ATI ($\beta = -0.16$, p < 0.0001), and increasing VRML ($\beta = -0.06$, p = 0.0001), but use increased with increasing TDI ($\beta = 0.09$, p < 0.0001) and increasing NDVI amplitude ($\beta = 0.27$, p < 0.0001). Although coyote probability of use for all of those covariates during summer 2020 did not differ between sexes, male transients had significantly higher overall probabilities of use than did male residents based on each covariate (Figure 14A-E). The k-folds cross-validation indicated that this model had adequate predictive capacity, with a mean Spearman rank correlation among folds of r = 0.71; model predictive performance was moderate (AUC = 0.64).



Figure 14. Predicted probability of coyote use during summer 2020 (May 2020–Oct. 2020), based on A) distance from water, B) surface texture, C) terrestrial development index, D) vector ruggedness measure local, and E) normalized difference vegetation index amplitude, from the top-ranked habitat selection model.

For winter 2021, three models were competing (<2 Δ AICc; Supplementary Table S3); however, two of the competing models were more general variants of the top-ranked model, with both competing models having just one additional covariate relative to the top-ranked model. Despite the addition of one parameter for each of those covariates, those models' log-likelihoods did not differ from that of the top-ranked model, suggesting the additional covariates were uninformative (Arnold 2010). Upon further inspection of the coefficient estimates for all three models, we found that both the NDVI amplitude and VRML covariates were uninformative. Therefore, we did not model-average the competing models and instead produced estimates from the top-ranked model only. This model indicated that the probability of coyote use declined with increasing distance from water sources ($\beta = -0.16$, p < 0.0001), increasing ATI ($\beta = -0.26$, p < 0.0001), and increasing TDI ($\beta = -0.17$, p < 0.0001). Coyote probability of use for all of those covariates during winter 2021 did not differ between sexes, and although transients of both sexes tended to have higher overall probabilities of use than residents, the differences between those classes were not statistically significant (Figure 15A-C). The k-folds cross-validation indicated that this model had deficient predictive capacity, with a mean Spearman rank correlation among folds of r = 0.46; model predictive performance was moderate (AUC = 0.60).



Figure 15. Predicted probability of coyote use during winter 2021 (Nov. 2020–Apr. 2021), based on A) distance from water, B) surface texture, and C) terrestrial development index, from the top-ranked habitat selection model.

For summer 2021, the top-ranked model received 90% of the weight relative to the other 23 considered models (Supplementary Table S4). This model indicated that the probability of coyote use declined with increasing distance from water sources ($\beta = -0.35$, p < 0.0001), increasing ATI ($\beta = -0.30$, p < 0.0001), and increasing TDI ($\beta = -0.23$, p < 0.0001), but use

increased with increasing VRML ($\beta = 0.04$, p = 0.01) and increasing NDVI amplitude ($\beta = 0.22$, p < 0.0001). Coyote probability of use for all of those covariates during summer 2021 was significantly higher for male residents than female residents, and female transients had significantly higher overall probabilities of use than did female residents based on each covariate (Figure 16A-E). The k-folds cross-validation indicated that this model had deficient predictive capacity, with a mean Spearman rank correlation among folds of r = 0.51; model predictive performance was moderate (AUC = 0.61).



Figure 16. Predicted probability of coyote use during summer 2021 (May 2021–Oct. 2021), based on A) distance from water, B) surface texture, C) terrestrial development index, D) vector ruggedness measure local, and E) normalized difference vegetation index amplitude, from the top-ranked habitat selection model.

In general, the top-ranked season × year habitat selection models predicted considerable temporal variation in probability of use for coyotes across the study area (Figure 17A-D). Notably, 7% of the study area had high probabilities of coyote use (P > 0.80) during summer 2020, compared to 0.39%, 0.16%, and 0% during summer 2021, winter 2020, and winter 2021, respectively. Moderate probabilities of coyote use (0.50 < P < 0.80) were estimated for 42%, 35%, and 32% of the study area during winter 2020, summer 2020, and summer 2021,

respectively. In contrast, most of the study area was estimated to have low probabilities of coyote use (P < 0.50) across all season × year combinations ($\geq 58\%$ of the study area); probabilities were lowest during winter 2021, when 71% of the study area was estimated to have P < 0.50 coyote use.



Figure 17. Spatial predicted probability of coyote use in the study area during A) winter 2020,
B) summer 2020, C) winter 2021, and D) summer 2021, from the top-ranked habitat selection models for each season × year combination. Note that the probability scales differ among the four panels, as indicated by the legends.

Black-tailed jackrabbits

For winter 2020, the top-ranked model received 60% of the weight relative to the other 23 considered models, though no other model was competing (i.e., <2 Δ AICc; Supplementary Table S5). This model indicated that the probability of jackrabbit use increased with increasing distance from water sources ($\beta = 0.06$, p = 0.08), increasing ATI ($\beta = 0.06$, p = 0.02), increasing TDI ($\beta = 0.09$, p < 0.0001), and increasing NDVI amplitude ($\beta = 0.11$, p < 0.0001), but use decreased with increasing VRML ($\beta = -0.06$, p = 0.006). Jackrabbit probability of use for all of those covariates during winter 2020 did not differ between sexes or residency statuses (Figure 18A-E). The k-folds cross-validation indicated that this model had relatively poor predictive





Figure 18. Predicted probability of jackrabbit use during winter 2020 (Nov. 2019–Apr. 2020), based on A) distance from water, B) surface texture, C) terrestrial development index, D) vector ruggedness measure local, and E) normalized difference vegetation index amplitude, from the top-ranked habitat selection model.

For summer 2020, the top-ranked model received 59% of the weight relative to the other 23 considered models (Supplementary Table S6). One model was competing (<2 Δ AICc) but it was a more general variant of the top-ranked model, with just one additional covariate relative to the top-ranked model. Despite the addition of one parameter for the extra covariate, the model's log-likelihood differed nominally from that of the top-ranked model (Δ LL = 0.65), suggesting the additional covariate was uninformative (Arnold 2010). Upon further inspection of the coefficient estimates, we found that the NDVI amplitude covariate in the competing model was uninformative. Therefore, we did not model-average the competing and top-ranked models and instead produced estimates from the top-ranked model only. This model indicated that the probability of jackrabbit use declined with increasing TPI (β = -1.11, *p* < 0.0001) and increasing VRML (β = -0.17, *p* < 0.0001), but use increased with increasing distance from water sources (β = 0.12, *p* = 0.08) and increasing TDI (β = 0.91, *p* < 0.0001). Jackrabbit probability of use for all of those covariates during summer 2020 did not significantly differ between sexes or residency

status, though there was weak evidence that transients may have had higher overall probabilities of use than residents (Figure 19A-D). The k-folds cross-validation indicated that this model had poor predictive capacity, with a mean Spearman rank correlation among folds of r = 0.35; however, model predictive performance was moderate (AUC = 0.67).



Figure 19. Predicted probability of jackrabbit use during summer 2020 (May 2020–Oct. 2020), based on A) distance from water, B) topographic position index, C) terrestrial development index, and D) vector ruggedness measure local, from the top-ranked habitat selection model.

For winter 2021, the top-ranked model received 65% of the weight relative to the other 23 considered models (Supplementary Table S7). One model was competing (<2 Δ AICc) but it was a more general variant of the top-ranked model, with just one additional covariate relative to the top-ranked model. Despite the addition of one parameter for the extra covariate, the model's log-likelihood differed nominally from that of the top-ranked model (Δ LL = 0.37), suggesting the additional covariate was uninformative (Arnold 2010). Upon further inspection of the coefficient estimates, we found that the VRML covariate in the competing model was uninformative. Therefore, we did not model-average the competing and top-ranked models and instead produced estimates from the top-ranked model only. This model indicated that the probability of jackrabbit use increased with increasing distance from water sources (β = 0.42, *p* < 0.0001), increasing TPI (β = 0.23, *p* < 0.0001), increasing TDI (β = 0.22, *p* < 0.0001), and increasing NDVI amplitude (β = 0.48, *p* < 0.0001). Jackrabbit probability of use for all of those
covariates during winter 2021 did not differ between residents and transients but evidence existed for males having a higher overall global (i.e., holding all covariates constant at their mean) probability of use than females ($\beta = 0.34$, p = 0.009; Figure 20A-D). The k-folds cross-validation indicated that this model had adequate predictive capacity, with a mean Spearman rank correlation among folds of r = 0.72; model predictive performance was moderate (AUC = 0.62).



Figure 20. Predicted probability of jackrabbit use during winter 2021 (Nov. 2020–Apr. 2021), based on A) distance from water, B) topographic position index, C) terrestrial development index, and D) normalized difference vegetation index amplitude, from the top-ranked habitat selection model.

For summer 2021, the top-ranked model received 68% of the weight relative to the other 23 considered models (Supplementary Table S8). One model was competing (<2 Δ AICc) but it was a nested version of the top-ranked model and excluded one covariate (VRML) that was present in the top-ranked model. Upon further inspection of the coefficient estimates, we found that the VRML covariate in the top-ranked model was informative, albeit weakly informative. Therefore, we did not model-average the competing and top-ranked models and instead produced estimates from the top-ranked model only. This model indicated that the probability of jackrabbit use increased with increasing distance from water sources ($\beta = 0.62$, p < 0.0001), increasing ATI ($\beta = 0.89$, p < 0.0001), increasing TDI ($\beta = 0.60$, p < 0.0001), and increasing NDVI amplitude (β

= 0.17, p = 0.004), but the probability of use declined with increasing VRML (β = -0.07, p = 0.07). Jackrabbit probability of use for all of those covariates during summer 2021 did not differ between sexes or residency statuses (Figure 21A-E). The k-folds cross-validation indicated that this model had deficient predictive capacity, with a mean Spearman rank correlation among folds of r = 0.51; however, model predictive performance was moderate (AUC = 0.67).



Figure 21A-E. Predicted probability of jackrabbit use during summer 2021 (May 2021–Oct. 2021), based on A) distance from water, B) surface texture, C) terrestrial development index, D) vector ruggedness measure local, and E) normalized difference vegetation index amplitude, from the top-ranked habitat selection model.

In general, the top-ranked season × year habitat selection models predicted considerable temporal variation in probability of use for jackrabbits across the study area (Figure 22A-D). Notably, 29% of the study area had high probabilities of jackrabbit use (P > 0.80) during summer 2020, compared to 18%, 15%, and 6% during summer 2021, winter 2021, and winter 2020, respectively. Moderate probabilities of jackrabbit use (0.50 < P < 0.80) were estimated for 46%, 43%, 36%, and 31% of the study area during summer 2020, winter 2021, winter, 2020, and summer 2021, respectively. In contrast, 58%, 51%, 42%, and 25% of the study area was estimated to have low probabilities of jackrabbit use (P < 0.50) during winter 2020, summer 2021, winter 2021, and summer 2020, respectively.



Figure 22A-D. Spatial predicted probability of jackrabbit use in the study area during **A**) winter 2020, **B**) summer 2020, **C**) winter 2021, and **D**) summer 2021, from the top-ranked habitat selection models for each season × year combination.

Survival and cause-specific mortality

Coyotes

Among the 21 monitored coyotes, a total of 5 (24%) died from the following causes: hunting (n = 2), vehicle collision (n = 2), and starvation (n = 1). We fit a total of 15 Cox proportional hazards models, 4 of which were competing ($\Delta AIC_c < 2$). The top-ranked model included only a year effect, the second-ranked model included only an age effect, the thirdranked model included only a sex effect, and the fourth-ranked model included only a residency status effect (Supplementary Table S9). Very weak support existed for the hazard ratio being higher during 2021 compared to 2019–2020 (HR = 4.18, 95% CI = 0.54–32.10), but no support existed for hazard ratios differing between ages (HR = 1.15, 95% CI = 0.70–1.86), sexes (HR = 0.49, 95% CI = 0.09–2.64), or residency statuses (HR = 0.52, 95% CI = 0.10–2.63). Estimated seasonal survival probabilities from the top-ranked model did not notably differ ($S_{summer} = 0.96$, 95% CI = 0.88–0.99; $S_{winter} = 0.94$, 95% CI = 0.84–0.99). Annual survival probabilities for coyotes were 0.95 and 0.81 during 2019–2020 and 2021, respectively (Figure 23A). Competing risks cause-specific mortality probabilities were very low, with hunting having the highest





Figure 23A-B. Coyote estimates of **A**) annual survival probabilities from the top-ranked Cox proportional hazards model and **B**) cause-specific mortality probabilities from a competing risks analysis using cumulative incidence functions.

Black-tailed jackrabbits

Among the 82 monitored jackrabbits having enough data to analyze, a total of 37 (45%) were confirmed to have died from the following causes: coyote predation (n = 6), kit fox predation (n = 6), predation by unknown predators (n = 17), and unknown causes of death (n = 8). We fit a total of 15 Cox proportional hazards models to each the optimistic (censors and unknown causes assumed alive; AA) and pessimistic (censors and unknown causes assumed dead; AD) jackrabbit datasets. For the AA data, 4 models were competing ($\Delta AIC_c < 2$); the topranked model included only a year effect, the second-ranked model included both age class and year effects, the third-ranked model included both residency status and year effects, and the fourth-ranked model included both sex and year effects (Supplementary Table S10). Very strong support existed for the hazard ratio progressively increasing by year (HR₂₀₂₀ = 2.79, 95% CI = 1.05–7.40; HR₂₀₂₁ = 5.54, 95% CI = 2.20–13.99), indicating declining survival probability over time. No support existed for hazard ratios differing between age classes (HR = 0.61, 95% CI = 0.25–1.47), residency status (HR = 1.30, 95% CI = 0.71–2.40), or sexes (HR_{Female} = 0.40, 95% CI = 0.16–1.02; HR_{Male} = 0.48, 95% CI = 0.19–1.20). Estimated seasonal optimistic survival

probabilities from the top-ranked model did not notably differ ($S_{summer} = 0.77, 95\%$ CI = 0.61–0.96; $S_{winter} = 0.72, 95\%$ CI = 0.53–0.97). Annual optimistic survival probabilities for jackrabbits were 0.75, 0.45, and 0.22 during 2019, 2020, and 2021, respectively (Figure 24A). Optimistic competing risks cause-specific mortality probabilities indicated that predation by unknown carnivores was the leading cause of death (M = 0.30, 95% CI = 0.15–0.46), followed by unknown causes of death (M = 0.13, 95% CI = 0.04–0.27), kit fox predation (M = 0.10, 95% CI = 0.03–0.20), and coyote predation (M = 0.08, 95% CI = 0.02–0.17; Figure 24C).



Figure 24A-D. Black-tailed jackrabbit estimates of A) optimistic and B) pessimistic annual survival probabilities from the top-ranked Cox proportional hazards models, and average annual C) optimistic and D) pessimistic cause-specific mortality probabilities from competing risks analyses using cumulative incidence functions.

For the AD data, 8 models were competing ($\Delta AIC_c < 2$); the top-ranked model included only residency status and the second-ranked model included only age class, both of which received equal model weight (w = 0.14; Supplementary Table S11). Three of the 8 competing AD models included a year effect, 3 included a sex effect, 4 included an age class effect, and 2 included a residency status effect. However, upon further inspection, we found that both residency status and age class were uninformative variables (Arnold 2010) and therefore we excluded all AD models that contained those effects from further consideration. This resulted in three plausible models; the top-ranked model included only a year effect, the second-ranked model included only a sex effect, and the third-ranked model included both year and sex effects. Weak support existed for the hazard ratio progressively increasing by year (HR₂₀₂₀ = 1.34, 95% CI = 0.64–2.82; HR₂₀₂₁ = 1.83, 95% CI = 0.96–3.45), and strong support existed for females having a lower hazard ratio than both unknown sex individuals and males (HR_{Female} = 0.51, 95% CI = 0.26–1.01), whereas males had a similar hazard ratio as unknown sex individuals (HR_{Male} = 0.73, 95% CI = 0.40–1.34). Some evidence existed, although weak, for pessimistic summer jackrabbit survival being higher than winter survival ($S_{summer} = 0.56, 95\%$ CI = 0.39–0.79; $S_{winter} = 0.32, 95\%$ CI = 0.16–0.63). Annual pessimistic survival probabilities for jackrabbits were 0.45, 0.35, and 0.24 during 2019, 2020, and 2021, respectively (Figure 24B). Pessimistic competing risks cause-specific mortality probabilities indicated that predation by unknown carnivores and unknown causes of death were the leading causes of mortality ($M_{Unknown} = 0.30, 95\%$ CI = 0.18–0.44; $M_{Pred-Unk} = 0.26, 95\%$ CI = 0.14–0.39), followed by kit fox predation (M = 0.09, 95% CI = 0.03–0.18), and coyote predation (M = 0.07, 95% CI = 0.02–0.15; Figure 24D).

Camera traps

At least 66 species or species groups (e.g., bats were not identified to the species level) were detected at camera traps placed in the study area from 2018-2021 (Table 1). Several species of reptile covered by Clark County's MSHCP were detected during the camera surveys, including Mojave desert tortoise (*Gopherus agassizi*), desert iguana (*Dipsosaurus dorsalis*), long-nosed leopard lizard (*Gambelia wislizenii*), sidewinder (*Crotalus cerastes*), Great Basin collared lizard (*Crotaphytus bicinctores*), and chuckwalla (*Sauromalus ater*). Bird species considered to be evaluation species in the MSHCP were observed as well, including Burrowing Owl (*Athene cunicularia*), Crissal Thrasher (*Toxostoma crissale*), Loggerhead Shrike (*Lanius ludovicianus*), and LeConte's Thrasher (*Toxostoma lecontei*), along with two watch list species, the Cactus Wren (*Campylorhynchus brunneicapillus*) and Golden Eagle (*Aquila chrysaetos*), as well as one covered species, Phainopepla (*Phainopepla nitens*). One evaluation species of mammal, the kit fox (*Vulpes macrotis*), was detected by camera traps.

Cameras that were strategically placed in washes detected far more species (n = 63) than randomly placed grid cameras (n = 41). However, grid cameras detected several species which were not detected on wash cameras, including verdin (*Auriparus glaviceps*), vesper sparrow (*Pooecetes gramineus*), and sidewinder (*Crotalis cerastes*). Species only detected on wash cameras included desert bighorn sheep (*Ovis canadensis*), western spotted skunk (*Spilogale gracilis*), desert cottontail (*Sylvilagus audubonii*), and Phainopepla. Many potential tortoise predators were detected on camera, but notably, no photos of mountain lions were recorded. Most species of primary concern to the predator-prey dynamics project (coyotes, black-tailed jackrabbits, kit fox, American badger) were detected at both camera types. However, desert cottontails (*Sylvilagus audubonii*) were only observed on strategically placed wash cameras. **Table 1**. Number of observations for selected species detected at camera stations in washes and random grids in the BCCE from 2018 to 2021. MSHCP Status: CS = Covered Species, HPES = High Priority Evaluation Species, LPES = Low Priority Evaluation Species, MPES = Medium Priority Evaluation Species, WLS = Watch List Species, None = No MSHCP Status.

Species	Scientific Name	MSHC P Status	Wash Cameras	Grid Cameras
Mammals	_		n	n
American Badger	Taxidea taxus	None	187	104
Bat	Unknown species	Various	10	-
Black-tailed Jackrabbit	Lepus californicus	None	23395	9993
Bobcat	Lynx rufus	None	133	4
Coyote	Canis latrans	None	2535	162
Desert Bighorn Sheep	Ovis canadensis nelsoni	None	61	-
Desert Cottontail	Sylvilagus audubonii	None	1935	-
Desert Woodrat	Neotoma lepida	None	369	632
Domestic Cat	Felis catus	None	1	-
Domestic Dog	Canis familiaris	None	30	6
Domestic Horse	Equus ferus caballus	None	2	-
Gray Fox	Urocyon cinereoargenteus	None	125	6
Kangaroo Rat	Dipodomys spp.	Various	1008	3375
Kit Fox	Vulpes macrotis	HPES	2330	2011
Ringtail	Bassariscus astutus	None	5	-
Round-tailed Ground	Xerospermophilus	None	18	57
Squirrei Spottod Slaunk	Spilogalo avagilia	Nono	20	
White tailed Antelone	Ammogne gracilis	None	20	-
Ground Squirrol		None	1661	852
Birds	leucurus			
Barn Owl	- Tyto alba	Nona	2	
Ball's Sparrow	1 yio uiou Artemisiospiza helli	None	2 1	- 23
Black tailed Gnateatcher	Polioptila malanura	None	1	23
Black-throated Sparrow	Amphispiza bilinaata	None	4	- 31
Bullock's Oriole	Ictorys bullockii	None	7 7	51
Burrowing Owl	Athene cunicularia	HPES	18	7
	Campylorhynchus	WL	10	7
Cactus Wren	brunneicapillus		4	/
Common Poorwill	Phalaenoptilus nuttallii	None	69	3
Common Raven	Corvus corax	None	162	50
Cooper's Hawk	Accipiter cooperii	None	4	-
Costa's Hummingbird	Calypte costae	None	1	-
Crissal Thrasher	Toxostoma crissale	LPES	8	-
Gambel's Quail	Callipepla gambelii	None	173	-
Golden Eagle	Aquila chrysaetos	WL	12	-
Great Horned Owl	Bubo virginianus	None	6	-

Species	Scientific Name	MSHC	Wash	Grid
		r Status	Cameras	Cameras
Greater Roadrunner	Geococcvx californianus	None	458	58
Green-tailed Towhee	Pipilo chlorurus	None	1	-
Horned Lark	Eremophila alpestris	None	4	94
LeConte's Thrasher	Toxostoma lecontei	MPES	438	249
Loggerhead Shrike	Lanius ludovicianus	LPES	97	9
Lesser Nighthawk	Chordeiles acutipennis	None	86	5
Mallard	Anas platyrhynchos	None	2	-
Mourning Dove	Zenaida macroura	None	84	3
Northern Harrier	Circus cyanus	None	4	1
Northern Mockingbird	Mimus polyglottos	None	49	3
Phainopepla	Phainopepla nitens	CS	18	-
Red-tailed Hawk	Buteo jamaicensis	None	9	10
Rock Wren	Salpinctes obsoletus	None	18	5
sage sparrow	Artemisiospiza spp.	None	2	3
Sage Thrasher	Oreoscoptes montanus	None	4	14
Say's Phoebe	Sayornis saya	None	20	-
Turkey Vulture	Cathartes aura	None	5	-
western flycatcher	Empidonax spp.	None	4	-
Western Meadowlark	Sturnella neglecta	None	2	17
White-crowned Sparrow	Zonotrichia leucophrys	None	16	1
Verdin	Auriparus flaviceps	None	-	1
Vesper Sparrow	Pooecetes gramineus	None	-	1
Reptiles	_			
Chuckwalla	Sauromalus ater	CS	5	-
Coachwhip	Coluber flagellum	None	3	8
Desert Iguana	Dipsosaurus dorsalis	CS	110	152
Desert Tortoise	Gopherus agassizii	CS	25	4
Great Basin Collared	Crotaphytus bicinctores	CS	1	-
Lizard	1 2			
Long-nosed Leopard	Gambelia wislizenii	CS	5	31
Sidewinder	Crotalis cerastes	CS	-	2
Southern Desert Horned	Phrynosoma platyrhinos	UDEC	1	10
Lizard	calidiarum	HPES	1	10
Whiptail Lizard	Aspidoscelis spp.	None	21	161
Yellow-backed Spiny		Mana	1	
Lizard	sceloporus unijormis	None	1	-
Zebra-tailed Lizard	Callisaurus draconoides	None	168	114
	# of sites		60	40
	# of observed species		63	41

Population density, size, and growth

Coyotes

Daily movement velocities varied substantially among individual coyotes, ranging from 15.68 km/day to 141.85 km/day (Figure 25). The Gamma mixed effects model estimated statistically significant differences in coyote mean movement velocities between seasons during each of the 3 years for which sufficient GPS-collar data were available (2019-2021). No clear seasonal pattern existed in coyote movement velocity differences, though movement velocities were higher during summer in both 2020 and 2021 (Figure 26A-B).



Figure 25. Distributions of seasonal movement velocities (km/day) for individual coyotes and jackrabbits, estimated from continuous-time movement models that were fit to location data acquired via GPS-collar/GPS-logger monitoring.





Across the 4-year period of continuous camera-trapping, seasonal estimates of coyote density ranged from 0.01 coyote/km² to 0.50 coyote/km², depending on camera-trap placement (Figure 27A). Using detection data from strategically placed cameras, which violated the REM assumption of animal movement being independent of camera-traps, resulted in coyote density estimates that were positively biased by 164–183%. Estimates based on detections from only the randomly placed cameras, which satisfied the REM assumption of animal movement being independent of camera-traps, indicated that coyotes inhabited the study area at consistently low densities (0.01–0.02 coyote/km²) with nominal variation among seasons and years. Applying those densities to the 2,770-km² study area delineated in the habitat selection analysis corresponded to coyote population size estimates of 28–55 total coyotes, which represented an average annual population growth rate of $\lambda = 1.16$ (95% CI = 1.15–1.18). The simple linear model and Pearson correlation test indicated that coyote densities were unrelated to seasonal mean monthly precipitation levels ($\beta = -0.001$, p = 0.66; r = -0.06, p = 0.81; Figure 28A).



Figure 27A-B. Seasonal density estimates of **A**) coyotes and **B**) black-tailed jackrabbits during 2018–2021 from unmarked random encounter models that analyzed detection data from randomly and strategically placed camera-traps in the study area.





Black-tailed jackrabbits

Daily movement velocities varied substantially among individual jackrabbits, ranging from 1.08 km/day to 97.40 km/day (Figure 26B). We note that the continuous-time movement models estimate velocities as km/hr, whereas the REM models require velocities as km/day; thus, we converted the km/hr estimated velocities to km/day, the latter of which do not represent true observed movements during our study (i.e., we did not observe any collared jackrabbits moving 97.40 km in one day). The Gamma mixed effects model estimated statistically significant differences in jackrabbit mean movement velocities between seasons during 2019 and 2021, whereas velocities were similar between seasons during 2020. No clear seasonal pattern existed in jackrabbit movement velocity differences (Figure 26B).

Across the 4-year period of continuous camera-trapping, seasonal estimates of jackrabbit density ranged from 2.77 jackrabbits/km² to 46.22 jackrabbits/km², depending on camera-trap placement (Figure 27B). Using detection data from strategically placed cameras, which violated the REM assumption of animal movement being independent of camera-traps, resulted in jackrabbit density estimates that were positively biased by 32–93%. Estimates based on detections from only the randomly placed cameras, which satisfied the REM assumption of

animal movement being independent of camera-traps, indicated that jackrabbits inhabited the study area at densities of 2.77–16.97 jackrabbits/km²), with substantial variation among seasons and years. Notably, the jackrabbit population exhibited undulations, initially increasing to a maximum density of 16.97 jackrabbits/km² by winter 2020, after which the population declined back to densities similar to those estimated for 2018–2019. Applying those densities to the 2,770-km² study area corresponded to jackrabbit population size estimates of 7,676–47,024 total jackrabbits. Although the jackrabbit population initially increased by 124% from summer 2018 to winter 2020, the average annual population growth rate across the entire 4-year monitoring period was $\lambda = 0.93$ (95% CI = 0.92–0.94), suggesting a cumulative population decline. The simple linear model and Pearson correlation test indicated that jackrabbit densities were significantly and positively related to seasonal mean monthly precipitation levels ($\beta = 0.79$, p = 0.03; r = 0.64, p = 0.004; Figure 28B).

Spotlight line transect surveys

Nine species of vertebrates were observed on spotlight line transect surveys during 2018, 2019, 2020, and 2021 (Supplementary Tables S12, S13, S14, and S15, respectively). Black-tailed jackrabbits, the most encountered animal, were observed on all surveys. The number of black-tailed jackrabbits detected in a single night of surveys ranged from 1 to 52 individuals. Most jackrabbits were detected \leq 30 m of the transect line, though they were also detected out to approximately 75 m. Black-tailed jackrabbits were the only species sighted on all spotlight transects.

Kangaroo rats (*Dipodomys* spp.) were the second most frequently observed taxon. Kangaroo rats were more frequently sighted on spotlight transects in 2020 and 2021 than in 2018 and 2019. Several other species were observed only on rare occasions, including coyotes, spotted skunks (*Spilogale gracilis*), and burrowing owls (*Athene cunicularia*; Supplementary Tables S12-S15). Additionally, the surveys regularly flushed small unidentified birds roosting in shrubs along the survey route. No attempt was made to count or identify these birds. Although not routinely counted during the surveys, lesser nighthawks (*Chordeiles minor*) and common poorwills (*Chordeiles acutipennis*) were regularly encountered during spotlight surveys as well.

Most mesocarnivores were infrequently sighted on spotlight transects. Kit foxes were the most frequently encountered carnivores in the BCCE on spotlight transects. They were observed during 63 to 90% of the surveys conducted (Supplementary Tables S12-S15). Coyotes were rarely observed. American badgers were also encountered on spotlight surveys, though infrequently and only during summer. We also observed only one spotted skunk during spotlight surveys throughout 2018, 2019, 2020, and 2021. We have yet to encounter any other carnivore species during road surveys in the BCCE, though we might expect to o

Camera traps placed at desert tortoise carcasses

Fifteen species were documented by the desert tortoise carcass surveillance cameras, including one species not detected on other camera types, the prairie falcon (*Falco mexicanus*). Coyotes and kit foxes had the highest observed visitation rates at mortality sites, with each species having visited 70% of camera-monitored carcasses. Most of the carcasses were located in the southern and eastern extent of the BCCE (Figure 29)Coyotes that we previously captured and marked were detected at 50% of tortoise carcasses. Coyotes were the most frequently observed species at monitored carcasses, with 27 independent detections.



Figure 29. Distributions of live and dead Mojave desert tortoises, in relation to local coyote GPS-collar locations in the Boulder City Conservation Easement in 2022.

DISCUSSION

Study area

The study of wildlife habitats in the 2,770-km² study area we established in the BCCE requires that we quantify spatially explicit habitat parameters, such as availability of water or vegetation productivity. While striving to establish these habitat parameters as GIS layers, we have found it to be a moving target because of the rapid changes in the landscape.

The addition of large solar energy generation plants was ongoing since before study initiation and there has been a recent surge in the development of new plants with associated powerlines and service roads as infrastructure for energy dissemination to the grid. Interstate highway 11 came online about the time that the study was initiated. While Interstate 11 is permeable to coyotes because of culverts and a wildlife overpass, it is an existential risk to coyotes that do not use those alternate routes to cross the highway. Vehicular recreation is ubiquitous across the BCCE on legal roads, as well as, unsanctioned cultural trails, and the BCCE is not alone in this regard. Availability of vehicles that are relatively safe and easy to drive has exploded since the Covid-19 epidemic drove people to open areas in numbers never before seen by land managers. While each of these factors present challenges, they all exist a backdrop of climate variability punctuated by the most severe drought we have experienced in memory.

Health evaluations and health indices

Coyotes

Coyotes are hosts for a wide variety of common diseases and parasites, such as sarcoptic mange (Sarcoptes scabiei), Rocky Mountain spotted fever (Rickettsia rickettsii), heartworm (Dirofilaria immitis), and Erlichiosis (Erlichia spp.). We examined coyotes for ectoparasites during 22 capture events, but did not detect any ticks, mites, or mosquitos. These results are in contrast to many previous reports regarding coyote disease loads. Rates of sarcoptic mange caused by mites exceeded 50% of captured coyotes in Texas and South Dakota (Pence and Windberg 1994, Chronert et al. 2007, respectively). Besides not observing any mites during captures, we also saw no signs of mange in more than 3,000 coyote trail cameracamera-trap photos during the study period. Large numbers of ticks and tick-borne diseases are also commonly reported in coyotes. Ticks were detected on 81% of captured coyotes in North Carolina (2015) and 50% of study animals in Georgia (Lydecker 2019). Tick borne diseases are prevalent in coyotes, with one study in Texas and Oklahoma showing that 60% of individuals had antibodies reactive to R. Rickettsii and at least 64% had antibodies reactive to Erlichia spp. (Starkey et al. 2013). Having observed no ticks on coyotes in the BCCE, we do not expect a high seroprevalence of tick-borne illnesses here. Anecdotally, there are few mosquitoes in the study area and they are only rarely prevalent for short periods after heavy monsoon rainfall. Moreover, we used satellite GPS collars to track coyotes for up to 24 months after capture, and no incidences of disease related mortality were observed. We did not collect coyote carcasses over the course of this study, and so no effort was made to search animals for helminth endoparasites, which are known to be common in some coyote populations (Henke 2002). Coyotes carry several pathogens which can be harmful to humans and domestic dogs. Because of this, continued surveillance of coyote disease incidence is warranted.

During captures, we weighed coyotes and assigned each animal a Body Condition Score to record the individual's nutritional condition. These scores are reported to the Nevada Department of Wildlife (NDOW), and do not have comparison in the literature. They are only valuable to us and NDOW because they allow us to track trends in body condition in the local population over time. Our Body Condition Score averaged 2.75±0.7 during the 2019 capture season, and 2.8±1.0 during the 2020 capture season. A Body Condition Score of 3 is reflective of "good, or average for species" body condition, while a score of 2 is "fair, thin, decreased muscle mass". There is wide variability in the weight of coyotes over their distribution, but an apparent west-east gradient exists of smaller coyotes in the Southwest to larger coyotes in the Northeast

(Golightly Jr 1997, Hinton et al. 2019). The variability in weights make comparisons to values from the Western U.S. important. Golightly reported that a 1951 study from New Mexico and a 1971 study from California found the same average weights, 11kg for male coyotes and 10kg for females. In the San Joaquin Valley of California researchers found that adult males averaged 12.7±0.3kg and females averaged 10.1±1.1kg (Cypher 1995). Across the entire western U.S., Hinton et al. (2019) found that the mean body weight was 12.7 kg and 11.0 kg for males and females, respectively. Males in our study averaged 11.7±1.3kg and females 9.7±0.7kg, which were both within the reported sex-specific weight ranges across the western U.S. Although our capture method provided some caloric reward via baiting at trap sites, this likely minimally influenced the weight of our study animals. We attempted to bait animals as little as possible so that we did not have an outsized impact on the nutritional condition of the animal. Additionally, the weights of our study animals do not notably differ from other values reported for coyotes in the western U.S., so we have little reason to believe that our capture method had a significant impact on the weight values we report. Our weight values, consistent with those found in the literature, along with the body condition scores, indicate that the coyote population in the BCCE was in good nutritional condition.

Black-tailed jackrabbit health status

We examined black-tailed jackrabbits for a variety of diseases and parasites they are known to host (citations). We also looked for signs of neurological distress as a proxy for some diseases (e.g., tularemia) (Caudell 2011). Ectoparasites include bot flies (*Cuterebra spp.*), and various tick species (*Otobius lagophilus, Dermacentor spp., Haemaphysalis* sp.) known to infect jackrabbits (Simes 2015). The diseases known as Tularemia, and Rocky Mountain spotted fever are also known for black-tailed jackrabbits, and the microbes causing them are *Francisella tularensis* and *Rickettsia rickettsia*, respectively.

We detected a low incidence of parasites relative to other reported values for jackrabbits in previous studies. We only found three *Cuterebra* sp. larvae parasitizing jackrabbits (1.5% of those examined). Larvae of *Cuterebra* have been reported to be locally abundant in jackrabbit populations, in which "excessive bot infestations obviously caused death...by blinding and debilitation" (Philip et al. 1955). One of the jackrabbits we captured succumbed to stress during capture, potentially a result of the underlying poor nutritional condition from the bot infection.

There were fifteen captured jackrabbits (7.5%) that were parasitized by ticks. We did not collect rabbits for our study, and therefore did not count the number of ticks on rabbits; however, the jackrabbits that we captured which were infected with ticks likely averaged fewer than five ticks per rabbit. By contrast, in southern Arizona, 50% of black-tailed jackrabbits carried ticks (Lipson and Kraussman 1988). A study in Utah did not report the percentage of black-tailed jackrabbits carrying ticks but collected approximately 8300 ticks from approximately 250 rabbits (Fremling 1955). There was some seasonal variation in the number of ticks observed, and in the early summer, those researchers collected approximately 100 ticks per rabbit with up to 447 ticks collected from one jackrabbit. A second study in Utah found similar numbers of ticks, collecting 7330 ticks from approximately 250 jackrabbits, with a maximum of 420 ticks on one jackrabbit (Rosasco 1957). The low incidence of ticks observed during the years we studied in the BCCE indicates there may be fewer vectors for tick borne diseases than have been observed in other jackrabbit populations.

We did not collect rabbits, and so were only able to examine rabbits for conspicuous ectoparasites and neurological distress. We were unable to examine rabbits for endoparasites and

no attempt was made to necropsy jackrabbits to search for internal helminth parasites, another group of organisms known to infect jackrabbits (Lipson and Krausman 1988, Lyons 1960).

Rabbit Hemorrhagic Disease Virus 2 (RHDV2) emerged in the southwestern United States in early 2020 after being first detected in New Mexico. Since then, it has spread throughout much of the rest of the Southwest. The disease is a highly pathogenic calcivirus, with high mortality in adult rabbits caused by hepatic necrosis and liver failure (Abrantes et al. 2012). Mass mortality events have been reported in native cottontail and jackrabbit species. We collected RHDV2 samples from captured jackrabbits in an attempt to monitor the effects of the virus' incursion into the study area and evaluate the ecosystem-level effects of RHDV2. There was concern that RHDV2 in the BCCE could lead to a decline of jackrabbits which could have a cascading effect on rabbit-dependent predators and their alternate prey species as predation pressure shifts (Monerroso et al. 2016). To date, RHDV2 has not been detected in the BCCE. Blood samples have been submitted to the USGS National Wildlife Health Lab from 41 jackrabbit individuals, and all have been RHDV2 negative. Moreover, no captured jackrabbits have exhibited symptoms consistent with RHDV2, such as hemorrhaging from the eyes, nose, and mouth. As such, we have no reason to believe that RHDV2 has arrived in the BCCE. The latest information about the distribution of RHDV2 can be found at USGS National Wildlife Health Center's Wildlife Health Information Sharing Partnership Event Reporting System (whispers.usgs.gov).

Home range size

The GPS technology we used to track and observe coyote and jackrabbit home ranges, movement patterns, and behaviors in this study provided insights that would otherwise not be possible, and these tools have rapidly become the standard for spatial ecology and predator-prey dynamics research. While using GPS technology for spatial ecology studies has become the standard, we now understand that, to be generalizable and comparable, the effective area of study must be quite large. For example, based on a spatial ecology study of coyotes in the eastern U.S., Hinton et al. (2015) suggested that study areas should be >2,500 km² to avoid bias in density, dispersal, and survival estimates. More recent studies have found that, for terrestrial carnivores in general, study areas should be multiple times larger than the average male home range size of the target species to obtain reliable demographic and movement-related parameter estimates (Tobler and Powell 2013, Suryawanshi et al. 2019, 2021, Nawaz et al. 2021, Murphy et al. 2022). However, for species like covotes and wolves that have multiple behavioral classes (i.e., residents and transients) with differential home range and movement characteristics (Hinton et al. 2015, Murphy et al. 2018), study areas often need to be much larger than expected. For instance, only 5 individual coyotes that were GPS-collared during our study were determined to be annual residents, suggesting that >75% of the covotes in the study area may have been transients with exceptionally large home range sizes that would necessitate an approximately 3,400-km² study area to obtain unbiased demographic parameter estimates.

Coyote home range size

Coyote home range studies have been ongoing in western North America for over fifty years (e.g., Robinson and Grand 1958, Knowlton 1972). Coyote research is frequently motivated by concerns about coyote influence on agricultural resources (Althoff and Gipson 1981, Stoddart et al. 2001,), game species (Berger et al. 2008, Ward et al. 2018), or more recently for their influence on species of conservation concern (Esque et al. 2010, Hinton et al. 2015, Woodruff et al. 2021). In their review of animal space use and coyote range expansions, Ellington and Murray

(2015) cited some 42 different studies. However, prior to the 1980's and 90's, field methods were not standardized, sample sizes were usually small because of the expense and logistics of tracking larger numbers, and technology could not provide the fine-resolution volumes of data that are typically required for accurately estimating home range sizes and analyzing habitat use via satellite technology.

Coyote populations are well-known to be comprised of two behavioral classes, residents and transients, that have different demographic contributions and space use requirements (Gese et al. 1988, Windberg and Knowlton 1988, Hinton et al. 2015, Murphy et al. 2018). Resident covotes defend a territory that may be occupied by breeders, juveniles, or pups in a pack against non-residents, both passively or aggressively, whereas transients do not defend territories and may wander over very large areas without fidelity to any one area and are usually not breeders (Hinton et al. 2015). Annual home range size estimates for resident coyotes in the BCCE (24 km² for males, and 29 km² for females) were within the range of annual home range estimates of 2.5 to 70 km² for the species across North America (Hinton et al. 2015, and citations therein). We speculated that home range sizes in the Mojave Desert would be larger than those in wetter, more productive ecosystems. Yet, the literature indicates that our estimates approximate the median of the size distribution for average annual home ranges of covotes across their geographic range (e.g., Kamler and Gipson 2000, Hinton et al. 2015). However, we caution that most previous studies that estimated coyote home range sizes used analytical methods that are now known to produce biased and inaccurate home range size estimates with poor confidence interval coverage (Noonan et al. 2019). Consequently, comparisons between our estimates and those from previous studies could be misleading.

Nevertheless, there may be an upper size limit for coyote territories that can be defended based on metabolic costs (Hinton et al 2015). We found that the average annual home range sizes between resident and transient coyotes differed by an order-of-magnitude. This difference was similar for coyotes in other systems, including the Great Plains of Oklahoma and eastern forests and agricultural lands of North Carolina (Kamler and Gipson 2000, Hinton et al. 2015, respectively). In consideration of annual home ranges, the ratio in our study was five residents to 14 transients, or 36:64, which is opposite the ratio found in eastern North Carolina of 70 % residents: 30% transients (Hinton et al. 2015). However, the ratio observed in eastern North Carolina was largely influenced by management practices, because the study area contained the non-essential experimental population of federally endangered red wolves (Canis rufus), within which all captured non-juvenile coyotes were surgically sterilized to prevent reproduction and then subsequently released back into the study area (Gese and Terletzky 2015, Hinton et al. 2015). This management action results in coyotes forming and maintaining long-term breeding pairs of residents that competitively exclude transients from territories, and territories not occupied by coyote breeding pairs are occupied by red wolf breeding pairs, which collectively mitigated the number of transient coyotes that could use the study area (Gese and Terletzky 2015, Gese et al. 2015). Similarly, a covote study in eastern Colorado observed a 78%:22% ratio of residents to transients (Gese et al. 1988), but the study area was located within a military training area where lethal management of coyotes was not allowed; therefore, the coyote population was effectively protected from processes that are known to increase the proportion of transients in a population (e.g., exploitation; Kilgo et al. 2017, Morin and Kelly 2017).

Average seasonal home range size estimates for resident male and female coyotes were not different between seasons in the BCCE, and were also within the range of other research results (Mills and Knowlton 1991, Hinton et al. 2015). Furthermore, summer seasonal home ranges for transient coyotes did not differ greatly between males and females, but there was a large difference between winter home range sizes for males and female transients. Transient male coyotes, in the BCCE, had substantially smaller summer home ranges than winter home ranges, while transient female coyotes had substantially smaller winter home ranges than summer home ranges, although the difference was smaller than for males. We speculate that the larger home range estimates for transient male coyotes in the winter season may reflect reproductive forays and responses to territorial defense by residents, whereas transient females having smaller home ranges during winter may reflect their higher reproductive value and associated potential availability as mates to form resident breeding pairs (Kilgo et al. 2017, Morin and Kelly 2017). We also had larger sample sizes of GPS-collared coyotes and more location data during the winter seasons, which may have resulted in summer home range size estimates that were biased. Alternatively, previous research indicates that coyote home range sizes increase during seasons when prey are scarce and there is speculation that mortality of transients during prey shortages may result in home range size increases for residents (Mills and Knowlton 1991). Resident coyotes tend to occupy higher quality habitats and have higher survival rates than transients (Kamler and Gipson 2000). Although this may be the case, we also consider that the interactions of transients, fluctuating prey availability, and access to resource subsidies may contribute to the patterns we have observed to date.

Evaluating differences in home range use between resident and transient coyotes may provide important insights into coyote population dynamics (Hinton et al. 2012), and this may be particularly useful as we seek to understand coyote use of the BCCE.

Black-tailed jackrabbit home range size

Home range configurations for black-tailed jackrabbits in the BCCE primarily occurred as elliptical/linear or approximately circular shapes and were divided about equally between those orientations. These configurations appeared to be generally associated with topographic features, where the non-circular home ranges occurred in narrow valleys or adjacent to more mountainous areas that restricted jackrabbit movement, whereas the circular home ranges were located in the open valley bottoms where movement is less constrained. In the Curlew Valley of northern Utah, black-tailed jackrabbit home range configurations were also generally elliptical in shape (Smith 1990).

Our continuous-time movement models identified 49 and 44 black-tailed jackrabbits in the BCCE as being resident and transient individuals, respectively. Only four individual jackrabbits were monitored across more than one season, due primarily to the combination of high mortality rates and collar malfunctions, which prevented estimating annual home range sizes. Among those four individuals, one adult male remained a transient during both seasons; one adult female transitioned from transiency during the first season to residency during the next season; one adult female maintained residency during both seasons; and one adult male transitioned from residency during the first season to transiency during the next season. Although we do not have social or behavioral observations to distinguish resident from transient blacktailed jackrabbits, such as we do for coyotes (Gese et al. 1988), most of the transient jackrabbits were adults (73%) and there was an approximately equal distribution of circular versus noncircular home range orientations among transients. These findings suggest that transiency in jackrabbits is unrelated to landscape characteristics (e.g., proximity to mountain range) or age/body size. Additionally, the proportion of transients in our sample of marked jackrabbits remained relatively constant across time (45-57%), suggesting that drought may not influence transiency in jackrabbits.

We could not find any previously published research on black-tailed jackrabbit home range or movements using GPS technology. As such, this appears to be a parallel advance to advances in coyote home range and movement research that occurred in the past 20 years once GPS collars were attached to coyotes. In the absence of GPS collars, VHF-telemetered blacktailed jackrabbits were frequently not found for weeks or perhaps never. In those cases, it was ultimately assumed in most cases that they died, which biases survivorship estimation. Using GPS in combination with VHF, we are gaining important new insights into jackrabbit ecology. It is still difficult to collect 100% of the data from jackrabbit studies, because the GPS collars do not accommodate satellited data downloads; thus, we must use VHF radios to find the GPS collars to download locations. However, with the robust amount of data we have secured already, it is apparent that black-tailed jackrabbit spatial ecology is more complicated than previously known, and that home range sizes are substantially larger than ever previously recorded.

Resident black-tailed jackrabbit home ranges are roughly twice as large in the winter (i.e., 69 ha M: 50 ha F) as in the summer (i.e., 33 ha M: 38 ha F) for both sexes. In contrast, the transient home range size estimates are roughly twice as large in the summer (584 ha M: 966 ha F) than in the winter (306 ha M: 637 ha F). Furthermore, the transient home ranges were five to 25 times the size of comparable resident home ranges by season. Unfortunately, there are few black-tailed jackrabbit home range studies with which to compare to the BCCE estimates (Simes et al. 2015). Size estimates for black-tailed jackrabbit home ranges provided on an annual basis ranged from <50 ha to >300 ha in a variety of habitat types across the western U.S. (Lechleitner 1958, French et al. 1965, Donoho 1971, Hungerford et al. 1974, Smith 1990, Harrison 2019). Previous home range studies provided annual home range estimations, but not seasonal ones; however, one study provided daytime and nighttime home range estimates (Harrison 2019). Black-tailed jackrabbit home range size and movements can be influenced by multiple interacting factors, including the availability and quality of cover plants, plant hydration status, water holding capacity of various soil types, surface water availability, predation pressure, recent weather history, and local climate factors (Flinders and Chapman 2003). Many of these are represented in the habitat selection analysis using resource selection functions that we discuss in the next section.

Habitat selection

Coyote habitat selection

We developed resource selection function models for coyote habitat selection across the BCCE. The models for summer 2020, winter 2020, and summer 2021 had adequate predictive performance measures and warranted further discussion of the driving factors involved in those models, while the model for winter 2021 had deficient predictive performance. NDVI, the vegetation greenup in response to precipitation, was the only factor having a positive influence on coyote use for all three models. We propose that this relationship is driven by the response of prey animals, particularly jackrabbits and other rodents, to the green vegetation and particularly during severe drought. Within the BCCE, these are probably prime hunting areas for coyotes. Distance to water (dWater), surface roughness (VRML), and terrestrial disturbance index (TDI) were all negatively related to increases in coyote habitat use in at least two of the three models.

Coyotes depend on surface water and regularly use water sources provided or enhanced by humans. In southern Arizona, coyote densities were greater in proximity to man-made water sources (Woodruff et al. 2021). Resource selection function results demonstrated the critical importance of water availability in shaping coyote use of the landscape in the BCCE. Throughout all seasons and years, both resident and transient coyotes selected for areas that were closer to water sources. Some surface waters in the BCCE are urban or suburban and related to Boulder City or solar energy generation plants. The movements of one male-female pair were centered around the sewage effluent south of Boulder City. Three other individual coyotes made regular visits to the water treatment facility ~200 m upstream from the effluent. Other individuals made regular visits through the town, likely acquiring water at will, as well as food resources. These examples of water acquisition were informative, though not unanticipated. However, based on GPS data, most other coyotes whose ranges were relatively far from urban development used surface water resources as well. One individual made multiple trips from the BCCE down to the Colorado River, and several other individuals made regular and frequent visits to wildlife guzzlers or other wildlife water developments. It is not clear exactly how coyotes use some of these guzzlers, because those designed for use by small animals have deterrents for larger animals like coyotes. Coyotes may obtain water directly from the guzzlers, or indirectly by capturing prey that visit the guzzlers. It is clear that coyotes repeatedly re-visit and use the guzzlers to acquire a critical resource (Figure 30). These anthropogenic sources of water (and food) are considered to be resource subsidies (Esque et al. 2010). These coyotes show clear movement biases in how they move across landscape by selecting routes that regularly and frequently intersect anthropogenic water sources. If coyotes were solely dependent on natural sources of water, such as springs and tinajas (natural surface water catchments from storms), then we speculate that the local population might be even smaller than our already low estimates.

The negative relationship with VRML seems counter-intuitive, as we had perceived more rugged and mountainous parts of the landscape to be where coyotes spent a lot of their time. We were also surprised to find a negative relationship between terrestrial disturbance index and coyote habitat use. We predicted that coyotes were attracted to the urban environment, roadsides, and solar generation plants. Our predictions were based on those features providing resource subsidies of food and water (Esque et al. 2010, Newsome et al. 2015, Larson et al. 2020)– although they also may present increased risk of vehicle collision or other complications. Indeed, one of the few study animals in the BCCE that was killed was hit by a vehicle collision on the Interstate 11 highway. Furthermore, a second coyote was killed by a hunter on the urban edge of the municipality of Boulder City. TDI had a positive relationship to coyote habitat use for the summer 2020 model. This was at the beginning of the drought and perhaps coyotes were beginning to require subsidies at this time.



Figure 30. Locations of where guzzlers are located that were used by coyots. Left: A landscapelevel view of the track of one coyote (indicated by red lines) revisiting several guzzlers (indicated by blue dots) in the Nelson Hills through the summer of 2020. Right: A close-up view illustrating the frequency of repeated guzzler (blue dot) use by a coyote (orange lines) on the edge of the BCCE.

In general, the top-ranked season × year habitat selection models predicted considerable temporal variation in probability of use for coyotes across the study area. Notably, 7% of the study area had high probabilities of coyote use (P > 0.80) during summer 2020, compared to 0.39%, 0.16%, and 0% during summer 2021, winter 2020, and winter 2021, respectively. Moderate probabilities of coyote use (0.50 < P < 0.80) were estimated for 42%, 35%, and 32% of the study area during winter 2020, summer 2020, and summer 2021, respectively. In contrast, most of the study area was estimated to have low probabilities of coyote use (P < 0.50) across all season × year combinations (\geq 58% of the study area); probabilities were lowest during winter 2021, when 71% of the study area was estimated to have P < 0.50 coyote use.

The temporal variation we observed for our top-ranked season × year habitat selection models was considerable. That combined with the low probability of use predicted among seasons and years indicates that coyotes select habitats that are adjacent to, or on the periphery of the BCCE, and that the BCCE may be suboptimal habitat that is used primarily by transient rather than resident coyotes. The high percentage of transient coyotes in the sample populations lends further evidence that this area may not be as preferred as nearby areas. A dominance of transient rather than resident coyotes in the BCCE presents multiple potential management issues, notably because transients sometimes have higher predation rates than residents and transients often have a wider dietary niche breadth than residents, increased predation of desert tortoises could result (Sacks et al. 1999, Lingle et al. 2022). However, the poor predictive performance for one of the coyote and three of the black-tailed jackrabbit habitat selection

models has stimulated us to consider whether we excluded an important habitat variable in the models or in some way misrepresented one of the variables that we incorporated. Future work will continue to focus on this important aspect of understanding habitat use.

Jackrabbit habitat selection

We modeled resource selection functions by seasons and years to understand how blacktailed jackrabbits interact with their habitat. Only one of the four models we created adequately describes resource selection and that was the model for winter of 2021. The top-ranked models for the other season × year combinations had poor predictive performance, indicating that our analysis likely omitted other ecological or environmental covariates that were also important to jackrabbit habitat selection. Nevertheless, during winter of 2021, we found that jackrabbits selected for areas that were further from water and located in less rugged terrain. Jackrabbits are well-adapted to living in habitats that rarely have surface water available. They require just 120 ml H₂O kg⁻¹ day⁻¹ to maintain water and depend largely on moisture in the vegetation they eat (Nagy et al. 1976). In the BCCE, surface water is only found at springs or tinajas in the mountains, and associated with the Colorado River, both of which are generally outside jackrabbit habitats and the areas that our models predicted higher probabilities of jackrabbit use. Within their range, water can be found at solar generation plants, the Boulder City Sewage effluent, and the periphery of suburban areas, and on rare occasions in the Eldorado Playa. Surface water at the solar plants that is available in ponds is probably not accessible to jackrabbits and would present a threat if they tried to access it. Some solar plants use water that creates puddles, but these large barren areas do not really provide the cover normally required for jackrabbits. Therefore, the negative association with water generally describes their traditional habitats. Furthermore, it is possible that coyotes' preferential selection for areas closer to surface water is a disincentive for black-tailed jackrabbits to frequent such areas that results in avoidance behavior by jackrabbits. Solar generation plants are a relatively new feature on the landscape and the interactions with wildlife have not been thoroughly studied, thus they require further attention to understand how they may influence wildlife.

Habitat with a high topographic position index (TPI) is represented by outwash plains (bajadas) below hilly and mountainous areas and the flatter valleys below these areas that are typical locales to find black-tailed jackrabbits. In the BCCE, the terrestrial disturbance index (TDI) is represented by suburban areas, roads and roadsides, and solar generation plants. Prior to these disturbances, jackrabbits inhabited all of these areas, and the physiography is consistent with areas they still use. Jackrabbits do not frequently inhabit the suburban edge, though they are occasionally observed in open parklands with native vegetation or on golf courses (TCE – personal observation). Jackrabbits are seen along roadsides with some frequency, and that is probably because they are nearly ubiquitous in the desert lowlands, but people travel mostly along the roads. Vegetation production is also enhanced on roadsides because of excess run-off from the nearly impermeable road surface. During a severe drought, the roadsides in the BCCE were the only place with green vegetation that is required for jackrabbits to meet their water requirements (Nagy et al. 1976). Furthermore, wildlife sometimes travel along roads and other linear disturbances in desert environments (Hromada et al. 2020), and although we have not analyzed this relationship, it is worth further consideration.

The positive relationship between black-tailed jackrabbits and solar generation plants is the most perplexing relationship we found. The BCCE is occupied only by traditional solar generation plants that denude the habitat 100% during construction and then strive to maintain zero vegetation production, which seemingly renders them useless to jackrabbits. Although they prefer "open" habitat, there is no clear benefit to them. However, during severe drought it is possible that the ancillary water that is used, or the rare precipitation events, have provided a run-off/run-on dynamic resulting in puddles on the periphery of the solar generation plants and this could attract jackrabbits if native or weedy vegetation were available while the jackrabbits are otherwise under duress during drought. This relationship also demands further attention. The greening of the desert following precipitation is represented in our models by NDVI. This is perhaps the most straightforward relationship to habitat variables that we have found. The greenup is extremely important to jackrabbits to meet their nutrition and hydration requirements. As we investigate this relationship further, we predict that finer grain habitat movements will also be linked to the pattern of greenup across the BCCE.

Survival and cause-specific mortality

Coyote survival and cause-specific mortality

Annual adult coyote survival probabilities for individuals within our study area, 0.95 during 2019-2020 and 0.81 during 2021, are quite high. The survival of coyotes in the BCCE is toward the upper range of reported values. Coyote survival estimates for harvestable populations, like the BCCE, have been documented to be as low as 0.47 for adults from an exploited population in Utah (Davison 1980), and 0.44 across age classes in Virginia (Morin et al. 2016). However, adult annual coyote survival has been reported to be as high as 0.98 across multiple years (Chamberlain and Leopold 2001), despite harvest being the prevalent cause of mortality.

Notably, our survival estimates only account for adult coyotes. Juvenile coyote survival estimates are not incorporated because we did not capture or monitor juvenile coyotes. Considering that BCCE adult survival is high, it is possible that juvenile survival is low, as has been reported in other populations (Windberg 1995, Morin 2016). Adult survival and abundance may regulate juvenile survival rates, and the two may be inversely related. (Windberg 1995, Morin 2016). It is surprising to see that coyote annual survival is as high as it is in an area open to harvest; the presence of the collars and ear tags may have kept some hunters from targeting our monitored animals. However, given our findings that the population may be dominated by transients, it is reasonable to assume that not only does the population have few juveniles due to a dearth of breeding pairs, but those transients may also be less vulnerable to harvest than residents (Nelson and Lloyd 2005).

Of 21 monitored coyotes, two died by hunting, two by vehicle collision, and one by starvation. Previous studies have reported that the majority of mortalities are human caused, usually a result of harvest or vehicle collisions (Gese 1989; Kamler and Gipson 2000; Morin 2016; Windberg 1985). Our study, during which 80% of recorded mortalities were a result of harvest or vehicle strike, are in keeping with these previous findings

Jackrabbit survival and cause-specific mortality

Survival estimates for black-tailed jackrabbits in the BCCE are within the range of published estimates ranging from 23% to 77 % (Stoddart 1970, Gross et al. 1974). Survivorship modeling for the BCCE indicated a general decline in jackrabbit survival through time from 2019 through 2021, whether we considered our optimistic models where unknown fates were assumed alive or our pessimistic models in which unknown ates were assumed to be mortalities. This pattern was consistent with a declining population during the time of the study, which was observed in the density and population growth rate estimates. The top three competing models for the optimistic modeling independently included age class, residency status, and sex each as

interactions with year as contributing factors to the survival pattern, while the top three competing models for pessimistic modeling included year, sex, and the interaction of the two as driving factors. The leading cause specific mortality factors were unknown predators, unknown causes, kit fox predation, and coyote predation, in that order, for both the optimistic and pessimistic models. The high incidence of unknown specific causes indicates that either kit foxes or coyotes could be the leading cause of mortality, or potentially some other source. We do not have mortality sensors on the telemetry equipment, and the rabbits were only visited on a biweekly or monthly basis, such that cause of mortality was difficult to determine.

Camera-traps placed at tortoise carcasses

Although mammalian carnivores were the most frequently observed visitors to desert tortoise carcasses, the visitation to carcasses does not identify them as the cause of mortality very effectively. As previously discussed, if carcasses are not investigated immediately after they are killed it becomes increasingly difficult to prove causation. One way to increase the information available for this investigation would be to use mortality sensors, although desert tortoises are notoriously sedentary, and this must be taken into consideration prior to investment in additional technology.

Population density, abundance, and growth

Coyote population density, size, and growth

Coyote density estimation is challenging, in large part because the species is generally cryptic, elusive, physically nondescript, and occupies landscapes at low densities. We elected to estimate coyote density using camera-traps and the random encounter model (REM) because of the potential utility in estimating density of unmarked populations, and coyotes do not have individually unique pelage patterns that can be used to definitively identify individuals in photographs with certainty (e.g., the unique rosette patterns on jaguars [*Panthera onca*]; Tobler and Powell 2013). If accurate and reliable density estimates can be obtained with REM, this could allow for a relatively cost-effective way to estimate coyote densities and monitor their population over time. However, REM has a very strict set of assumptions and associated requirements for obtaining reliable density estimates, which study designs often violate or the assumptions are rendered intractable by the ecology of some species.

One of the primary assumptions of REM is that animal detections and movements are independent of the camera-traps, which requires that cameras be placed entirely randomly with respect to the landscape (Rowcliffe et al. 2008). However, coyotes and most other medium- and large-bodied carnivores do not use landscapes randomly; consequently, randomly placed cameras that ignore coyote movement ecology are expected to yield low detection rates for the species. Indeed, the randomly placed grid cameras produced low detection rates of coyotes compared to the strategically placed cameras, which may have negatively biased the REM density estimates from the randomly placed camera data.

Comparing our estimated coyote densities to previously published estimates is difficult because of the lack of standardization in estimation methods (e.g., Murphy et al. 2022). Moreover, historical density values were often based on antiquated statistical techniques with poor reliability, most of which produce derived *indices* of density rather than *estimates* of density with quantifiable measures of uncertainty. Knowlton (1972), in reviewing a number of previous coyote surveys using those density-derivation methods, surmised based on indices that coyotes likely existed at densities of 0.2-0.4 coyotes/km² across their range. However, coyotes have since

colonized large portions of North America that were not reflected in Knowlton's (1972) review, and many of those colonized areas have much more productive habitats and prey resources than coyotes' native range in the western U.S. (Hody and Kays 2020). Our REM estimates of coyote density from only the randomly placed cameras were within the range of reported densities for the species, albeit towards the lower bound of the range, and were most similar to spatially explicit estimates for coyotes in the Great Basin and Sonoran deserts (Lonsinger et al.2018, Woodruff et al. 2021). Collectively, the densities estimated by Lonsinger et al. (2018), Woodruff et al. (2021), and our study in the BCCE suggest that coyotes may occupy American deserts at lower densities than previously postulated. Based on the results of our home range analysis, we suspect that the low densities are at least partially a reflection of the local population at BCCE being comprised primarily of transients that have larger home range sizes, with comparatively few resident breeding pairs. However, the REM that we used to estimate density is incapable of accounting for demographic and detection heterogeneity that arises in coyote populations between the two behavioral classes. Accommodating the differential detection and movement rates of residents and transients, which we detected in our home range size analysis, is critical to obtaining accurate population density estimates for coyotes (Murphy et al. 2018, Ruprecht et al. 2021), and failure to account for the two classes in modeling frameworks can negatively bias density estimates (Murphy et al. 2018). Thus, we suspect that our coyote density estimates based on the randomly placed cameras may be slight underestimates.

Nevertheless, coyote densities in the West are presumed to be heavily influenced by lagomorph population trends, particularly jackrabbits. For instance, researchers in Idaho estimated covote densities during 1979-1995 and found that covote density varied from 0.001 to 0.0139 coyotes/km², and that this variation reflected population-level responses to fluctuations in local jackrabbit densities (Stoddart et al. 2001). Across our 4-year study, we observed no such relationship between coyote and jackrabbit densities, suggesting that coyotes in the BCCE may not be as reliant on jackrabbits as they are in other western ecosystems. However, a three to fouryear time-lag between jackrabbit population declines and corresponding coyote population declines may exist (Stoddart et al. 2001); thus, given the peak in jackrabbit density at BCCE occurred during winter 2019-2020, our study may not have been of sufficient duration to detect a potential covote population response. Furthermore, anthropogenic resource subsidization of food and water sources also likely impacts covote density in the BCCE and may temper the population-level effects of jackrabbit declines. For example, researchers in southern California examined the influence of anthropogenic foods on coyote density and found that subsidization may bolster coyote densities (Fuller 2001). A more recent study in the Sonoran Desert examined coyote densities in two study areas, one with a higher density of artificial water sources than the other (Woodruff et al. 2021). That study found that coyote densities in the area with artificial water sources (0.11 coyotes/km²) were double the densities in the area with comparatively fewer artificial water sources (0.05 coyotes/km²).

Black-tailed jackrabbit population density, size, and growth

Density estimates for black-tailed jackrabbits in the BCCE between 2018 through 2021 ranged from 2.77 to 16.97 jackrabbits/km². These density values are within the range of other density estimates across the west, but relatively low compared to the past eight decades that range from 2 jackrabbits/km² to 1,258 jackrabbits/km² (Leichleitner 1958, French et al. 1965, Gross et al. 1974, Anderson and Shumar 1986). The population estimation for the BCCE represents a relatively short sampling time during a period of unusually strong drought conditions, and we should expect a rebound if wetter conditions prevail in the near term, given

our finding of a strong positive relationship between jackrabbit density and precipitation levels. Furthermore, some of the historical estimates of black-tailed jackrabbit densities were severely overestimated due to sampling bias of large jackrabbit aggregations in localized areas (e.g., Leichleitner 1958) and the use of analytical methods that are known to positively bias density estimates. Black-tailed jackrabbit population densities fluctuate through time and they are cyclic in northern populations (Leichleitner 1958), but densities track environmental conditions such as drought more closely in southerly populations (Simes et al. 2015), such as the BCCE.

Extrapolating our density estimate for black-tailed jackrabbits across the 2,770 -km² study area provides a population size of 7,676–47,024 total jackrabbits in the BCCE. To put such large population size estimates into perspective, French et al. (1965) compared the estimation for the number of jackrabbits for their study area in Idaho to the estimation for the number of coyotes in the area and found there to be 1,100 black-tailed jackrabbits per coyote. A similar extrapolation using data from the BCCE provides an estimate of 274 to 855 jackrabbits per coyote during from 2018 to 2021. The estimation from Idaho was during a peak jackrabbit population fluctuation. However, our jackrabbit abundance estimates for the BCCE are likely overestimates, because, based on our habitat selection analysis, not all of the entire 2,770-km² study area was comprised of suitable habitat. Our habitat selection models estimated that at maximum, approximately 1,773 km² of the study area, or 64%, had >0.50 probability of jackrabbit use. Applying our density estimates to that area results in a jackrabbit population size of 4,913 to 30,098 total jackrabbits, which represents approximately 223 to 547 jackrabbits per coyote.

While we observed a population increase of 124% between the summer of 2018 to the winter of 2020, we then observed a severe drop in population density. The estimate for population growth known as λ (lambda) was 0.93 (95% CI = 92-94) in the BCCE across the entire 4-year study period and this suggests a cumulative population decline. Our analyses indicate that the population decline was strongly related to the drought that occurred at this time.

Density estimation caveats

As noted in the Methods, we obtained camera detection zone measurements from a single camera-trap, from which we calculated d and θ , and we applied those camera parameter values to all deployed camera-traps. This approach violated a primary assumption of random encounter models that detection zones vary among camera-traps with differences in habitat and landscape features that are present at each camera-trap (Rowcliffe et al. 2008). After considering this oversight, we determined that post-hoc measurements were not feasible because of changes over time with the camera placements and failure of some cameras. However, considering the very open nature of the habitat surveyed by the randomly placed grid cameras, which had very few obstructions, we believe that any detection zone variation among those cameras was likely minimal and therefore the impact on density estimations may have been minimal. With the acquisition of new cameras for which we will acquire camera-specific calculations of detection zones, we can provide more insight into the potential consequences of said deficiency.

Recent studies have found that REM density estimates can be positively biased, but the causes of this have not yet been definitively identified and have remained speculative to date (Cusack et al. 2015, Twining et al. 2022). By placing camera-traps both randomly and strategically in the study area, we were able to directly investigate the consequences of violating a fundamental REM assumption – that animal movement is independent of camera-traps (Rowcliffe et al. 2008). Our findings revealed that strategically placing cameras in locations that are more likely to detect the target species, which violates the independence assumption of REM,

causes substantial positive bias in density estimates, potentially as much as +200%. This finding has critical implications for the interpretation of density estimates from previous studies that used REM for a wide range of species around the globe. Many species for which REM has been applied are imperiled, but multiple studies violated the REM independence assumption by deploying camera-traps strategically, which may have resulted in conservation or management decisions being unknowingly based on severe overestimates of population density (e.g., Cusack et al. 2015, Loonam et al. 2020). Specific to the BCCE, we strongly advise against making any management decisions for coyotes or jackrabbits based on density estimates that were produced from detection data acquired at strategically placed cameras, as those estimates are unreliable.

Spotlight line transect surveys

Spotlight transect surveys were discontinued in 2022 because of extremely low capture rates and the need to put more emphasis on radio-telemetry and camera trap surveys. Spotlight transect surveys have provided useful information however, this research project requires higher resolution in the data we use to try and understand population dynamics than can be provide by relative abundances. The relative abundance approach is particularly useful for extremely large surveys areas such as the state of Nevada, and for which the logistics and costs for that large of an area would be unfeasible.

Management Considerations

With the goal of this project to gain a better understanding of the population dynamics and community interdependencies of Mojave desert tortoises, black-tailed jackrabbits, and their predators – coyotes, toward a strategy to mitigate future tortoise translocations from being severely impacted by coyote predation, we consider that it is appropriate to begin discussions about management considerations prior to the end of the project.

We suggest that discussion about potential ways to reduce anthropogenic subsidies to coyotes is important, and that topics for discussion might include ways to reduce subsidies associated with city dumps, the Boulder City sewage effluent, golf courses, solar plants and other water sources, a place to start.

A second area for consideration is weaponized tortoises. In this regard there are a variety of ways that have been suggested to dissuade mammalian predators. Materials may be attached to live tortoises that can emit particularly bad odors or tastes to curious coyotes. A potentially highly effective nonlethal method could be distributing baits treated with ziram (zinc dimethyl dithio-carbamate) throughout a tortoise release area 7-10 days prior to translocations, or at tortoise carcasses, and then additional placement of ziram-treated baits near tortoise burrows post-release (Baker et al. 2005, Clark County et al. 2022). Alternatively, tortoise decoys may be used to deploy materials to teach coyotes that tortoises are not a good food source (Tim Shields, personal communication).

Finally, various methods of reproductive interference with coyotes have been experimented with and are worth considering. Surgical sterilization of adult coyotes has been used to effectively reduce coyote predation on domestic lambs and wild pronghorn fawns by as much as 90% (Bromley and Gese 2001, Seidler et al. 2014). The population-level effects of surgical sterilization can be substantial, potentially suppressing canid population size by >70% for 10 years after implementation (Conner et al. 2008). Removal of adult coyotes and their litters or eliminating the litters alone has reduced predation of domestic sheep (Till and Knowlton 1983), though the effects of removals or lethal management are typically always ephemeral (Kilgo et al. 2014, 2017; Minnie et al. 2016). A variety of chemical methods of contraception have been studied for decades and most of them involve endocrine disruption, however, a contraceptive vaccine has not been developed for coyotes at this time (Padodara et al. 2022). Experiments were completed to understand if coyote pairs that did not reproduce would reduce predation on livestock and this was proven successful.

There are important caveats to any management actions that seek to modify wildlife populations for desired outcomes. We suggest the following items as further discussion topics for consideration while the data are still being collected on population dynamics. Coyote populations are driven by resources. Removal of coyotes may only be temporary if resource subsidies are not addressed. With regard to age structure of BCCE population –lethal management of adult coyotes may exacerbate the issue by providing opportunities to more juveniles or other transients. Any of these methods may have high social and monetary cost and involve long-term, ongoing maintenance.

Future Plans

Plans for Phase II of desert tortoise predator-prey dynamics in the Boulder City Conservation Easement include acquiring new wildlife/trail cameras to replace those damaged by normal use in the past 4 years. The sun deteriorates sensors on the cameras and they are not refurbishable. As the new cameras are deployed, they will be re-distributed to accommodate the most useful analytical methods and calibrated for use in density estimations. The camera data provides high resolution data that is much more useful for the purposes of this research project than the road surveys. While road surveys provide a broad-brush estimation of abundance and can be useful for estimations for very large-scale studies – such as state-wide studies, we will focus on camera surveys. We also will explore upgrading jackrabbit GPS units to satellite units if the budget allows. The data structure we are using for storage and analysis is being re-designed to accommodate different analytical tools than we previously used.

CONCLUSION

Phase I of this research project occurred during a period of unprecedented drought in our lifetimes. By comparing black-tailed jackrabbit density estimates with mean monthly precipitation we concluded that their population decline was strongly related to the drought. Black-tailed jackrabbits are affected by drought through food availability and hydration because they depend on the plants they eat for essential water. While coyotes certainly preyed on some of the jackrabbits in the study, direct cause for mortality often was unresolved. Based on previous predator-prey studies across the West involving coyotes and jackrabbits, one might expect coyote densities to track black-tailed jackrabbit densities. However, we did not find this to be the case during the 4-year duration of our study. Instead, we found coyote density to be generally unresponsive to the drought, though coyote populations have been known to lag behind a decline in prey species. As an alternative to that, we have hypothesized that coyotes were somewhat invariant to the decline in rabbit densities, because of the availability of subsidized food resources from the nearby suburban environment.

The results of the research may also be complicated by the social mixture of coyotes including residents and transient coyotes. Recent research, in only the past 5 years, has indicated that social status within the population can have important implications for coyote population demography, spatial ecology, and perhaps affect other aspects of coyote ecology. More research into these dynamics is warranted, and necessary to gain a better idea of the predator and prey dynamics in the BCCE.

While the importance of social status in coyotes has been documented in the literature, our use of GPS collars on black-tailed jackrabbits has opened up a completely new area of research for understanding jackrabbit ecology. We are unable to find previous work involving GPS collars on jackrabbits. Because of this innovation we learned that jackrabbits also have social status. Our ability to classify the social categories as resident and transient was made possible with the recent advent of novel continuous-time movement models, which provide a more realistic characterization of animal movement and space use. While the social structure of coyotes is somewhat known, and are related to other aspects of social status and reproductive biology in important ways, we know very little about how residency versus transiency affect jackrabbit ecology. Our continued work on this topic will seek to define the ramifications of jackrabbits being resident versus transient.

REFERENCES CITED

- Abrantes, J., W. van der Loo, J.L. Pendu, and P. Esteves. 2012. Rabbit haemorrhagic disease (RHD) and rabbit haemorrhagic disease virus (RHDV): a review. Veterinary Research 43. https://doi.org/10.1186/1297-9716-43-12.
- Altemus, M.M. 2016. Antelope jackrabbit (*Lepus alleni*) spatial ecology, habitat characteristics, and overlap with the endangered pima pineapple cactus (*Coryphantha scheeri var. Robustispina*). Unpublished M.Sc. Thesis. University of Arizona, Tucson, Arizona, USA.
- Althoff, D.P., and P.S. Gipson. 1981. Coyote family spatial relationships with reference to poultry losses. Journal of Wildlife Management 45:641-649.
- Andelt, W.F., 1985. Behavioral ecology of coyotes in south Texas. Wildlife Monographs 94:3-45.
- Andelt, W.F., and P.S. Gipson. 1979. Home range, activity, and daily movements of coyotes. Journal of Wildlife Management 43:944-951.
- Anderson, J. E., and M. L. Shumar. 1986. Impacts of black-tailed jackrabbits at peak population densities on sagebrush-steppe vegetation. Journal of Range Management 39:152.
- Arjo WM, and D.H. Pletscher.1999. Behavioral responses of coyotes to wolf recolonization in northwestern Montana. Canadian Journal of Zoology 77: 1919–1927. https://doi.org/10.1139/z99-177.
- Arnold, T.W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. Journal of Wildlife Management 74:1175-1178.
- Averill-Murray, R.C., C.H. Fleming, and J.D. Riedle. 2020. Reptile home ranges revisited: A case study of space use of Sonoran Desert tortoises (*Gopherus morafkai*). Herpetological Conservation and Biology 15:253-271.
- Baker, S.E., S.A. Ellwood, R. Watkins, and D.W. MacDonald. 2005. Non-lethal control of wildlife: Using chemical repellents as feeding deterrents for the European badger *Meles meles*. Journal of Applied Ecology 42:921-931.

- Balph, D.F. 1971. Sampling small mammal populations in Curlew Valley methodological study. US International Biological Program, Desert Biome, Logan, Utah, USA.
- Bastille-Rousseau, G., and G. Wittemyer. 2019. Leveraging multidimensional heterogeneity in resource selection to define movement tactics of animals. Ecology Letters 22:1417-1427.
- Bauer, J.W., K.A. Logan, L.L. Sweanor, and W.M. Boyce. 2005. Scavenging behavior in puma. Southwestern Naturalist 50:466-471.
- Beasley, J.C., Z.H. Olson, N. Selva, and T.L. DeVault. 2019. Ecological functions of vertebrate scavenging. Pg. 125-127 in P.P. Olea, P. Mateo-Tomas, and J.A. Sanchez-Zapata (Eds.). *Carrion ecology and management*. Springer Nature, Switzerland.
- Berger, K.M., E.M. Gese, and J. Berger. 2008. Indirect effects and traditional trophic cascades: A test involving wolves, coyotes, and pronghorn. Ecology 89:818-828.
- Bisi, F., S. Newey, M. Nodari, L.A. Wauters, A. Harrison, S. Thirgood, and A. Martinoli. 2011. The strong and the hungry: bias in capture methods for mountain hares *Lepus timidus*. Wildlife Biology 17:311-316.
- Bivand, R.S., E. Pebesma, and V. Gomez-Rubio. 2013. *Applied spatial data analysis with R, 2nd edition*. Springer, New York, USA.
- Blejwas, K.M., C.L. Williams, G.T. Shin, D.R. McCullough, and M.M. Jaeger. 2006. Salivary DNA evidence convicts breeding male coyotes of killing sheep. Journal of Wildlife Management 70:1087-1093.
- Booth, J.G., G. Casella, H. Friedl, and J.P. Hobert. 2003. Negative binomial loglinear mixed models. Statistical Modeling 3:179-191.
- Boyce, M.S., P.R. Vernier, S.E. Nielsen, and F.K.A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modelling 157:281-300.
- Bronson, F.H., and O.W. Tiemeier. 1959. The relationship of precipitation and black-tailed jack rabbit populations in Kansas. Ecology 40:194-198.
- Brooks, M.E., K. Kristensen, K.J. van Benthem, A. Magnusson, C.W. Berg, A. Nielsen, H.J. Skaug, M. Maechler, and B.M. Bolker. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. The R Journal 9:378-400.
- Burnham, K.P., and D.R. Anderson. 2002. *Model selection and multimodel inference: A practical information-theoretic approach*. Springer-Verlag, New York, USA.
- Calenge, C. 2006. The package *adehabitat* for the R software: Tool for the analysis of space and habitat use by animals. Ecological Modelling 197:516-519.
- Caravaggi, A., P.B. Banks, A.C. Burton, C.M.V. Finlay, P.M. Haswell, M.W. Hayward, M.J. Rowcliffe, and M.D. Wood. 2017. A review of camera trapping for conservation behaviour research. Remote Sensing in Ecology and Conservation 3:109-122.
- Caravaggi, A., M. Zaccaroni, F. Riga, S.C. Schai-Braun, J.T.A. Dick, W.I. Montgomery, and N. Reid. 2016. An invasive-native mammalian species replacement process captured by

camera trap survey random encounter models. Remote Sensing in Ecology and Conservation 2:45-58.

- Carr, N.B., I.I.F. Leinwand, and D.J.A. Wood. 2017. A multiscale index of landscape intactness for the Western United States. Pg. 55-74 in *Multiscale guidance and tools for implementing a landscape approach to resource management in the Bureau of Land Management*. U.S. Geological Survey Open-File Report 2016-1207. U.S. Geological Survey, Reston, USA.
- Calabrese, J.M., C.H. Fleming, and E. Gurarie. 2016. *ctmm*: An R package for analyzing animal relocation data as a continuous-time stochastic process. Methods in Ecology and Evolution 7:1124-1132.
- Caudell, J.N., and D. Zimmerman. 2011. Indiana Wildlife Disease News 6:16.
- Chamberlain, M.J., and B.D. Leopold. 2001. Survival and cause-specific mortality of adult coyotes (*Canis latrans*) in central Mississippi. American Midland Naturalist 145:414-418.
- Chronert, J.M., J.A. Jenks, D.E. Roddy, M.A. Wild, and J.G. Powers. 2007. Effects of sarcoptic mange on coyotes at Wind Cave National Park. Journal of Wildlife Management 71:1987-1992.
- Clark County. 2000. Clark County Multiple Species Habitat Conservation Plan and Environmental Impact Statement. 550 pp.
- Clark County. 2021. Boulder City Conservation Easement Management Plan. 135 pp. https://files.clarkcountynv.gov/clarknv/Environmental%20Sustainability/Desert%20Cons ervation/Management%20Plans/BCCE%20Management%20Plan%20Version%203.5_fi nal%202021.pdf. 45 p. Plus appendices. March 2021. 129 pp.
- Clark, F.W. 1972. Influence of jackrabbit density on coyote population change. Journal of Wildlife Management 36:343-356.
- Collins, G.H., S.L. Petersen, C.A. Carr, and L. Pielstick. 2014. Testing VHF/GPS collar design and safety in the study of free-roaming horses. PLoS one 9:e103189.
- Conner, M.M., M.R. Ebinger, and F.F. Knowlton. 2008. Evaluating coyote management strategies using a spatially explicit, individual-based, socially structured population model. Ecological Modelling 219:234-247.
- Cornely, J.E. 1980. Home ranges and diets of coyotes in Joshua Tree National Monument in relation to prey densities. National Park Service/University of Nevada, Las Vegas. Contribution #009/14. Unpublished Dissertation.
- Cusack, J. J., A. Swanson, T. Coulson, C. Packer, C. Carbone, A. J. Dickman, M. Kosmala, C. Lintott, and J. M. Rowcliffe. 2015. Applying a random encounter model to estimate lion density from camera traps in Serengeti National Park, Tanzania. Journal of Wildlife Management 79:1014-1021.
- Cypher, B.L. 1995. Coyote morphometric characteristics and mass dynamics in the San Joaquin Valley, California. Southwestern Naturalist 40:360-365.

- Dilts, T.E., M.E. Blum, K.T. Shoemaker, P.J Weisberg, and K.M. Stewart. In Prep. Topographic ruggedness indices in ecology: past, present and future.
- Donoho, H.S. 1971. Dispersion and dispersal of white-tailed and black-tailed jackrabbits, Pawnee National Grasslands. U.S. International Biological Program, Grassland Biome, Colorado State University, Fort Collins, CO. Technical Report No 96. 55 pp.
- Duchesne, T., D. Fortin, and N. Courbin. 2010. Mixed conditional logistic regression for habitat selection studies. Journal of Animal Ecology 79:548-555.
- Ellington, E.H. and D.L. Murray. 2015. Influence of hybridization on animal space use: A case study using coyote range expansion. Oikos 124:535-542. https://doi.org/10.1111/oik.01824.
- Emblidge, P.G., K.E. Nussear, T.C. Esque, C.M. Aiello, and A.D. Walde. 2015. Severe predation on a population of threatened desert tortoises: The American Badger as a novel predator. Endangered Species Research 28:109-116.
- Esque, T.C., K.E. Nussear, K.K. Drake, A.D. Walde, K.H. Berry, R.C. Averill-Murray, A.P. Woodman, W.I. Boarman, P.A. Medica, J. Mack, and J.S. Heaton. 2010. Effects of subsidized predators, resource variability, and human population density on desert tortoise populations in the Mojave Desert, USA. Endangered Species Research 12:167-177.
- Fleming, C.H., and J.M. Calabrese. 2017. A new kernel density estimator for accurate homerange and species-range area estimation. Methods in Ecology and Evolution 8:571-579.
- Fleming, C.H., J.M. Calabrese, T. Mueller, K.A. Olson, P. Leimgruber, and W.F. Fagan. 2014a. From fine-scale foraging to home ranges: A semivariance approach to identifying movement modes across spatiotemporal scales. American Naturalist 183:E154-E167.
- Fleming, C.H., J.M. Calabrese, T. Mueller, K.A. Olson, P. Leimgruber, and W.F. Fagan. 2014b. Non-Markovian maximum likelihood estimation of autocorrelated movement processes. Methods in Ecology and Evolution 5:462-472.
- Fleming, C.H., W.F. Fagan, T. Mueller, K.A. Olson, P. Leimgruber, and J.M. Calabrese. 2015. Rigorous home-range estimation with movement data: A new autocorrelated kerneldensity estimator. Ecology 96:1182-1188.
- Fleming, C.H., M.J. Noonan, E.P. Medici, and J.M. Calabrese. 2019. Overcoming the challenge of small effective sample sizes in home-range estimation. Methods in Ecology and Evolution 10:1679-1689.
- Fleming, C.H., D. Sheldon, W.F. Fagan, P. Leimgruber, T. Mueller, D. Nandintsetseg, M.J. Noonan, K.A. Olson, E. Setyawan, A. Sianipar, and J.M. Calabrese. 2018. Correcting for missing and irregular data in home-range estimation. Ecological Applications 28:1003-1010.
- Flinders, J.T., and Chapman, J.A. 2003. Black-tailed Jackrabbit *Lepus californicus* and allies. Pages 126-146 *in* G.A. Feldhamer, B.C. Thompson, and J.A. Chapman, editors. Wild mammals of North America: biology, management, and conservation. The Johns Hopkins University Press, Baltimore, Maryland, USA.

- Frehner, E.H., E.R. Buechley, T. Christensen, and C.H. Sekercioglu. 2017. Subterranean caching of domestic cow (*Bos taurus*) carcasses by American badgers (*Taxidea taxus*) in the Great Basin Desert, Utah. Western North American Naturalist 77:124-129.
- Fremling, C.R. 1955. Seasonal abundance of the tick Dermacentor parumapertus. Ecology 36:162-163.
- French, N. R., R. McBride, and J. Detmer. 1965. Fertility and population density of the blacktailed jackrabbit. Journal of Wildlife Management 29:14-26.
- Garshelis, D.L., and C.R. McLaughlin. 1998. Review and evaluation of breakaway devices for bear radio collars. Ursus 10:459-465.
- Gese, E.M., F.F. Knowlton, J.R. Adams, K. Beck, T.K. Fuller, D.L. Murray, T.D. Steury, M.K. Stoskopf, W.T. Waddell, and L.P. Waits. 2015. Managing hybridization of a recovering endangered species: The red wolf *Canis rufus* as a case study. Current Zoology 61:191– 205.
- Gese, E.M., O.J. Rongstad, and W.R. Mytton. 1988. Home range and habitat use of coyotes in southeastern Colorado. Journal of Wildlife Management 52:640-646.
- Gese, E.M., O.J. Rongstad, and W.R. Mytton. 1989. Population dynamics of coyotes in southeastern Colorado. Journal of Wildlife Management 53(1):174-181.
- Gese, E.M., and P.A. Terletzky. 2015. Using the "placeholder" concept to reduce genetic introgression of an endangered carnivore. Biological Conservation 192:11-19.
- Gier, H.T. 1968. Coyotes in Kansas. Agricultural Experiment Station, Kansas State University, Manhattan, KS. Bulletin 393. 120 pp.
- Gipson, P.S., W.B. Ballard, R.M. Nowak, and L.D. Mech. 2000. Accuracy and precision of estimating age of gray wolves by tooth wear. Journal of Wildlife Management 64:752-758.
- Gotelli, N.J. 2008. A primer of ecology, 4th edition. Sinauer Associates, Sunderland, MA, USA.
- Gray, B. 2020. *cmprsk*: Subdistribution analysis of competing risks. R package version 2.2-10. <u>https://cran.r-project.org/package=comprsk</u>.
- Greger, P.D., and P.A. Medica. 2009. *Gopherus agassizii* (desert tortoise) predation/mountain lions. Herpetological Review 40:75–77.
- Gross, J.E., L.C. Stoddart, and F.H. Wagner. 1974. Demographic analysis of a northern Utah jackrabbit population. Wildlife Monographs 40:3-68.
- Grueber, C.E., S. Nakagawa, R.J. Laws, and I.G. Jamieson. 2011. Multimodel inference in ecology and evolution: Challenges and solutions. Journal of Evolutionary Biology 24:699-711.
- Gurarie, E., and O. Ovaskainen. 2011. Characteristic spatial and temporal scales unify models of animal movement. American Naturalist 178:113-123.

- Harris G., R. Thompson, J.L. Childs, and J.G. Sanderson. 2010. Automatic storage and analysis of camera trap data. Bulletin of the Ecological Society of America 91:352-360.
- Harrison, X.A., L. Donaldson, M.E. Correa-Cano, J. Evans, D.N. Fisher, C.E.D. Goodwin, B.S. Robinson, D.J. Hodgson, and R. Inger. 2018. A brief introduction to mixed effects modelling and multi-model inference in ecology. PeerJ 6:e4794.
- Harrison, R.L., 2019. Sylvilagus audubonii and Lepus californicus home range sizes in the Chihuahuan Desert. Western North American Naturalist 79:603-609. doi.org/10.3398/064.079.0415.
- Haskell, H.S., and H.G. Reynolds. 1947. Growth, developmental food requirements, and breeding activity of the California Jack Rabbit. Journal of Mammalogy Vol. 28:129-136.
- Heisey, D.M., and T.K. Fuller. 1985. Evaluation of survival and cause-specific mortality rates using telemetry data. Journal of Wildlife Management 49:668-674.
- Heisey, D.M., and B.R. Patterson. 2006. A review of methods to estimate cause-specific mortality in the presence of competing risks. Journal of Wildlife Management 70:1544-1555.
- Henke, S.E., D.B. Pence, and F.C. Bryant. 2002. Effect of short-term coyote removal on populations of coyote helminths. Journal of Wildlife Diseases 38:54-67.
- Hijmans, R.J., and J. van Etten. 2012. *raster*: Geographic analysis and modeling with raster data. R package version 2.0-12. <u>http://cran.r-roject.org/package=raster</u>.
- Hinton, J.W., M.J. Chamberlain, F.T. van Manen. 2012. Long-distance movements of transient coyotes in eastern North Carolina. American Midland Naturalist 168: 281–288. http://dx.doi.org/10.1674/0003-0031-168.2.281.
- Hinton, J.W., E. Heppenheimer, K.M. West, D. Caudill, M.L. Karlin, J.C. Kilgo, J.J. Mayer, K.V. Miller, M. Walch, B. vonHoldt, and M.J. Chamberlain. 2019. Geographic patterns in morphometric and genetic variation for coyote populations with emphasis on southeastern coyotes. Ecology and Evolution 9:3389-3404.
- Hinton, J.W., F.T. van Manen, and M.J. Chamberlain. 2015. Space use and habitat selection by resident and transient coyotes (*Canis latrans*). PLoS ONE 10:e0132203.
- Hody, J.W., and R. Kays. 2020. Mapping the expansion of coyotes (*Canis latrans*) across North and Central America. Zookeys 759:81-97.
- Hromada, S.J., T.C. Esque, A.G. Vandergast, K.E. Dutcher, C.I. Mitchell, M.E. Gray, T. Chang, B.G. Dickson, and K.E. Nussear. 2020. Using movement to inform conservation corridor design for Mojave desert tortoise. *Movement Ecology* 8:1-18.
- Hungerford, C.R., C.H. Lowe, and R.L. Madsen. 1974. Population studies of the desert cottontail (Sylvilagus audubonii), black-tailed jackrabbit (Lepus californicus) and Allen's jackrabbit (Lepus alleni) in the Sonoran Desert. U.S. International Biological Program, Desert Biome, Utah State University, Logan, UT. Research Memorandum 74-23. 22 pp.

- Inman, R.D., K.E. Nussear, T.C. Esque, A.G. Vandergast, S.A. Hathaway, D.A. Wood, K.R. Barr, and R.N. Fisher. 2014. Mapping habitat for multiple species in the desert Southwest. U.S. Geological Survey Open-File Report 2014-1134. U.S. Geological Survey, Reston, USA.
- Jedrzejewski, W., H.S. Robinson, M. Abarca, K.A. Zeller, G. Velasquez, E.A.D. Paemelaere, J.F. Goldberg, E. Payan, R. Hoogesteijn, E.O. Boede, K. Schmidt, M. Lampo, A.L. Viloria, R. Carreno, N. Robinson, P.M. Lukacs, J.J. Nowak, R. Salom-Perez, F. Castaneda, V. Boron, H. Quigley. 2018. Estimating large carnivore populations at global scale based on spatial predictions of density and distribution – Application to the jaguar (*Panthera onca*). PLoS ONE 13:e0194719.
- Johnson, C.J., Nielsen, S.E., E.H. Merrill, T.L. McDonald, and M.S. Boyce. 2006. Resource selection functions based on use-availability data: Theoretical motivation and evaluation methods. Journal of Wildlife Management 70:347-357.
- Johnson, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65-71.
- Johnston, M., L. Bould, M. O'Donoghue, M. Holdsworth, P. Marmion, R. Bilney, A.E. Reside, D. Caldwell, R. Gaborov, and T. Gentles. 2014. Field efficacy of Curiosity® bait for management of a feral cat population at Roxby Downs, South Australia. Technical Report Series No. 253. Arthur Rylah Institute for Environmental Research, Heidelberg, Victoria, Australia.
- Julien, Y., and J.A. Sobrino. 2008. NDVI seasonal amplitude and its variability. International Journal of Remote Sensing 29:17-18.
- Kamler, J.F., W.B. Ballard, P.R. Lemons, R.L. Gilliland, and K. Mote. 2005. Home range and habitat use of coyotes in an area of native prairie, farmland, and CRP fields. American Midland Naturalist 153:396-404.
- Kamler, J.F., and P.S. Gipson. 2000. Space and habitat use by resident and transient coyotes. Canadian Journal of Zoology 78: 2106–2111. https://doi.org/10.1139/z00-153.
- Karelus, D.L., B.W. Geary, L.A. Harveson, and P.M. Harveson. 2021. Movement ecology and space-use by mountain lions in West Texas. Global Ecology and Conservation 31:e01859.
- Kays, R.W., and K.M. Slauson. 2008. Remote Cameras. *In* Noninvasive Survey Methods for Carnivores. I. Long, R.A., P. MacKay, W.J. Zielinski, and J. C. Rey, eds. Island Press, Washington, D.C. USA. Pp. 110-141.
- Keith, L.B. 1983. Role of food in hare population cycles. Oikos 40:385-395.
- Kilgo, J.C., H.S. Ray, M. Vukovich, M.J. Goode, and C. Ruth. 2012. Predation by coyotes on white-tailed deer neonates in South Carolina. Journal of Wildlife Management 76:1420-1430.
- Kilgo, J.C., C.E. Shaw, M. Vukovich, M. J. Conroy, and C. Ruth. 2017. Reproductive characteristics of a coyote population before and during exploitation. Journal of Wildlife Management 81:1386-1393.
- Kilgo, J.C., M. Vukovich, H.S. Ray, C.E. Shaw, and C. Ruth. 2014. Coyote removal, understory cover, and survival of white-tailed deer neonates. Journal of Wildlife Management 78:1261-1271.
- Kim, J.H. 2019. Multicollinearity and misleading statistical results. Korean Journal of Anesthesiology 72:558-569.
- Knowlton, F. F. 1972. Preliminary interpretations of coyote population mechanics with some management implications. Journal of Wildlife Management 36:369-382.
 - Knowlton, F. F., E. M. Gese, and M. M. Jaeger. 1999. Coyote Depredation Control: An interface between Biology and Management. Journal of Range Management 52:398.
- Knowlton, F.F., P.E. Martin, and J.C. Haug. 1968. A telemetric monitor for detecting animal activity. Journal of Wildlife Management 32:943-948.
- Larson RN, J.L. Brown, T. Karels, and S.P.D. Riley. 2020. Effects of urbanization on resource use and individual specialization in coyotes (*Canis latrans*) in southern California. PLoS ONE 15(2): e0228881. <u>https://doi.org/10.1371/journal.pone.0228881.</u>
- Laufenberg, J.S., J.D. Clark, M.J. Hooker, C.L. Lowe, K.C. O'Connell-Goode, J.C. Troxler, M.M. Davidson, M.J. Chamberlain, and R.B. Chandler. 2016. Demographic rates and population viability of black bears in Louisiana. Wildlife Monograph 194:1-37. https://doi.org/10.1002/wmon.1018.
- Laundré, J.W., and B.L. Keller. 1984. Home-range size of coyotes: A critical review. Journal of Wildlife Management 48:127-139.
- Lechleitner, R.R. 1958. Movements, density, and mortality in a black-tailed jackrabbit population. Journal of Wildlife Management 22:371-384.
- Leopold B.D., and Chamberlain M.J. 2001. Carnivorous furbearers. *In* J.G. Dickson, *ed*. Wildlife of southern forests: habitat and management. Washington: Hancock House Publishers. 248–277 pp.
- Lindsey, C.T., J.J. Nugent, J.W. Wilde, and S.J. Johnson. 2014. Hanford site black-tailed jackrabbit monitoring report for fiscal year 2013. Richland, Washington, USA. Doi:10.2172/1123702.
- Lingle, S., C.-J. Breiter, D.B. Schowalter, and J.F. Wilmshurst. 2022. Prairie dogs, cattle subsidies and alternative prey: Seasonal and spatial variation in coyote diet in a temperate grassland. Wildlife Biology 2022:e01048.
- Lipson M.P., and P.R. Krausman. 1988. Parasites of desert leporids in the Picacho Mountains, Arizona. Southwestern Naturalist 33:487-488.
- Lonsinger, R.C., P.M. Lukacs, E.M. Gese, R.N. Knight, and L.P. Waits. 2018. Estimating densities for sympatric kit foxes (*Vulpes macrotis*) and coyotes (*Canis latrans*) using noninvasive genetic sampling. Canadian Journal of Zoology 96:1080-1089.

- Loonam, K. E., D. E. Ausband, P. M. Lukacs, M. S. Mitchell, and H. S. Robinson. 2020. Estimating abundance of an unmarked, low-density species using cameras. Journal of Wildlife Management 85:87-96.
- Lydecker, H.W., P.B. Banks, and D.F. Hochuli. 2019. Counting ticks (Acari: Ixodida) on hosts is complex: a review and comparison of methods. Journal of Medical Entomology 56:1527-1533.
- Lyons, E.T., M.F. Hansen, and O.W. Tiemeier. 1960. Helminth parasites of black-tailed jack rabbit in southwestern Kansas. Transactions of the Kansas Academy of Science 63:135-140.
- Manly, B., L. McDonald, D. Thomas, T. McDonald, and W. Erickson. 2002. *Resource selection by animals*. Kluwer Academic Publishers, Dordrecht, Netherlands.
- McGregor, M., and D. Jones. 2016. Tattoo pens as a low-cost approach to in field identification of medium sized mammals. Wildlife Society Bulletin 40:169-173.
- Meek, P., and P. Fleming. 2014. Camera trapping: wildlife management and research. Csiro Publishing VIC, Australia.Mills, L.S., and F.F. Knowlton. 1991. Coyote space use in relation to prey abundance. Canadian Journal of Zoology 69:1516-1521.
- Minnie, L., A. Gaylard, and G.I.H. Kerley. 2016. Compensatory life-history responses of a mesopredator may undermine carnivore management efforts. Journal of Applied Ecology 53:379-387.
- Monerroso P., G. Garrote, A. Serronha, E. Santos, M. Delibes-Mateos, J. Abrantes, R. Perez de Ayala, F. Silvestre, J. Carvalho, I. Vasco, and A.M. Lopes. 2016. Disease-mediated bottom-up regulation: An emergent virus affects a keystone prey, and alters the dynamics of trophic webs. Scientific Reports 6:1-9.
- Morin, D.J., and M.J. Kelly. 2017. The dynamic nature of territoriality, transience and biding in an exploited coyote population. Wildlife Biology 1:1-13.
- Morin, D.J., M.J. Kelly, and L.P. Waits. 2016. Monitoring coyote population dynamics with fecal DNA and spatial-capture recapture. Journal of Wildlife Management 80(5):824-836.
- Murphy, S.M., B.C. Augustine, J.R. Adams, L.P. Waits, and J.J. Cox. 2018. Integrating multiple genetic detection methods to estimate population density of social and territorial carnivores. Ecosphere 9:e02479. https://doi.org/10.1002/ecs2.2479.
- Murphy, S.M., R.A. Beausoleil, H. Stewart, and J.J. Cox. 2022. Review of puma density estimates reveals sources of bias and variation, and the need for standardization. Global Ecology and Conservation 35:e02109.
- Murray, D.L., and B.R. Patterson. 2006. Wildlife survival estimation: Recent advances and future directions. Journal of Wildlife Management 70:1499-1503.
- Nagy, K.A, V.H. Shoemaker, and W.R. Costa. 1976. Water, electrolyte, and nitrogen budgets of jackrabbits (*Lepus californicus*) in the Mojave Desert. Physiological Zoology 49:351-363. https://doi.org/10.1086/physzool.49.3.30155693.

- Nawaz M.A., B.U. Khan, A. Mahmood, M. Younas, and C. Sutherland. 2021. An empirical demonstration of the effect of study design on density estimations. Scientific Reports 11:1-9.
- Nelson, T.A., and D.M. Lloyd. 2005. Demographics and condition of coyotes in Illinois. American Midland Naturalist 153:418-427.
- Newsome, S.D., H.M. Garbe, E.C. Wilson, S.D. Gehrt. 2015. Individual variation in anthropogenic resource use in an urban carnivore. Oecologia 178:115–128. DOI 10.1007/s00442-014-3205-2.
- Noonan, M.J., M.A. Tucker, and C.H. Fleming. 2019. A comprehensive analysis of autocorrelation and bias in home range estimation. Ecological Monographs 89:e01344.
- Northrup, J.M., M.B. Hooten, C.R. Anderson Jr, and G. Wittemyer. 2013. Practical guidance on characterizing availability in resource selection functions under a use-availability design. Ecology 94:1456-1463.
- Nowicki, S.A., R.D. Inman, T.C. Esque, K.E. Nussear, and C.S. Edwards. 2019. Spatially consistent high-resolution land surface temperature mosaics for thermophysical mapping of the Mojave Desert. Sensors 19:2669. https://doi.org/10.3390/s19122669.
- Nussear, K.E., T.C. Esque, R.D. Inman, K.A. Thomas, L. Gass, C.S.A. Wallace, J.B. Blainey, D.M. Miller, and R.H. Webb. 2009. Modeling habitat of the desert tortoise (*Gopherus agassizii*) in the Mojave and parts of the Sonoran Deserts of California, Nevada, Utah, and Arizona. U.S. Geological Survey open-file report 2009-1102. 18 pp.
- Padodara, V.K., V.K. Singh, A.B. Odedara, A.A. Vasava, A.K. Sharma, and V.M. Mehta. 2022 Modern approaches to contraception in domestic and wild animals: A Review. Journal of Global Ecology and Environment 16(1): 14-25, 2022.
- Pearce, J., and S. Ferrier. 2000. Evaluating the predictive performance of habitat models developed using logistic regression. Ecological Modelling 133:225-245.
- Pebesma, E.J., and R.S. Bivand. 2005. S classes and methods for spatial data: the sp package. R news 5:9-13.
- Pence, D.B., and L.A. Windberg. 1994. Impact of a sarcoptic mange epizootic on a coyote population. Journal of Wildlife Management 58:624-633.
- Philip, C.B., J.F. Bell, and C.L. Larson. 1955. Evidence of infectious diseases and parasites in a peak population of black-tailed jack rabbits in Nevada. Journal of Wildlife Management 19:225-233.
- Platt, S.G., G.T. Salmon, S.M. Miller, and T.R. Rainwater. 2010. Scavenging by a bobcat, *Lynx rufus*. Canadian Field-Naturalist 124:265-267.
 - Pollock, K.H., S.R. Winterstein, C.M. Bunck, and P.D. Curtis. 1989. Survival analysis in telemetry studies: The staggered entry design. Journal of Wildlife Management 53:7-15.
 - R Core Team. 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <u>https://www.R-project.org/</u>.

- Ralls, K., and P. J. White. 1995. Predation on San Joaquin kit foxes by larger canids. Journal of Mammalogy 76:723.
- Revelle, W. 2022. *Psych*: Procedures for psychological, psychometric, and personality research. R package version 2.2.9. <u>https://cran.r-project.org/package=psych</u>.
- Robin, X., N. Turck, A. Hainard, N. Tiberti, F. Lisacek, J.-C. Sanchez, and M. Muller. 2011. *pROC*: An open-source package for R and S+ to analyze and compare ROC curves. BMC bioinformatics 12:1-8.
- Robinson, W.B., and E.F. Grand. 1958. Comparative movements of bobcats and coyotes as disclosed by tagging. Journal of Wildlife Management 22: 117-122.
- Rogers, A.M., M.R. Gibson, T. Pockette, J.L. Alexander, and J.F. Dwyer. 2014. Scavenging of migratory bird carcasses in the Sonoran Desert. Southwestern Naturalist 59:544-549.
- Rosasco, M.E. 1957. Seasonal abundance of the tick Dermacentor parumapertus on the blacktailed jack rabbit with notes on other ectoparasites. Journal of Mammalogy 38:485-490.
- Rovero, F. and D. Spitale. 2016. Presence/absence and species inventory. Pages 43-67 *in* F. Rovero, and F. Zimmerman, eds. Camera trapping for wildlife research. Pelagic Publishing, Exeter, UK.
- Rowcliffe, J.M., J. Field, S.T. Turvey, and C. Carbone. 2008. Estimating animal density using camera traps without the need for individual recognition. Journal of Applied Ecology 45:1228-1236.
- Ruprecht, J.S., C.E. Eriksson, T.D. Forrester, D.A. Clark, M.J. Wisdom, M.M. Rowland, B.K. Johnson, and T. Levi. 2021. Evaluating and integrating spatial capture-recapture models with data of variable individual identifiability. Ecological Applications 31:e02405.
- Rusch, D.H. 1965. Some movements of black-tailed jackrabbits in northern Utah. *M.S. Thesis*, Utah State University, Logan, Utah, USA.
- Sacks, B.N., M.M. Jaeger, J.C.C. Neale, and D.R. McCullough. 1999. Territoriality and breeding status of coyotes relative to sheep predation. Journal of Wildlife Management 63:593-605.
- Sanderson, J.G. and G. Harris. 2014. Automatic camera trap data organization, storage and analysis without entering data by hand from keyboard. *In* Camera trapping Wildlife Management and Research, Meek, P and P. Fleming *eds*. Csiro Publishing VIC, Australia.
- Sandmeier, F.C., C.R. Tracy, S. duPré, and K. Hunter. 2009. Upper respiratory tract disease (URTD) as a threat to desert tortoise populations: A reevaluation. Biological Conservation 142:1255–1268. https://doi.org/10.1016/j.biocon.2009.02.001.
- Sappington M. J., K.M. Longshore, and D.B. Thompson. 2007. Quantifying landscape ruggedness for animal habitat analysis: a case study using bighorn sheep in the Mojave Desert. Journal of Wildlife Management 71:1419-1426. <u>https://doi.org/10.2193/2005-723</u>.

- Schai-Braun, S.C., H.G. Rödel, and K. Häcklander. 2012. The influence of daylight regime on diurnal locomotor activity patterns of the European hare (*Lepus europaeus*) during summer. Mammalian Biology 77:434-440.
- Schemnitz, S.D., G.R. Batcheller, M.J. Lovallo, H.B. White, and M.W. Fall. 2009. Capturing and handling wild animals. Pages 232-269. *in* N.J. Silvy, editor. *The Wildlife Techniques Manual*. Johns Hopkins University Press, Baltimore, Maryland, USA.
- Schober, P., C. Boer, and L.A. Schwarte. 2018. Correlation coefficients: Appropriate use and interpretation. Anesthesia and Analgesia 126:1763-1768.
- Shivik, J.A., D.J. Martin, M.J. Pipas, J. Turnan, and T.J. DeLiberto. 2010. Initial comparison: jaws, cables, and cage traps to capture coyotes. Wildlife Society Bulletin 33:1375-1383.
- Sikes, R.S, and the Animal Care and Use Committee of the American Society of Mammalogists. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. Journal of Mammalogy 97:663-688.
 - Simes, M. T., K. M. Longshore, K. E. Nussear, G. L. Beatty, D. E. Brown, and T. C. Esque. 2015. Black-tailed and white-tailed jackrabbits in the American west: History, ecology, ecological significance, and survey methods. Western North American Naturalist 75:491–519.
- Smith, G.W. 1990. Home range and activity patterns of black-tailed jackrabbits. Great Basin Naturalist 50:249-256.
- Smith, G.W., L.C. Stoddart, and F.F. Knowlton. 2002. Long-distance movements of black-tailed jackrabbits. Journal of Wildlife Management 66:463-469.
- Smith, G.W., and N.C. Nydegger. 1985. A spotlight, line-transect method for surveying jack rabbits. Journal of Wildlife Management 49:699-702.
- Starkey, L.A., M. D. West, A.W. Barrett, J.A. Saucier, T.P. O'Connor, K.L. Paras, M.H. Reiskind, M.V. Reichard, and S.E. Little. 2013. Prevalence of Antibodies to Spotted Fever Group Rickettsia spp. and Ehrlichia spp. in Coyotes (Canis latrans) in Oklahoma and Texas, USA. Journal of Wildlife Diseases 49:670-673.
- Stoddart, L.C. 1970. A telemetric method for detecting jackrabbit mortality. Journal of Wildlife Management 34:501-507.
- Stoddart, L.C., R.E. Griffiths, and F.F. Knowlton. 2001. Coyote responses to changing jackrabbit abundance affect sheep predation. Journal of Range Management 54:15-20.
- Suryawanshi, K.R., M. Khanyari, K. Sharma, P. Lkhagvajav, and C. Mishra. 2019. Sampling bias in snow leopard population estimation studies. Population Ecology 61:268-276.
- Suryawanshi, K.R., A. Reddy, M. Sharma, M. Khanyari, A. Bijoor, D. Rathore, H. Jaggi, A. Khara, A. Malgaonkar, A. Ghoshal, and J. Patel. 2021. Estimating snow leopard and pretty populations at large spatial scales. Ecological Solutions and Evidence 2:e12115.

- Therneau, T.M. 2021. *A package for survival analysis in R*. R package version 3.2-11. <u>https://cran.r-project.org/package=survival</u>.
- Tiemeier, O.W. 1965. Bionomics. The black-tailed jackrabbit in Kansas, Kansas Agricultural Experimental Station Bulletin #140, Kansas State University, Manhattan, USA.
- Therneau, T.M., and P.M. Grambsch. 2000. *Modeling survival data: Extending the Cox model*. Springer-Verlag, New York, USA.
- Tobler, M.W., and G.V. Powell. 2013. Estimating jaguar densities with camera traps: problems with current designs and recommendations for future studies. Biological conservation 159:109-118.
- Twining, J.P., C. McFarlane, D. O'Meara, C. O'Reilly, M. Reyne, W.I. Montgomery, S. Helyar, D.G. Tosh, and B.C. Augustine. 2022. A comparison of density estimation methods for monitoring marked and unmarked animal populations. Ecosphere 13:e4165.
- Uhlenbeck, G.E., and L.S. Ornstein. 1930. On the theory of the Brownian motion. Physical Review 36:823-841.
- Clark County, Bureau of Land Management, U.S. Fish and Wildlife Service, and U.S. Geological Survey. 2022. Translocation plan for the Stump Springs regional augmentation site, Clark County, Nevada. U.S. Fish and Wildlife Service, Reno, USA.
- Vatcheva, K.P., M. Lee, J.B. McCormick, and M.H. Rahbar. 2016. Multicollinearity in regression analyses conducted in epidemiologic studies. Epidemiology 6:227.
- Ward, J.N., J.W. Hinton, K.L. Johannsen, M.L. Karlin, K.V. Miller, M.J. Chamberlain. 2018. Home range size, vegetation density, and season influences prey use by coyotes (*Canis latrans*). PLoS ONE 13(10): e0203703. https://doi.org/10.1371/journal.pone.0203703.
- Western Regional Climate Center. 2022. *Climate data: Boulder City, Nevada (261071)*. Western Regional Climate Center, Reno, USA. <u>https://wrcc.dri.edu/cgi-bin/cliMAIN.pl?nv1071</u>.
- Windberg, L.A. 1995. Demography of a high-density coyote population. Canadian Journal of Zoology 73:942–954.
- Windberg, L.A., H.L. Anderson, R.M. Engeman. 1995. Survival of coyotes in southern Texas. Journal of Wildlife Management 49(2):301-307.
- Windberg, L.A., and F.F. Knowlton. 1988. Management implications of coyote spacing patterns in southern Texas. Journal of Wildlife Management 52:632-640.
- Woodbury, A.M. 1955. Ecology of the Great Salt Lake Desert: I. An annual cycle of the desert jackrabbit. Ecology 36:353-356.
- Woodruff, S.P., D.R. Eacker, and L.P. Waits. 2021. Estimating coyote densities with local, discrete Bayesian capture-recapture models. Journal of Wildlife Management 85:73-86. <u>https://doi.org/10.1002/jwmg.21967.</u>
- Wywialowski, A.P., and F.F. Knowlton. 1983. Effect of simulated radio-transmitters on captive black-tailed jackrabbits. Pages 1-11 in D.G. Pincock, ed. *Proceedings of the 4th*

International Conference on Wildlife Biotelemetry. Applied Microelectronics Institute and Technical University of Nova Scotia, Halifax, Nova Scotia, Canada.

Zuur, A.F., E.N. Ieno, and C.S. Elphick. 2010. A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution 1:3-14.

SUPPLEMENTARY TABLES

Supplementary Table S1. Model selection of generalized linear mixed models explaining coyote habitat selection during winter 2020 (Nov. 2019 – Apr. 2020). Covariates were animal sex, residency status (Status), distance to water (dWater), topographic position index (TPI), surface texture (ATI), terrestrial development index (TDI), vector ruggedness mean local (VRML), and normalized difference vegetation index amplitude (NDVIamp). Random intercepts for individuals (1|ID) were included in all models.

Model	Ka	LL ^b	AICc ^c	$\Delta AICc^{d}$	W_i^e
Use ~ Sex × Status + dWater + TPI + TDI + VRML + NDVIamp + $(1 ID)$	10	-6769.25	13558.52	0.00	0.98
Use ~ Sex × Status + dWater + TPI + VRML + NDVIamp + $(1 ID)$	9	-6774.14	13566.30	7.78	0.02
Use ~ Sex × Status + dWater + TPI + TDI + NDVIamp + $(1 ID)$	9	-6793.54	13605.10	46.58	0.00
Use ~ Sex × Status + dWater + TPI + NDVIamp + $(1 ID)$	8	-6796.92	13609.85	51.33	0.00
Use ~ Sex × Status + dWater + ATI + TDI + VRML + NDVIamp + $(1 ID)$	10	-6808.59	13637.20	78.69	0.00
Use ~ Sex × Status + dWater + TDI + VRML + NDVIamp + $(1 ID)$	9	-6811.22	13640.46	81.95	0.00
Use ~ Sex × Status + dWater + ATI + VRML + NDVIamp + $(1 ID)$	9	-6814.27	13646.56	88.04	0.00
Use ~ Sex × Status + dWater + ATI + TDI + NDVIamp + $(1 ID)$	9	-6814.39	13646.80	88.28	0.00
Use ~ Sex × Status + dWater + VRML + NDVIamp + $(1 ID)$	8	-6816.02	13648.05	89.53	0.00
Use ~ Sex × Status + dWater + ATI + NDVIamp + $(1 ID)$	8	-6819.78	13655.56	97.05	0.00
Use ~ Sex × Status + dWater + TDI + NDVIamp + $(1 ID)$	8	-6821.00	13658.02	99.50	0.00
Use ~ Sex × Status + dWater + NDVIamp + $(1 ID)$	7	-6824.84	13663.69	105.17	0.00
Use ~ Sex × Status + dWater + TPI + TDI + VRML + $(1 ID)$	9	-6844.32	13706.65	148.14	0.00
Use ~ Sex × Status + dWater + TPI + VRML + $(1 ID)$	8	-6854.86	13725.74	167.22	0.00
Use ~ Sex × Status + dWater + TPI + TDI + $(1 ID)$	8	-6877.26	13770.54	212.02	0.00
Use \sim Sex \times Status + dWater + TPI + (1 ID)	7	-6885.37	13784.76	226.24	0.00
Use ~ Sex × Status + dWater + ATI + TDI + VRML + (1 ID)	9	-6885.90	13789.81	231.30	0.00
Use ~ Sex × Status + dWater + TDI + VRML + $(1 ID)$	8	-6888.47	13792.95	234.43	0.00
Use ~ Sex × Status + dWater + ATI + TDI + $(1 ID)$	8	-6895.55	13807.12	248.60	0.00
Use ~ Sex × Status + dWater + ATI + VRML + $(1 ID)$	8	-6897.33	13810.68	252.16	0.00
Use ~ Sex × Status + dWater + VRML + $(1 ID)$	7	-6898.69	13811.40	252.88	0.00
Use ~ Sex × Status + dWater + TDI + $(1 ID)$	7	-6903.59	13821.19	262.67	0.00
Use ~ Sex × Status + dWater + ATI + $(1 ID)$	7	-6906.62	13827.26	268.74	0.00
Use ~ Sex × Status + dWater + (1 ID)	6	-6912.23	13836.47	277.95	0.00

Supplementary Table S2. Model selection of generalized linear mixed models explaining coyote habitat selection during summer 2020 (May 2020 – Oct. 2020). Covariates were animal sex, residency status (Status), distance to water (dWater), topographic position index (TPI), surface texture (ATI), terrestrial development index (TDI), vector ruggedness mean local (VRML), and normalized difference vegetation index amplitude (NDVIamp). Random intercepts for individuals (1|ID) were included in all models.

Model	Ka	LL ^b	AICc ^c	$\Delta AICc^{d}$	w_i^{e}
Use ~ Sex × Status + dWater + ATI + TDI + VRML + NDVIamp + $(1 ID)$	10	-16986.26	33992.53	0.00	1.00
Use ~ Sex × Status + dWater + ATI + TDI + NDVIamp + $(1 ID)$	9	-16994.25	34006.51	13.98	0.00
Use ~ Sex × Status + dWater + ATI + VRML + NDVIamp + $(1 ID)$	9	-17002.00	34022.00	29.48	0.00
Use ~ Sex × Status + dWater + ATI + NDVIamp + $(1 ID)$	8	-17009.98	34035.97	43.44	0.00
$Use \sim Sex \times Status + dWater + TPI + TDI + VRML + NDVIamp + (1 ID)$	10	-17009.91	34039.83	47.30	0.00
Use ~ Sex × Status + dWater + TDI + VRML + NDVIamp + $(1 ID)$	9	-17011.74	34041.49	48.96	0.00
Use ~ Sex × Status + dWater + TDI + NDVIamp + (1 ID)	8	-17031.49	34078.99	86.46	0.00
Use ~ Sex × Status + dWater + TPI + TDI + NDVIamp + $(1 ID)$	9	-17031.41	34080.83	88.30	0.00
Use ~ Sex × Status + dWater + TPI + VRML + NDVIamp + $(1 ID)$	9	-17037.45	34092.90	100.37	0.00
Use ~ Sex × Status + dWater + VRML + NDVIamp + $(1 ID)$	8	-17038.50	34093.00	100.47	0.00
Use ~ Sex × Status + dWater + NDVIamp + $(1 ID)$	7	-17061.54	34137.08	144.55	0.00
Use ~ Sex × Status + dWater + TPI + NDVIamp + $(1 ID)$	8	-17061.52	34139.05	146.52	0.00
Use ~ Sex × Status + dWater + TPI + TDI + VRML + $(1 ID)$	9	-17087.54	34193.09	200.56	0.00
Use ~ Sex × Status + dWater + TPI + TDI + $(1 ID)$	8	-17110.62	34237.25	244.72	0.00
Use ~ Sex × Status + dWater + TPI + VRML + $(1 ID)$	8	-17115.48	34246.97	254.44	0.00
Use ~ Sex × Status + dWater + ATI + TDI + VRML + $(1 ID)$	9	-17115.48	34248.97	256.44	0.00
Use ~ Sex × Status + dWater + TDI + VRML + $(1 ID)$	8	-17117.72	34251.44	258.91	0.00
Use ~ Sex × Status + dWater + ATI + TDI + $(1 ID)$	8	-17124.36	34264.72	272.19	0.00
Use ~ Sex × Status + dWater + TDI + $(1 ID)$	7	-17130.48	34274.96	282.43	0.00
Use ~ Sex × Status + dWater + ATI + VRML + $(1 ID)$	8	-17135.05	34286.11	293.58	0.00
Use \sim Sex \times Status + dWater + TPI + (1 ID)	7	-17141.00	34296.01	303.48	0.00
Use ~ Sex × Status + dWater + VRML + $(1 ID)$	7	-17141.26	34296.52	303.99	0.00
Use ~ Sex × Status + dWater + ATI + $(1 ID)$	7	-17143.94	34301.88	309.35	0.00
Use ~ Sex × Status + dWater + (1 ID)	6	-17156.55	34325.10	332.57	0.00

Supplementary Table S3. Model selection of generalized linear mixed models explaining coyote habitat selection during winter 2021 (Nov. 2020 – Apr. 2021). Covariates were animal sex, residency status (Status), distance to water (dWater), topographic position index (TPI), surface texture (ATI), terrestrial development index (TDI), vector ruggedness mean local (VRML), and normalized difference vegetation index amplitude (NDVIamp). Random intercepts for individuals (1|ID) were included in all models.

Model	Ka	LL ^b	AICc ^c	$\Delta AICc^{d}$	w_i^e
Use ~ Sex × Status + dWater + ATI + TDI + $(1 ID)$	8	-21715.58	43447.16	0.00	0.49
Use ~ Sex × Status + dWater + ATI + TDI + NDVIamp + $(1 ID)$	9	-21715.43	43448.87	1.71	0.21
Use ~ Sex × Status + dWater + ATI + TDI + VRML + $(1 ID)$	9	-21715.44	43448.89	1.73	0.21
Use ~ Sex × Status + dWater + ATI + TDI + VRML + NDVIamp + $(1 ID)$	10	-21715.30	43450.60	3.44	0.09
Use ~ Sex × Status + dWater + ATI + NDVIamp + $(1 ID)$	8	-21794.15	43604.31	157.15	0.00
Use ~ Sex × Status + dWater + ATI + VRML + NDVIamp + $(1 ID)$	9	-21794.00	43606.00	158.84	0.00
Use ~ Sex × Status + dWater + ATI + $(1 ID)$	7	-21800.71	43615.42	168.26	0.00
Use ~ Sex × Status + dWater + ATI + VRML + $(1 ID)$	8	-21800.55	43617.10	169.94	0.00
$Use \sim Sex \times Status + dWater + TPI + TDI + VRML + NDVIamp + (1 ID)$	10	-21840.84	43701.69	254.53	0.00
Use ~ Sex × Status + dWater + TPI + TDI + VRML + $(1 ID)$	9	-21845.24	43708.48	261.32	0.00
Use ~ Sex × Status + dWater + TDI + VRML + NDVIamp + $(1 ID)$	9	-21861.67	43741.35	294.19	0.00
Use ~ Sex × Status + dWater + TDI + VRML + $(1 ID)$	8	-21862.77	43741.55	294.38	0.00
Use ~ Sex × Status + dWater + TPI + TDI + NDVIamp + $(1 ID)$	9	-21863.67	43745.35	298.19	0.00
$Use \sim Sex \times Status + dWater + TPI + VRML + NDVIamp + (1 ID)$	9	-21865.13	43748.26	301.10	0.00
Use ~ Sex × Status + dWater + TPI + TDI + $(1 ID)$	8	-21867.59	43751.18	304.02	0.00
Use ~ Sex × Status + dWater + TDI + NDVIamp + $(1 ID)$	8	-21874.39	43764.78	317.62	0.00
Use ~ Sex × Status + dWater + TDI + $(1 ID)$	7	-21875.92	43765.85	318.69	0.00
Use ~ Sex × Status + dWater + TPI + VRML + $(1 ID)$	8	-21880.53	43777.06	329.90	0.00
Use ~ Sex × Status + dWater + TPI + NDVIamp + $(1 ID)$	8	-21888.22	43792.45	345.29	0.00
Use ~ Sex × Status + dWater + TPI + $(1 ID)$	7	-21902.65	43819.29	372.13	0.00
Use ~ Sex × Status + dWater + VRML + NDVIamp + $(1 ID)$	8	-21905.20	43826.39	379.23	0.00
Use ~ Sex × Status + dWater + VRML + $(1 ID)$	7	-21913.27	43840.55	393.39	0.00
Use ~ Sex × Status + dWater + NDVIamp + $(1 ID)$	7	-21913.96	43841.92	394.76	0.00
Use ~ Sex × Status + dWater + (1 ID)	6	-21922.24	43856.49	409.33	0.00

Supplementary Table S4. Model selection of generalized linear mixed models explaining coyote habitat selection during summer 2021 (May 2021 – Oct. 2021). Covariates were animal sex, residency status (Status), distance to water (dWater), topographic position index (TPI), surface texture (ATI), terrestrial development index (TDI), vector ruggedness mean local (VRML), and normalized difference vegetation index amplitude (NDVIamp). Random intercepts for individuals (1|ID) were included in all models.

Model	K ^a	LL ^b	AICc ^c	$\Delta AICc^{d}$	w_i^e
Use ~ Sex × Status + dWater + ATI + TDI + VRML + NDVIamp + $(1 ID)$	10	-14533.67	29087.35	0.00	0.90
Use ~ Sex × Status + dWater + ATI + TDI + NDVIamp + $(1 ID)$	9	-14536.87	29091.75	4.40	0.10
Use ~ Sex × Status + dWater + ATI + TDI + $(1 ID)$	8	-14617.08	29250.17	162.82	0.00
Use ~ Sex × Status + dWater + ATI + TDI + VRML + $(1 ID)$	9	-14616.17	29250.35	163.00	0.00
Use ~ Sex × Status + dWater + TPI + TDI + NDVIamp + $(1 ID)$	9	-14635.50	29289.01	201.66	0.00
Use ~ Sex × Status + dWater + ATI + VRML + NDVIamp + $(1 ID)$	9	-14635.87	29289.76	202.41	0.00
Use ~ Sex × Status + dWater + TPI + TDI + VRML + NDVIamp + $(1 ID)$	10	-14635.29	29290.60	203.25	0.00
Use ~ Sex × Status + dWater + ATI + NDVIamp + $(1 ID)$	8	-14638.86	29293.72	206.37	0.00
$Use \sim Sex \times Status + dWater + TDI + VRML + NDVIamp + (1 ID)$	9	-14653.90	29325.80	238.45	0.00
Use ~ Sex × Status + dWater + TDI + NDVIamp + $(1 ID)$	8	-14656.37	29328.75	241.40	0.00
Use ~ Sex × Status + dWater + ATI + VRML + $(1 ID)$	8	-14681.74	29379.50	292.14	0.00
Use ~ Sex × Status + dWater + ATI + $(1 ID)$	7	-14682.98	29379.96	292.61	0.00
Use ~ Sex × Status + dWater + TPI + TDI + $(1 ID)$	8	-14684.62	29385.24	297.89	0.00
Use ~ Sex × Status + dWater + TPI + TDI + VRML + $(1 ID)$	9	-14683.84	29385.69	298.34	0.00
Use ~ Sex × Status + dWater + TDI + VRML + $(1 ID)$	8	-14691.70	29399.41	312.06	0.00
Use ~ Sex × Status + dWater + TDI + $(1 ID)$	7	-14694.30	29402.61	315.26	0.00
Use ~ Sex × Status + dWater + TPI + NDVIamp + $(1 ID)$	8	-14707.13	29430.26	342.91	0.00
Use ~ Sex × Status + dWater + TPI + VRML + NDVIamp + $(1 ID)$	9	-14706.96	29431.92	344.57	0.00
Use ~ Sex × Status + dWater + NDVIamp + $(1 ID)$	7	-14712.05	29438.11	350.76	0.00
Use ~ Sex × Status + dWater + VRML + NDVIamp + $(1 ID)$	8	-14711.10	29438.20	350.85	0.00
Use \sim Sex \times Status + dWater + TPI + (1 ID)	7	-14733.29	29480.58	393.23	0.00
Use ~ Sex × Status + dWater + TPI + VRML + $(1 ID)$	8	-14732.76	29481.53	394.18	0.00
Use ~ Sex × Status + dWater + VRML + $(1 ID)$	7	-14734.10	29482.21	394.86	0.00
Use ~ Sex × Status + dWater + (1 ID)	6	-14735.21	29482.41	395.06	0.00

Supplementary Table S5. Model selection of generalized linear mixed models explaining jackrabbit habitat selection during winter 2020 (Nov. 2019 – Apr. 2020). Covariates were animal sex, residency status (Status), distance to water (dWater), topographic position index (TPI), surface texture (ATI), terrestrial development index (TDI), vector ruggedness mean local (VRML), and normalized difference vegetation index amplitude (NDVIamp). Random intercepts for individuals (1|ID) were included in all models.

Model	Ka	LL ^b	AICc ^c	$\Delta AICc^{d}$	W_i^e
Use ~ Sex × Status + dWater + ATI + TDI + VRML + NDVIamp + $(1 ID)$	11	-7401.06	14824.15	0.00	0.60
Use ~ Sex × Status + dWater + TPI + TDI + VRML + NDVIamp + $(1 ID)$	11	-7402.45	14826.92	2.77	0.15
Use ~ Sex × Status + dWater + TPI + TDI + NDVIamp + $(1 ID)$	10	-7403.71	14827.43	3.28	0.12
Use ~ Sex × Status + dWater + TDI + VRML + NDVIamp + $(1 ID)$	10	-7403.98	14827.98	3.83	0.09
Use ~ Sex × Status + dWater + ATI + TDI + NDVIamp + $(1 ID)$	10	-7405.24	14830.51	6.36	0.03
Use ~ Sex × Status + dWater + TDI + NDVIamp + $(1 ID)$	9	-7406.69	14831.39	7.24	0.02
Use ~ Sex × Status + dWater + ATI + TDI + VRML + $(1 ID)$	10	-7409.43	14838.89	14.74	0.00
Use ~ Sex × Status + dWater + ATI + VRML + NDVIamp + $(1 ID)$	10	-7409.66	14839.34	15.19	0.00
Use ~ Sex × Status + dWater + VRML + NDVIamp + $(1 ID)$	9	-7411.03	14840.08	15.93	0.00
Use ~ Sex × Status + dWater + TPI + VRML + NDVIamp + $(1 ID)$	10	-7410.03	14840.09	15.94	0.00
Use ~ Sex × Status + dWater + TPI + NDVIamp + $(1 ID)$	9	-7411.44	14840.9	16.75	0.00
Use ~ Sex × Status + dWater + TDI + VRML + $(1 ID)$	9	-7412.17	14842.35	18.20	0.00
Use ~ Sex × Status + dWater + NDVIamp + $(1 ID)$	8	-7413.68	14843.37	19.22	0.00
Use ~ Sex × Status + dWater + TPI + TDI + VRML + $(1 ID)$	10	-7412.04	14844.10	19.95	0.00
Use ~ Sex × Status + dWater + ATI + NDVIamp + $(1 ID)$	9	-7413.18	14844.39	20.24	0.00
Use ~ Sex × Status + dWater + ATI + TDI + $(1 ID)$	9	-7413.42	14844.85	20.70	0.00
Use ~ Sex × Status + dWater + TDI + $(1 ID)$	8	-7414.76	14845.53	21.38	0.00
Use ~ Sex × Status + dWater + TPI + TDI + $(1 ID)$	9	-7414.00	14846.02	21.87	0.00
Use ~ Sex × Status + dWater + ATI + VRML + $(1 ID)$	9	-7416.93	14851.87	27.72	0.00
Use ~ Sex × Status + dWater + VRML + $(1 ID)$	8	-7418.26	14852.53	28.38	0.00
Use ~ Sex × Status + dWater + TPI + VRML + $(1 ID)$	9	-7418.22	14854.46	30.31	0.00
Use ~ Sex × Status + dWater + (1 ID)	7	-7420.79	14855.6	31.45	0.00
Use ~ Sex × Status + dWater + TPI + $(1 ID)$	8	-7420.28	14856.58	32.43	0.00
Use ~ Sex × Status + dWater + ATI + $(1 ID)$	8	-7420.31	14856.64	32.49	0.00

Supplementary Table S6. Model selection of generalized linear mixed models explaining jackrabbit habitat selection during summer 2020 (May 2020 – Oct. 2020). Covariates were animal sex, residency status (Status), distance to water (dWater), topographic position index (TPI), surface texture (ATI), terrestrial development index (TDI), vector ruggedness mean local (VRML), and normalized difference vegetation index amplitude (NDVIamp). Random intercepts for individuals (1|ID) were included in all models.

Model	Ka	LL ^b	AICc ^c	$\Delta AICc^{d}$	w_i^e
Use ~ Sex × Status + dWater + TPI + TDI + VRML + $(1 ID)$	10	-8785.47	17590.95	0.00	0.59
Use ~ Sex × Status + dWater + TPI + TDI + VRML + NDVIamp + $(1 ID)$	11	-8784.82	17591.66	0.71	0.41
Use ~ Sex × Status + dWater + TPI + TDI + $(1 ID)$	9	-8822.87	17663.76	72.80	0.00
Use ~ Sex × Status + dWater + TPI + TDI + NDVIamp + $(1 ID)$	10	-8821.89	17663.79	72.84	0.00
Use ~ Sex × Status + dWater + TPI + VRML + NDVIamp + $(1 ID)$	10	-8990.17	18000.35	409.40	0.00
Use ~ Sex × Status + dWater + TPI + VRML + $(1 ID)$	9	-8991.21	18000.42	409.47	0.00
Use ~ Sex × Status + dWater + ATI + TDI + VRML + NDVIamp + $(1 ID)$	11	-9022.51	18067.03	476.08	0.00
Use ~ Sex × Status + dWater + ATI + TDI + VRML + $(1 ID)$	10	-9024.70	18069.41	478.46	0.00
Use ~ Sex × Status + dWater + TPI + $(1 ID)$	8	-9030.34	18076.70	485.74	0.00
Use ~ Sex × Status + dWater + TPI + NDVIamp + $(1 ID)$	9	-9029.69	18077.40	486.45	0.00
Use ~ Sex × Status + dWater + ATI + TDI + NDVIamp + $(1 ID)$	10	-9039.25	18098.51	507.56	0.00
Use ~ Sex × Status + dWater + ATI + TDI + $(1 ID)$	9	-9041.34	18100.70	509.75	0.00
Use ~ Sex × Status + dWater + TDI + VRML + NDVIamp + $(1 ID)$	10	-9085.78	18191.58	600.63	0.00
Use ~ Sex × Status + dWater + TDI + VRML + $(1 ID)$	9	-9087.58	18193.17	602.22	0.00
Use ~ Sex × Status + dWater + TDI + NDVIamp + $(1 ID)$	9	-9093.32	18204.66	613.70	0.00
Use ~ Sex × Status + dWater + TDI + $(1 ID)$	8	-9094.71	18205.42	614.47	0.00
Use ~ Sex × Status + dWater + ATI + VRML + $(1 ID)$	9	-9296.21	18610.43	1019.48	0.00
Use ~ Sex × Status + dWater + ATI + VRML + NDVIamp + $(1 ID)$	10	-9295.56	18611.14	1020.19	0.00
Use ~ Sex × Status + dWater + ATI + $(1 ID)$	8	-9310.16	18636.32	1045.37	0.00
Use ~ Sex × Status + dWater + ATI + NDVIamp + $(1 ID)$	9	-9309.51	18637.03	1046.08	0.00
Use ~ Sex × Status + dWater + VRML + NDVIamp + $(1 ID)$	9	-9315.74	18649.50	1058.55	0.00
Use ~ Sex × Status + dWater + VRML + $(1 ID)$	8	-9318.32	18652.65	1061.70	0.00
Use ~ Sex × Status + dWater + NDVIamp + $(1 ID)$	8	-9323.84	18663.69	1072.74	0.00
Use ~ Sex × Status + dWater + (1 ID)	7	-9325.65	18665.31	1074.36	0.00

Supplementary Table S7. Model selection of generalized linear mixed models explaining jackrabbit habitat selection during winter 2021 (Nov. 2020 – Apr. 2021). Covariates were animal sex, residency status (Status), distance to water (dWater), topographic position index (TPI), surface texture (ATI), terrestrial development index (TDI), vector ruggedness mean local (VRML), and normalized difference vegetation index amplitude (NDVIamp). Random intercepts for individuals (1|ID) were included in all models.

Model	Ka	LL ^b	AICc ^c	$\Delta AICc^{d}$	W_i^e
Use ~ Sex × Status + dWater + TPI + TDI + NDVIamp + $(1 ID)$	10	-5597.42	11214.87	0.00	0.65
Use ~ Sex × Status + dWater + TPI + TDI + VRML + NDVIamp + $(1 ID)$	11	-5597.05	11216.12	1.26	0.35
Use ~ Sex × Status + dWater + TDI + NDVIamp + $(1 ID)$	9	-5604.12	11226.26	11.39	0.00
Use ~ Sex × Status + dWater + TDI + VRML + NDVIamp + $(1 ID)$	10	-5603.89	11227.80	12.93	0.00
Use ~ Sex × Status + dWater + ATI + TDI + NDVIamp + $(1 ID)$	10	-5604.11	11228.25	13.38	0.00
$Use \sim Sex \times Status + dWater + ATI + TDI + VRML + NDVIamp + (1 ID)$	11	-5603.87	11229.78	14.91	0.00
Use ~ Sex × Status + dWater + TPI + NDVIamp + $(1 ID)$	9	-5612.20	11242.42	27.55	0.00
Use ~ Sex × Status + dWater + TPI + VRML + NDVIamp + $(1 ID)$	10	-5611.92	11243.88	29.01	0.00
Use ~ Sex × Status + dWater + NDVIamp + $(1 ID)$	8	-5615.03	11246.08	31.22	0.00
Use ~ Sex × Status + dWater + VRML + NDVIamp + $(1 ID)$	9	-5614.83	11247.67	32.81	0.00
Use ~ Sex × Status + dWater + ATI + NDVIamp + $(1 ID)$	9	-5614.91	11247.84	32.97	0.00
Use ~ Sex × Status + dWater + ATI + VRML + NDVIamp + $(1 ID)$	10	-5614.68	11249.38	34.51	0.00
Use ~ Sex × Status + dWater + TDI + $(1 ID)$	8	-5668.93	11353.87	139.01	0.00
Use ~ Sex × Status + dWater + ATI + TDI + $(1 ID)$	9	-5668.28	11354.58	139.71	0.00
Use ~ Sex × Status + dWater + TDI + VRML + $(1 ID)$	9	-5668.60	11355.22	140.35	0.00
Use ~ Sex × Status + dWater + TPI + TDI + $(1 ID)$	9	-5668.82	11355.66	140.79	0.00
Use ~ Sex × Status + dWater + ATI + TDI + VRML + $(1 ID)$	10	-5667.85	11355.74	140.87	0.00
Use ~ Sex × Status + dWater + TPI + TDI + VRML + $(1 ID)$	10	-5668.50	11357.03	142.17	0.00
Use ~ Sex × Status + dWater + TPI + $(1 ID)$	8	-5741.28	11498.58	283.71	0.00
Use ~ Sex × Status + dWater + TPI + VRML + $(1 ID)$	9	-5741.03	11500.08	285.21	0.00
Use ~ Sex × Status + dWater + ATI + $(1 ID)$	8	-5762.27	11540.55	325.69	0.00
Use ~ Sex × Status + dWater + ATI + VRML + $(1 ID)$	9	-5761.79	11541.61	326.74	0.00
Use \sim Sex \times Status + dWater + (1 ID)	7	-5771.64	11557.30	342.43	0.00
Use ~ Sex × Status + dWater + VRML + $(1 ID)$	8	-5771.33	11558.67	343.80	0.00

Supplementary Table S8. Model selection of generalized linear mixed models explaining jackrabbit habitat selection during summer 2021 (May 2021 – Oct. 2021). Covariates were animal sex, residency status (Status), distance to water (dWater), topographic position index (TPI), surface texture (ATI), terrestrial development index (TDI), vector ruggedness mean local (VRML), and normalized difference vegetation index amplitude (NDVIamp). Random intercepts for individuals (1|ID) were included in all models.

Model	K^{a}	LL ^b	AICc ^c	$\Delta AICc^{d}$	w_i^e
Use ~ Sex × Status + dWater + ATI + TDI + VRML + NDVIamp + $(1 ID)$	11	-3005.89	6033.83	0.00	0.68
Use ~ Sex × Status + dWater + ATI + TDI + NDVIamp + $(1 ID)$	10	-3007.72	6035.49	1.66	0.30
Use ~ Sex × Status + dWater + ATI + TDI + VRML + $(1 ID)$	10	-3010.40	6040.85	7.01	0.02
Use ~ Sex × Status + dWater + ATI + TDI + $(1 ID)$	9	-3012.29	6042.62	8.78	0.01
Use ~ Sex × Status + dWater + TPI + TDI + VRML + NDVIamp + $(1 ID)$	11	-3033.36	6088.78	54.94	0.00
Use ~ Sex × Status + dWater + TPI + TDI + NDVIamp + $(1 ID)$	10	-3034.58	6089.22	55.38	0.00
Use ~ Sex × Status + dWater + TPI + TDI + VRML + $(1 ID)$	10	-3047.20	6114.45	80.62	0.00
Use ~ Sex × Status + dWater + TPI + TDI + $(1 ID)$	9	-3048.40	6114.84	81.01	0.00
Use ~ Sex × Status + dWater + TDI + NDVIamp + $(1 ID)$	9	-3054.73	6127.51	93.67	0.00
Use ~ Sex × Status + dWater + TDI + VRML + NDVIamp + $(1 ID)$	10	-3054.73	6129.51	95.68	0.00
Use ~ Sex × Status + dWater + TDI + $(1 ID)$	8	-3078.23	6172.50	138.67	0.00
Use ~ Sex × Status + dWater + TDI + VRML + $(1 ID)$	9	-3078.21	6174.45	140.62	0.00
Use ~ Sex × Status + dWater + ATI + VRML + NDVIamp + $(1 ID)$	10	-3089.26	6198.57	164.73	0.00
Use ~ Sex × Status + dWater + ATI + NDVIamp + $(1 ID)$	9	-3091.22	6200.48	166.64	0.00
Use ~ Sex × Status + dWater + TPI + VRML + NDVIamp + $(1 ID)$	10	-3095.24	6210.54	176.70	0.00
Use ~ Sex × Status + dWater + TPI + NDVIamp + $(1 ID)$	9	-3097.26	6212.55	178.72	0.00
Use ~ Sex × Status + dWater + ATI + VRML + $(1 ID)$	9	-3102.38	6222.79	188.96	0.00
Use ~ Sex × Status + dWater + ATI + $(1 ID)$	8	-3104.43	6224.89	191.06	0.00
Use ~ Sex × Status + dWater + TPI + VRML + $(1 ID)$	9	-3114.41	6246.87	213.04	0.00
Use ~ Sex × Status + dWater + TPI + $(1 ID)$	8	-3116.00	6248.04	214.21	0.00
Use ~ Sex × Status + dWater + NDVIamp + $(1 ID)$	8	-3118.74	6253.51	219.68	0.00
Use ~ Sex × Status + dWater + VRML + NDVIamp + $(1 ID)$	9	-3118.65	6255.34	221.51	0.00
Use ~ Sex × Status + dWater + (1 ID)	7	-3138.19	6290.40	256.56	0.00
Use ~ Sex × Status + dWater + VRML + $(1 ID)$	8	-3138.18	6292.40	258.56	0.00

Model	LL ^a	AICc ^b	ΔAICc ^c	w_i^{d}
Year + Strata (Season) + Cluster (ID)	-14.04	31.42	0.00	0.35
Age + Strata (Season) + Cluster (ID)	-14.56	32.45	1.03	0.21
Sex + Strata (Season) + Cluster (ID)	-14.70	32.72	1.30	0.18
Residency + Strata (Season) + Cluster (ID)	-14.74	32.82	1.40	0.17
Year + Age + Strata (Season) + Cluster (ID)	-13.38	36.75	5.33	0.02
Year + Residency + Strata (Season) + Cluster (ID)	-13.81	37.63	6.21	0.02
Year + Sex + Strata (Season) + Cluster (ID)	-13.89	37.78	6.36	0.02
Age + Sex + Strata (Season) + Cluster (ID)	-14.30	38.61	7.19	0.01
Age + Residency + Strata (Season) + Cluster (ID)	-14.40	38.79	7.37	0.01
Residency + Sex + Strata (Season) + Cluster (ID)	-14.48	38.97	7.55	0.01
Year + Age + Sex + Strata (Season) + Cluster (ID)	-13.17	56.34	24.92	0.00
Year + Age + Residency + Strata (Season) + Cluster (ID)	-13.18	56.36	24.94	0.00
Year + Sex + Residency + Strata (Season) + Cluster (ID)	-13.73	57.45	26.03	0.00
Age + Sex + Residency + Strata (Season) + Cluster (ID)	-14.18	58.36	26.94	0.00
Year + Age + Sex + Residency + Strata (Season) + Cluster (ID)	-13.06	60.55	29.13	0.00

Supplementary Table S9. Model selection of Cox proportional hazards models explaining annual coyote survival.

Model	LL ^a	AICc ^b	ΔAICc ^c	w_i^{d}
Year + Strata (Season) + Cluster (ID)	-112.80	230.00	0.00	0.35
Year + Age + Strata (Season) + Cluster (ID)	-112.38	231.53	1.53	0.16
Year + Residency + Strata (Season) + Cluster (ID)	-112.50	231.76	1.76	0.15
Year + Sex + Strata (Season) + Cluster (ID)	-111.31	231.91	1.91	0.14
Year + Age + Residency + Strata (Season) + Cluster (ID)	-112.07	233.44	3.44	0.06
Year + Age + Sex + Strata (Season) + Cluster (ID)	-110.76	233.50	3.50	0.06
Year + Residency + Sex + Strata (Season) + Cluster (ID)	-110.85	233.68	3.68	0.06
Year + Age + Sex + Residency + Strata (Season) + Cluster (ID)	-110.26	235.39	5.39	0.02
Residency + Strata (Season) + Cluster (ID)	-119.50	241.16	11.16	0.01
Age + Strata (Season) + Cluster (ID)	-119.73	241.62	11.62	0.00
Sex + Strata (Season) + Cluster (ID)	-119.06	242.51	12.51	0.00
Age + Residency + Strata (Season) + Cluster (ID)	-119.50	243.39	13.39	0.00
Sex + Residency + Strata (Season) + Cluster (ID)	-118.73	244.23	14.23	0.00
Age + Sex + Residency + Strata (Season) + Cluster (ID)	-119.06	244.88	14.88	0.00
Age + Sex + Residency + Strata (Season) + Cluster (ID)	-118.72	246.74	16.74	0.00

Supplementary Table S10. Model selection of Cox proportional hazards models explaining annual optimistic (censors assumed alive; AA) black-tailed jackrabbit survival.

Model	LL ^a	AICc ^b	ΔAICc ^c	W_i^{d}
Residency + Strata (Season) + Cluster (ID)	-154.43	310.99	0.00	0.14
Age + Strata (Season) + Cluster (ID)	-154.44	311.01	0.02	0.14
Year + Strata (Season) + Cluster (ID)	-153.46	311.21	0.23	0.12
Sex + Strata (Season) + Cluster (ID)	-153.50	311.32	0.31	0.12
Year + Age + Strata (Season) + Cluster (ID)	-152.73	312.07	1.06	0.08
Year + Sex + Strata (Season) + Cluster (ID)	-151.77	312.52	1.51	0.06
Age + Residency + Strata (Season) + Cluster (ID)	-154.10	312.52	1.51	0.06
Age + Sex + Strata (Season) + Cluster (ID)	-153.18	312.96	1.95	0.05
Year + Residency + Strata (Season) + Cluster (ID)	-153.21	313.02	2.01	0.02
Residency + Sex + Strata (Season) + Cluster (ID)	-153.26	313.12	2.11	0.05
Year + Age + Sex + Strata (Season) + Cluster (ID)	-151.00	313.44	2.43	0.04
Year + Age + Residency + Strata (Season) + Cluster (ID)	-152.46	313.88	2.89	0.03
Year + Sex + Residency + Strata (Season) + Cluster (ID)	-151.61	314.67	3.66	0.02
Age + Sex + Residency + Strata (Season) + Cluster (ID)	-152.95	314.87	3.86	0.02
Year + Age + Sex + Residency + Strata (Season) + Cluster (ID)	-150.83	315.70	4.71	0.01

Supplementary Table S11. Model selection of Cox proportional hazards models explaining annual pessimistic (censors assumed dead; AD) black-tailed jackrabbit survival.

Supplementary Table S12. Monthly species occurrence and relative abundance observed on spotlight transects in the BCCE, Clark County, NV from February to December 2018.

Survey Effort	Jan	Feb	March	April	May	June	July	August	Sept	Oct	Nov	Dec	Total Nights Surveyed	Total km Surveyed
# Nights Surveyed	-	1	1	1	1	3	3	3	3	3	3	3	25	-
# of km surveyed	-	27.6	27.6	27.6	27.6	82.8	82.8	82.8	82.8	82.8	82.8	82.8	-	690
Species Observed													Total observed	% Surveys observed
American Badger	-	-	-	-	-	-	2	-	-	-	-	-	2	9.1%
Black-tailed Jackrabbit	-	8	4	14	11	8	12	11	13	9	29	33	152	100%
Burrowing Owl	-	-	-	-	-	-	-	1	-	-	-	-	1	9.1%
Coyote	-	-	1	-	-	-	-	-	-	-	-	-	1	9.1%
Kangaroo Rat	-	-	2	3	2	5	8	15	3	4	2	1	45	90.9%
Kit Fox	-	-	1	-	2	1	2	-	1	-	1	2	10	63.6%
Woodrat	-	-	-	-	-	1	-	1	-	-	-	-	2	18.2%
Rodent	-	-	1	1	-	-	1	3	2	1	1	-	10	63.6%
Spotted Skunk	-	-	-	-	1	-	-	-	-	-	-	-	1	9.1%
Total Animals Observed	-	8	9	18	16	15	25	31	19	14	33	36	224	

Supplementary Table S13. Monthly species occurrence and relative abundance observed on spotlight transects in the BCCE, Clark County, NV from January to December 2019.

Survey Effort	Jan	Feb	March	April	May	June	July	August	Sept	Oct	Nov	Dec	Total Nights Surveyed	Total km Surveyed
# Nights Surveyed	3	2	1	3	3	3	3	3	3	3	3	3	33	-
# of km surveyed	82.8	55.2	27.6	82.8	82.8	82.8	82.8	82.8	82.8	82.8	82.8	82.8	-	910.8
Species Observed													Total observed	% Surveys observed
American Badger	-	-	-	-	-	-	-	-	-	-	-	-	0	0%
Black-tailed Jackrabbit	17	15	4	20	51	29	15	17	12	7	6	7	200	100%
Burrowing Owl	-	-	-	-	-	-	-	-	-	-	-	-	0	0%
Coyote	-	-	-	1	-	-	-	-	-	-	-	-	1	8%
Kangaroo Rat	2	2	-	6	-	1	1	11	7	7	-	12	49	75%
Kit Fox	-	1	-	1	4	1	3	3	1	3	1	-	18	75%
Woodrat	-	-	-	-	-	-	-	-	-	-	-	-	0	0%
Rodent	-	-	-	3	2	1	1	1	9	-	2	-	19	58%
Spotted Skunk	-	-	-	-	-	-	-	-	-	-	-	-	0	0%
Total Animals Observed	19	18	4	31	57	32	20	32	29	17	9	19	287	

Supplementary Table S14. Monthly species occurrence and relative abundance observed on spotlight transects in the BCCE, Clark County, NV from January to December 2020. Spotlight surveys were not conducted in April, May, or June of 2020, due to the Covid-19 outbreak and associated lock down; surveys were reinitiated once acceptable safety measures were instituted to make spotlight survey methods practicable.

Survey Effort	Jan	Feb	March	April	May	June	July	August	Sept	Oct	Nov	Dec	Total Nights Surveyed	Total km Surveyed
# Nights Surveyed	2	3	3	-	-	-	3	3	3	3	3	6	29	-
# of km surveyed	55.2	82.8	82.8	-	-	-	82.8	82.8	82.8	82.8	82.8	165.6	-	800.4
Species Observed													Total observed	% Surveys observed
American Badger	-	-	-	-	-	-	1	1	-	-	-	-	2	20%
Black-tailed Jackrabbit	10	8	16	-	-	-	20	20	9	5	5	20	113	100%
Burrowing Owl	-	-	-	-	-	-	1	-	-	-	-	-	1	10%
Coyote	-	-	-	-	-	-	-	-	-	-	-	-	0	0%
Kangaroo Rat	2	-	9	-	-	-	28	61	10	55	37	38	240	90%
Kit Fox	-	2	1	-	-	-	2	-	2	1	2	10	20	80%
Woodrat	-	-	-	-	-	-	-	-	-	-	-	-	0	0%
Rodent	-	-	1	-	-	-	4	-	0	-	-	1	6	60%
Spotted Skunk	-	-	-	-	-	-	-	-	-	-	-	-	0	0%
Total Animals Observed	12	10	27	-	-	-	56	83	21	61	44	69	382	

Survey Effort	Jan	Feb	March	April	May	June	July	August	Sept	Oct	Nov	Dec	Total Nights Surveyed	Total km Surveyed
# Nights Surveyed	3	3	3	3	3	3	3	3	3	3	-	-	30	-
# of km surveyed	82.8	82.8	82.8	82.8	82.8	82.8	82.8	82.8	82.8	82.8	-	-	-	828
Species Observed													Total observed	% Surveys observed
American Badger	-	-	-	-	-	-	-	-	-	-	-	-	0	0%
Black-tailed Jackrabbit	11	11	8	14	7	4	2	4	3	7	-	-	71	100%
Burrowing Owl	-	-	-	-	-	-	-	-	-	-	-	-	0	0%
Coyote	2	-	-	1	-	-	3	-	-	1	-	-	7	30%
Kangaroo Rat	24	4	45	23	40	49	227	119	61	36	-	-	628	100%
Kit Fox	2	3	4	2	4	4	3	-	1	4	-	-	27	90%
Woodrat	-	-	-	-	-	-	-	-	-	-	-	-	0	0%
Rodent	2	-	2	-	-	-	-	2	-	-	-	-	6	30%
Spotted Skunk	-	-	-	-	-	-	-	-	-	-	-	-	0	0%
Total Animals Observed	41	18	59	40	51	57	235	125	65	48	-	-	739	

Supplementary Table S15. Monthly species occurrence and relative abundance observed on spotlight transects in the BCCE, Clark County, NV from January to October 2021. Spotlight surveys concluded in October 2021.