Title

Multi-scale approaches to wildlife ecology and conservation in arid environments

Permalink

https://escholarship.org/uc/item/12k9k5hv

Author

Schmidt, Greta

Publication Date

2024

Peer reviewed|Thesis/dissertation

Multi-scale Approaches to Wildlife Ecology and Conservation in Arid Environments

By

GRETA SCHMIDT
DISSERTATION

Submitted in partial satisfaction of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

Ecology

in the

OFFICE OF GRADUATE STUDIES

of the

UNIVERSITY OF CALIFORNIA

DAVIS

And

SAN DIEGO STATE UNIVERSITY

Approved:

_____

Rebecca Lewison, Chair

_____

Kevin Hovel

_____

Justine Smith

Committee in Charge

2024

i

TABLE OF CONTENTS

Acknowledgments

Completing a PhD is like running a sprint and a marathon at the same time. Without the support I've received from mentors, colleagues, friends, and family during my years in graduate school I would not be submitting this dissertation on time, if at all. I offer these acknowledgments as an inadequate but sincere expression of my gratitude.

Thanks to my qualifying exam committee, Marissa Baskett, Andy Sih, Eric Post, Luke Miller, and especially Kevin Hovel for making the round-trip journey from San Diego to Davis. Thanks to Justine Smith, my UC Davis mentor, for welcoming me into the lab and providing thoughtful direction and insight. As members of my dissertation committee, Kevin and Justine have been supportive and provided valuable feedback to improve this work.

To my advisor, Becca Lewison, thank you for everything. Especially in these past six months your guidance and confidence in me made all the difference, but I can look back over the past seven years and see how much I've learned from you and benefitted from your mentorship. I so admire the work you put in for your students, and the joy and humor you bring to that hard work.

This research would not have been possible without the participation of many collaborators. In particular, Stephanie Fuest has been a key mentor, generous with her time and knowledge. Stephanie facilitated the data sharing for Chapters 2 & 3. Thanks to the members of the Sonoran Pronghorn Recovery Team and greater Sonoran Desert research network who contributed data: Aaron Alvidrez, Jill Bright, Stephanie Fuest, Peter Holm, Roger Joos, and Paul Sitzmann. Infinite thanks to everyone whose hard work across many years went into collecting the data.

Thanks to the Conservation Ecology Lab members I've had the privilege to know over the years. I feel so lucky to have been a part of such a kind, collaborative group of people who appreciate good snacks. In particular Dr. Nima Farchadi provided great inspiration and friendship, being always one year ahead and very obviously the senior member of the lab. Jaz Llamas, any time you walked into the lab it brightened my day. Thanks for the best blanket in the world, I promise I won't let my dogs eat it. Erica Mills, thanks for all the mental health walks to Trader Joe's and weekend birding excursions, they always boosted my mood. Corey Kramer, Daniel Gordon, Troy Wynne, and Megan Jennings - your community was an integral part of my PhD experience. Megan Jennings, thanks especially for sharing your San Diego bobcat dataset, collaborating on the publication that became Chapter 1 was a great experience.

Thanks to Smith lab members Ellie Bolas, Olivia Feldman, and Emily Leonhardt, who made me feel so welcome, helped me navigate a year on the UC Davis campus, and cultivated a lab environment that was supportive, fun, and inspiring.

Thanks to the greater SDSU graduate student community, in particular the 2020 JDPE cohort: Lupita Barajas, Xavius Boone, Craig Fischer, Ana Gomez, and Lily McIntire. The importance of your solidarity, community, and friendship as we navigated this program together can't be overstated. We're an amazing group of scientists, even if we disagree about wetlands.

Thanks to the team at Cabeza Prieta National Wildlife Refuge for welcoming me and providing support and understanding as I worked to finish this degree. I've learned so much in such a short time - my years in academia did not cover how to haul a 1,000 gallon water trailer, for example - and I look forward to what else I'll learn in this beautiful corner of Arizona.

To my parents, Roy Schmidt and Kirsten Olson, thank you for unconditional love and support, including providing a place to live and work in Summer 2023. Sorry that my dogs taught your dog bad habits. To my sister Inga, I can't imagine a better friend in life and I'm excited to support you on your journey back to school.

To Craig Fischer, I'm sorry but I'm just thinking of the right words to say.

To Emmy Lou and Ted Hunt, thanks for being dogs.

Abstract

Ecology aims to understand the links between processes and patterns in the natural world. Scale plays an integral role, because processes at one scale, large or small, can shape patterns observed at disparate scales. Ecological research typically considers scale in terms of space, time, and biotic organization, and across these three dimensions no single scale provides a definitive lens through which to consider any given ecological phenomenon. This is because the motivations of the observer inform which scales are meaningful. In particular, the diverse goals set by wildlife conservation and management efforts can cover a wide range of scales in space, time, and organization.

Modern conservation faces the challenge of maintaining biodiversity and ecosystem function amid widespread habitat alteration and climate change. The challenge is intensified in arid environments, where resources are scarce and ephemeral in space and time, and plants and animals are often existing at their physiological limits for factors like temperature and water. Wildlife conservation in arid environments can benefit from strategies that increase species' resilience, providing the opportunity to adapt as changes occur. Effective approaches include protecting habitats that serve as climate refugia or facilitate movement, increasing permeability for mobile species, supplementing critical resources, and undertaking captive breeding, reintroduction, and translocation of particularly vulnerable species.

My dissertation examines multi-scale approaches to wildlife ecology and conservation in arid environments, emphasizing how these frameworks can inform our understanding of human impacts on wildlife and guide effective conservation strategies. Chapter 1 explores the influence of development and urbanization on bobcats (*Lynx rufus*) in San Diego County, focusing on individual and population-level space use. Results showed that at the individual level, bobcats

prefer areas characterized by low elevation and low development intensity. In a region like San Diego County where development is concentrated at lower elevations along the western coastline, this suggests constraints on preferred habitats for this species. At the population level, we observed a contrasting pattern, where bobcat densities were higher in developed areas relative to wildland spaces. This suggests that, while individual animals select against development, patterns of population density are governed by development-related movement barriers. Recognizing these contrasting relationships across scales of organization can inform future conservation action in this region to ensure wildlife persistence in developed areas, including identifying movement corridors and prioritizing areas for preservation.

Chapter 2 is set in the Sonoran Desert in southwest Arizona and investigates seasonal patterns of post-translocation mortality risk for the Sonoran pronghorn (*Antilocapra americana sonoriensis*), a federally endangered ungulate that has been the focus of a long-term captive breeding and reintroduction program. At the scale of the study area, long-term drought conditions elevated mortality risk in the fall, winter, and spring, while increased experience reduced mortality risk in the early summer and summer monsoon seasons. At the scale of individual space use, increased human footprint elevated mortality risk year-round, and a lack of water access further increased mortality risk in summer months. Mortality risk for translocated Sonoran pronghorn is influenced by both large-scale climatic conditions and small-scale habitat contexts. A consideration of both scales can provide insight for informing effective translocation practices in current and future reintroduction areas.

Chapter 3 remains in the Sonoran desert but expands from a single-species focus to consider the large mammal community, exploring seasonal variation in occurrence and interactions at managed water sources. As expected, single-species occupancy at waters varied

seasonally and was generally higher in summer months, confirming that these waters represent an important resource to multiple members of the large mammal community. Although species occupancy was elevated across water sites during the summer, similar seasonal patterns did not necessarily equate to high predicted co-occurrence, refining expectations for species overlap at sites. At a finer temporal scale we measured both potential and direct interactions. Potential for interactions to occur increased in summer months, as did direct interactions. Direct species interactions were higher as a function of relative species abundance and high antagonism class, but were also impacted by drought severity in the summer monsoon and fall-winter seasons. Active water management is likely to become more prevalent as conditions in the Sonoran Desert trend hotter and more prone to periods of severe drought. As desert ecosystems continue to experience anthropogenic change, thoughtful approaches to water management that account for the influence on species interactions and other unintended effects will be valuable for ensuring that this strategy achieves desired conservation and management objectives.

These research efforts integrate multiple scales in space, time, and organization to deepen our understanding of human impacts on wildlife and inform conservation strategies in arid environments. When conducting observational ecological studies in natural systems, describing patterns is a simpler task than uncovering underlying processes. By considering multiple scales in space, time, and organization, we can derive insight into the processes that underlie patterns of interest.

CHAPTER 1

Bobcats in southern California respond to urbanization at multiple scales[1]

Abstract

Urban areas impact wildlife populations through multiple pathways, notably habitat fragmentation and degradation. Wildlife can respond to development and other human-driven environmental change at multiple scales, from the individual to the population level, ultimately driving biodiversity patterns and processes in built and adjacent natural landscapes. However, multiple scales of space use are rarely considered in an integrated framework. Focusing on bobcats, a species associated with intermediate sensitivity to development, we explored factors affecting multi-scale space use and population density across San Diego County, a region in southern California characterized by a pronounced development gradient. We used remote camera data and GPS collar data in an integrated spatial capture-recapture + resource selection function approach. At the individual scale, bobcats selected against developed areas, while at the population level, bobcat densities were higher in habitat patches surrounded by development, suggesting that bobcat populations in these areas may be experiencing home range pile-up, a manifestation of the fence effect. Our results provide an integrated multi-scale view of the impacts of human-modified landscapes on wildlife, confirming that research on space use at the individual and population levels should be considered jointly to advance understanding of the mechanisms driving wildlife response to development. This approach has promise to improve conservation and management efforts for urban wildlife.

Keywords

development gradient, fence effect, Bobcat (*Lynx rufus*), resource selection function, spatial capture-recapture, urban wildlife

Introduction

Over the past two decades, populations in urban areas worldwide grew by 1.6 billion people and projections estimate an increase of 2.5 billion people in the world's towns and cities over the next 35 years (UN DESA 2014, Sanderson et al. 2018). Although associated land use change and development have increased more slowly than the rate of urban population growth (Angel 2012, Venter et al. 2016), the corresponding habitat reduction, degradation, and fragmentation have been implicated in biodiversity loss (Hanski 2011). Some urban areas have already experienced concentrated development and densification, resulting in increased pressure particularly where biodiversity hotspots overlap with areas of intense urban development (Venter et al. 2016). The term urban areas or urbanized areas encompasses a range of built, biotic, and abiotic landscape features, as well as social and demographic factors, across a gradient of development intensity (Moll et al. 2019), with implications for variable responses from wildlife populations to these changes.

While many wildlife species successfully use developed, urbanized landscapes, (Barrett et al. 2019), anthropogenic impacts in urban areas also have well-documented negative effects on wildlife (Santini et al 2019, Suraci et al. 2021). Species' responses to developed landscape features can vary based on intrinsic life history characteristics such as reproductive strategy, dietary guild, and cognitive ability (Barett et al. 2019, Suraci et al 2021), as well as extrinsic factors including locale (Fidino et al. 2021), co-occurring disturbances (Nickel et al. 2020), and development intensity (Šálek et al. 2014, Lewis et al. 2015). Even within species that have

adapted to urbanized environments, there is evidence of variable responses to environmental

conditions and site characteristics depending on where animals are found along the development

gradient (Lewis et al. 2015, Fidino et al. 2021). Responses can also vary over multiple scales of

space use, such that individual responses to landscape development may differ from population-

level responses for the same species (Šálek et al. 2014).

Urbanization and related land conversion exert considerable influence on space use at the

individual level (Riley et al. 2010, Leighton et al. 2021) as well as patterns of abundance and

distribution at the population level through multiple pathways (Randa and Yunger 2006,

Ordeñana et al. 2010, Parsons et al. 2019). For example, more abundant prey or other food

subsidies may lead to increased population density in developed areas (Bino et al. 2010).

Alternatively, increases in population densities may be a result of the fence effect (Krebs et al.

1969) whereby constrained populations experience increased density and potentially home range

pile-up because of dispersal barriers or impediments (Riley et al. 2006). The former can indicate

synurbanization, or adaptation to urban conditions (Santini et al. 2019), whereas the latter may

precede eventual genetic degradation or population decline (e.g., Gustafson et al. 2019), which

can occur over multigenerational time lags or after a significant mortality event such as an

epizootic outbreak (Ruell et al. 2009, Serieys et al. 2015). Because previous research has

typically considered the effects of urbanization on wildlife at individual and population-level

scales independently (Young et al. 2019a, 2019b), there has been limited exploration of

potentially concurrent or even contrasting factors that influence wildlife response to

urbanization. A multi-scale integrated approach can provide clearer insight into the mechanisms

driving wildlife response to anthropogenic land use change (Lewis et al. 2015) and can also help

identify factors that may underlie wildlife responses in a multi-site context (Magle et al. 2019, Fidino et al. 2021).

Mammalian carnivores exhibit a diversity of behavioral and life history traits, with implications for species-specific differences in survival and persistence in urbanized landscapes (Crooks 2002, Riley et al. 2010, Schell et al. 2021, Suraci et al. 2021). Consequently, a large body of research has focused on exploring carnivore movement, space use, and population dynamics in urban settings (Crooks 2002, Ordeñana et al. 2010, Crooks et al. 2011, Šálek et al. 2014). Bobcats (*Lynx rufus*), in particular, are associated with developed and urbanized areas, yet also experience negative effects from altered landscapes over time (Riley et al. 2006, Ruell et al. 2009, Serieys et al. 2018). Although bobcats are habitat generalists, they have been found to exhibit intermediate sensitivity to urbanization and habitat fragmentation (Crooks 2002, Lombardi et al. 2017, Young et al. 2019a), perhaps because they are obligate carnivores with reduced dietary plasticity relative to more omnivorous carnivores like coyotes, raccoons, and foxes. Research on bobcats in developed landscapes has demonstrated negative relationships with urbanization and bobcat resource selection, density, and occupancy (Lewis et al. 2015, Lombardi et al. 2017), while other studies have reported high bobcat densities in urban areas (Young et al. 2019b). Bobcat populations have been vulnerable to the fence effect in some urban settings (Riley et al. 2006), but the effect has not been detected in others (Lewis et al. 2015). Because of their moderate sensitivity to landscape disturbance, bobcats have been used as a model carnivore species to explore both individual and population-level responses to urban gradients in a range of ecosystems (Lewis et al. 2015, Lombardi et al. 2017, Young et al. 2019a, 2019b, Smith et al. 2020).

To better understand individual space use and movement as well as spatial patterns at the population-level, new multi-scaled analytical methods have been developed and tested that afford population-level inference informed by individual-level data (Royle et al. 2013b, Scharf and Buderman 2020, Glennie et al. 2021, Converse et al. 2022). In particular, joint frameworks used to estimate density and resource selection have demonstrated improved inference of space use across multiple scales and increased precision of density estimates, which presents a methodological opportunity to identify drivers of both individual and population-level responses to environmental change and human modified landscape features (Royle et al. 2013b, Linden et al. 2018, Paterson et al. 2019). These methods merge spatial capture-recapture (SCR), a hierarchical approach to estimating density that accounts for variability in detection probability relative to locations of detectors and individuals (Borchers and Efford 2008, Royle and Young 2008), with third-order resource selection functions (RSF), which describe patterns of space use at the individual level using fine-scale location data (Manly et al. 2002, Royle et al. 2013b). Previous applications of integrated SCR-RSF models have demonstrated this framework's ability to capture variability in space use at the individual level, which informs the interpretation of landscape characteristics driving patterns in density (Linden et al. 2018), and increases precision and accuracy of SCR model parameter estimates (Royle et al. 2013b, Paterson et al. 2019). For wildlife populations with space use that varies relative to habitat and landscape characteristics, integrating these two frameworks can leverage multiple data types gathered at the individual level (e.g., capture-recapture, telemetry) to reduce bias in density estimation and provide a more robust linkage between space use at both individual and population scales (Royle et al. 2013b).

Here, we sought to identify factors that influence individual resource selection and population density of bobcats in a southern California landscape characterized by a strong

development gradient using an integrated SCR-RSF model. In southern California, bobcats occupy habitat that extends across an urbanized landscape gradient, typically from intensively developed coastal areas to inland towards suburban, rural, and wildland landscapes, providing an opportunity to explore factors driving multi-scale responses to urbanization. Additionally, southern California has a rich history of urban carnivore research that can provide context and comparison to understand wildlife movement and space use in response to urbanization (Crooks 2002, Riley et al. 2006, 2010, Ruell et al. 2009, Ordeñana et al. 2010, Tracey et al. 2013, Alonso et al. 2015, Dunagan et al. 2019). We also compare our findings to bobcat research in human-modified landscapes at other sites within their U.S. range to consider evidence of the fence effect or home range pile-up across regions. Understanding multi-scale responses to a marked development gradient can inform land management, conservation action, and connectivity planning to facilitate more effective wildlife management in southern California, a developed landscape with an expanding human footprint.

Methods

Study area

We conducted our research in San Diego County, CA, USA. San Diego County is characterized by a pronounced development gradient with more developed and urbanized areas along the western coastline and a steady decline of development intensity towards the east of the County, where there are large expanses of protected lands including Anza Borrego and Palomar State Parks, and Cleveland National Forest. We monitored bobcats with remote cameras and GPS collars along this gradient, focusing on three local roadways that bisect conserved habitat patches and natural lands set aside to maintain landscape connectivity as part of San Diego's Multiple Species Conservation Program (Greer 2004). We broadly categorized the study area

from east - west as urban, wildland urban interface (WUI), and wildland (Figure 1). The three categories were defined based on a combination of housing density, observed land use, road density, and impervious surface values. The urban site was dominated by moderate to high density development with >100 units/km^2, as well as suburban development interspersed with commercial business parks. Average road density in the urban area was 17.7 km/km^2 and the average percent impervious surface across the area was 28.6%. In the WUI zone, high density exurban land use was dominant (12-50 units/km^2) with some low density exurban and suburban development and conserved recreational and multiple use lands. Average road density in this area was 5.45 km/km^2 and the average percent impervious surface was 5.0%. Finally, the wildland zone was dominated by parks, recreational or conserved lands, and multiple use lands along with some low-density exurban development (0-3 units/km^2). Some agricultural lands were present in the western part of this zone. Average road density was 2.48 km/km^2 and average percent impervious surface was 1.1%. Elevation across the study area ranged from sea level at the coast to 1000 m in the inland foothills. Habitat type in the study area varied with both elevation and distance from the coast, but was predominantly a shrubland ecosystem. Habitats across these areas included coastal sage scrub dominated by California sagebrush (*Artemisia californica*), chaparral habitat types generally dominated by scrub oak (*Quercus berberidifolia*) or chamise (*Adenostoma fasciculatum*), oak woodland with coast live oak (*Quercus agrifolia*), grasslands dominated by non-native annual grasses, riparian zones with an oak (*Quercus agrifolia*) or sycamore (*Platanus racemosa*) overstory and herbaceous understory, as well as urban and altered areas. The Mediterranean-climate of the study region is characterized by hot, dry summers and mild, wet winters with annual precipitation often less than 300 mm.

Remote camera sampling and individual identification

We established 36 remote camera stations along a roughly 2-km^2 grid across the study area, based on the minimum expected home range for bobcats in southern California (Lyren et al. 2006, Ruell et al. 2009, Alonso et al. 2015). We used two camera models: Cuddeback Expert white-flash (Cuddeback, Green Bay, WI, USA) and the LTL Acorn 5210A 940 infrared camera (Old Boys Outdoors, Stone Mountain, GA, USA). Cameras were active between November 2011 and January 2013 and set to capture images 24 hours per day with a one-minute delay between triggered photos. We processed bobcat images using Adobe Bridge (Adobe Systems Incorporated, San Jose, CA, USA). Photographs were discarded if they were too blurry, out of focus, overexposed, or captured only a partial view of the animal. Sex could not be reliably determined. We classified all retained bobcat pictures as having a left or right orientation, because bobcats lack bilateral symmetry in their pelage markings (Heilbrun et al. 2006, McClintock et al. 2013).

We compared photographs within left- and right-oriented datasets using pelt-pattern matching software, Wild-ID (Bolger et al. 2012). Wild-ID uses image-matching algorithms to select the most likely identification matches for each bobcat image. Although Wild-ID guides its users to crop only the relevant part of the animal and exclude the surrounding area from the pictures, for bobcats, this was not advisable because the lower extremities can have diagnostic markings.

Three observers performed individual identifications with the software, and novel identifications were made when a pelt displayed a minimum of three distinct natural markings, which included any clearly defined pattern or grouping in one specific area, such as an inner leg. When comparing different pictures of the same putative individual, we required matching natural markings at two different points on the body, or at least three matching points between multiple

pictures (Supplemental Figure S1). Positive individual identifications were confirmed by a majority consensus among observers and independent expert opinion when necessary. Additionally, collared individuals identified by a numbered ear tag or collar or individuals photographed on both flanks within a single series of images were considered part of both the left- and right-orientation datasets.

Animal capture and telemetry

Prior to and concurrent with remote camera sampling efforts, bobcats were trapped in baited cage traps (61cm x 43cm x 109cm) and sedated with a combination of ketamine HCl and xylazine HCL. Project staff conducted all trapping, collaring, and tracking efforts (California Department of Fish and Game Scientific Collecting Permit #SCP-009632, IACUC Protocol # 10-09-027L) between 2009 and 2012. Animals were weighed, measured, ear tagged, and fitted with one of two GPS collar brands (TCG181 or TCG271, Sirtrack Ltd., Havelock North, New Zealand; Quantum 4000, Telemetry Solutions, Concord, California, USA). Collars collected fine-scale locational fixes eight times per day five days/week and 48 times per day two days/week over six to nine months. To ensure sufficient accuracy and limit erroneous locations, only fixes made with greater than or equal to three satellites and less than or equal to a horizontal dilution of precision of five were retained in the telemetry dataset (Lewis et al. 2007). To examine differences in home range territory size along a gradient of development, we calculated local convex hull home ranges (LoCoH; Getz and Wilmers 2004) for each individual using the adaptive kernel method (a = 18km) using the adehabitatHR package (Calenge 2006). For each individual, we also calculated the percentage of its home range that overlapped with the home ranges of other collared individuals to provide a qualitative assessment of home range overlap across the study area.

SCR-RSF model development

To evaluate the effect of urbanization on bobcat resource selection and population density, we used camera trap data and telemetry data in an integrated SCR-RSF model approach (Royle et al. 2013b, Linden et al. 2018). SCR is a hierarchical density estimation method consisting of an encounter model describing spatial variation in individual detection probability and a spatial process (i.e., density) model describing the distribution of individuals in the population. The encounter model includes a function describing how detection probability declines with distance from an animal's latent home range center, also known as its activity center. SCR-RSFs expand the SCR encounter model to allow for variation in space use probability according to local landscape features. The parameters to be estimated in the SCR-RSF encounter model include baseline detection probability, the spatial scale parameter of the distance function (i.e., sigma), and the probability of use given selected habitat covariates. In the density model, baseline density and coefficients describing spatial variation in density are the parameters to be estimated.

All models were fitted in R v 4.1.0 (R Core Team 2021) using the oSCR package, employing maximum-likelihood methods (Sutherland et al. 2019). Fitting the SCR-RSF model requires capture-recapture histories of individuals detected at traps across temporal sampling occasions, complementary telemetry data, a discretized area known as the state space over which density and abundance are estimated, and an additional discretized layer matching the state space used for integrating the RSF. Individual, trap-specific, and landscape-level covariates can accommodate heterogeneity in parameters in the encounter and density models.

We fit models separately for the left and right-sided bobcat datasets. While methods exist to probabilistically resolve partial identities, e.g., unilateral versus bilateral identification, in SCR

frameworks (Augustine et al. 2018), these do not yet accommodate landscape covariates in either the encounter or density models, which was a primary objective of our research. Datasets containing partial and complete identities can potentially yield either positively or negatively biased estimates (Augustine et al. 2018). However, previous research has shown that failing to account for spatial heterogeneity can also bias estimates, in some cases severely (Royle et al. 2013b, Howe et al. 2013). Therefore, we chose to evaluate left- and right-sided datasets separately, favoring the accommodation of landscape covariates describing spatial heterogeneity at multiple scales in our model.

Remote cameras were active between 30 November 2011 and 7 February 2013. We used photo data collected from 30 November 2011 through 25 December 2012 in our analyses to balance meeting assumptions of population closure while maximizing available recaptures and spatial recaptures. Using a full year of monitoring data in an SCR analysis has the potential to violate the assumption of demographic closure and may negatively bias detection estimates, leading to positive bias in density (Royle et al. 2013a). However, because the late fall beginning and early winter end of our monitoring period coincides with the timing of dispersal of yearlings from their natal territories, the degree to which closure was violated by emigration and immigration within this timeframe was likely minimal. For this period, we created encounter histories for individual bobcats detected at camera locations, dividing the entire 56-week study period into 28 bi-weekly sampling occasions. We accounted for variable camera activity in the trap operation matrix in the oSCR framework, where camera locations are coded as '1' if active, and '0' if inactive during each bi-weekly sampling occasion. We used a Poisson encounter model, allowing for multiple detections of an individual at a single detector per sampling

11

occasion and proceeded with model building and selection using this specification. We used the

half-normal distance function in our encounter model (Royle et al. 2013a).

To create a state space, we used previous knowledge of bobcat home range sizes in

southern California, which have been reported between $2 - 20$ km^2 (Riley et al. 2006, 2010,

Poessel et al. 2014). Using the half-normal detection model such that $\sigma \times \sqrt{5.99} =$

95% $HR\ radius$, these previously reported home range sizes suggest that the expected value for

sigma would be roughly $0.8 - 2.5$ km (Royle et al. 2013a, Sun et al. 2014). Standard

recommendations to avoid estimate bias suggest that the buffer to create the state space extent be

3 times the sigma value, and pixel resolution of the state space be between ½ sigma and sigma

(Sutherland et al. 2019). Therefore, we buffered the sampling array by 8 km to account for

expected sigma as well as for the anticipated influence of landscape covariates on space use, and

set the pixel resolution to 0.25 km^2. For the RSF surface, we used the same extent and resolution

as the state space. Given the 8 km buffer size and 0.25 km^2 resolution, our state space and RSF

surface were each represented by a 1,275.50 km^2 area of 5,102 pixels (Figure 1).

Telemetry data provides additional information to the encounter model that can be used

to estimate sigma and inform a heterogeneous space use model where the activity center

placement on the landscape and space use around it are sensitive to habitat covariates. We

integrated our telemetry dataset with the capture-recapture data using established methods

available in oSCR, where telemetry locations are summarized as counts for each collared

individual on pixels in the state space (Linden et al. 2018, Sutherland et al. 2019). To avoid serial

autocorrelation and ensure the independence of locations over time, we randomly thinned

telemetry data, using only 10% of each individual's full location dataset (Royle et al. 2013b).

Any individuals that still retained a large number (>100) of locations were thinned again to

ultimately keep only 1% of their full location dataset, in part because large amounts of telemetry data may contain extreme movements that are not reflective of typical movement and space-use patterns, and can preclude model convergence. Because two collared individuals were also recorded using remote camera methods, we used the dependent telemetry setting in oSCR, which implements the model described in Linden et al. (2018).

To evaluate site and occasion-specific heterogeneity in the encounter model, we selected covariates expected to influence detection probability. Site-specific factors included binary covariates describing camera type used (Cuddeback, LTL Acorn), recreation level (High, Low), and landscape surrounding the camera site (Linkage, Core). We defined recreation level based on remote camera detections of humans or animals associated with human recreational activity (e.g., domestic dogs, horses) standardized to the number of camera nights each station was active. Sites with a recreation level greater than 15 human detections per camera night were classified as 'High' and sites below this threshold were classified as 'Low'. Landscape surrounding the camera was classified as 'Core' if the site was located in relatively contiguous designated protected areas ranging in size from 5 km^2 to 230 km^2 or as 'Linkage' if the site was located in unprotected but primarily natural lands between core areas. We also tested season as an occasion-specific covariate (Wet [October - April], Dry [May - September]). Individual level covariates, such as sex, can also be included in the encounter model. Because sex could not be reliably determined from the remote camera records, there is a potential for negatively biased estimates if home range sizes vary among individuals by sex (Tobler and Powell 2013). However, case studies and simulations exploring unmodeled sex-specific heterogeneity in the encounter model have shown that the incurred density estimate bias is typically negligible (Efford and Mowat 2013). For bobcats in southern California, home range size differences

between males and females have been documented, but the magnitude of size differences varies across studies, and is often mediated by landscape features including roads and development (Riley et al. 2003, Poessel et al. 2014)

To evaluate state space-wide spatial heterogeneity in individual space use and population density, we selected landscape covariates to parametrize the encounter model and density model. Previous research on multi-species landscape connectivity in southern California found that water, topography, and development affected bobcat movement (Jennings et al. 2020). As part of this analysis, Jennings et al. 2020 tested a suite of environmental variables at eight ecological neighborhood distances, derived from the ranges of movements seen in bobcat telemetry data, ranging from 170 m to 2000 m. Road density at two different scales, 465m and 1000m, was found to affect bobcat movement. Therefore, we considered distance to water, elevation, percent impervious surface, which is considered a proxy for development and urbanization, and road density at two ecological neighborhoods (465 m, 1000 m, McGarigal et al. 2016, Jennings et al. 2020) as candidate habitat covariates both for the encounter model, which includes the RSF (individual-level space use), and the density model (population-level space use). All habitat covariates were aggregated to the state space/RSF surface resolution, centered by subtracting each covariate layer by its mean, and then scaled by dividing centered layers by their standard deviations using the scale() function in the raster package (Hijmans and van Etten 2012).

SCR-RSF model selection approach

We used a multi-step model fitting approach common in SCR studies (Sutherland et al. 2018, Kendall et al. 2019) that first resolves a best supported encounter model before adding covariates to the density model, similar to a build-up approach (Morin et al. 2020). We identified the best-supported model at each step through AIC-based model selection (Arnold 2010,

Sutherland et al. 2018, Horn et al. 2020). We considered models supported if they were within ΔAIC $\leq$ 2 of the top-ranked model. First, we evaluated trap and occasion-specific covariates on detection probability. Second, we incorporated landscape covariates on the RSF surface into the encounter model, including up to two landscape covariates in a single model. We did not pair habitat variables with a Pearson's correlation coefficient $> |0.65|$. Next, we used the best supported encounter model to compare six candidate models describing landscape-level variation in density, using the landscape covariates extracted to the state space in a univariate context. At each step, we evaluated the sign of the covariate coefficients across left and right-side models, considered whether the relationships were consistent, and removed covariates that were inconsistent for both left and right-sided datasets from consideration in that model selection step.

We used the best-supported model to estimate density and map spatial variation in relative probability of use and bobcat density across our study area. We calculated relative probability of use across the study area individually for each covariate included in the RSF while holding other RSF covariates at their mean, as well as calculating a relative probability of use across the study area for the full RSF using the formulae detailed in Royle et al. (2013a) and Linden et al. (2018). To qualitatively evaluate differences in density across the three original camera arrays (urban, WUI, wildland), we used an ad-hoc approach and created a 3 km buffer around traps in each region and took the mean and standard deviation of per-pixel density values that fell within each buffer. We interpret the resulting values as a qualitative assessment of differences in density across the three study area regions. For clarity, we report only the left-sided SCR-RSF results in the main text, and the right-sided results can be found in Supplemental Tables S1 - S4 and Supplemental Figures S2 – S3.

Results

Sampling data

Between 30 November 2011 and 25 December 2012, we collected 1,434 images of bobcats. Of these, 462 were identifiable to the individual level. We identified 56 left-sided individuals, 57 right-sided individuals, and 17 individuals with both flanks known.

We captured 19 bobcats (14 males, 5 females), collared 17 individuals, and retrieved data from eight collars (7 males, 1 female). The duration of tracking for an individual lasted between 11 and 465 days. After filtering for precision and excluding one collared male that dispersed during the monitoring period, our telemetry dataset comprised 3,961 locations from seven bobcats for home range analysis.

Home range evaluation

Home range sizes calculated with GPS telemetry data ranged from 2.79 km^2 to 5.13 km^2 in the wildland region of the study area (Figure 3 left panel). The smallest home range was for a female bobcat at that site. In the urban region of the study area, home ranges varied from 1.05 km^2 to 5.26 km^2 (Figure 3 right panel). While we did observe overlap among home ranges in the wildland site, the largest degree of overlap (35.3% and 60.7%) was for males overlapping the home range of a collared female. Overlap among male home ranges ranged from 0 to 5.0%. In contrast, there was a much greater degree of overlap among male home ranges in the urban site, ranging from 3.26% to 51.8% (Figure 4, Supplemental Table S5).

SCR-RSF

Capture-recapture summaries for the left + both-sided dataset and right + both-sided dataset are included in Supplemental Table S6. Capture-recapture dataset sample sizes (e.g., total detections, recaptures, spatial recaptures) were comparable across datasets. After thinning the telemetry data, we used a total of 239 locations in our SCR-RSF integration. The number of

unique state space pixels used by each collared individual ranged from 8 - 17. 10 camera trap detections were of collared individuals that contributed telemetry data to the SCR-RSF encounter model selection evaluating trap and occasion-specific covariates on detection probability strongly supported an effect of recreation level at the detector site (AICwt = 1, Table 1, Step 1). When we added RSF covariates, the model including elevation and percent impervious surface had the greatest support (AICwt = 0.90, Table 1, Step 2).

Density model selection yielded three competing best-supported models which included percent impervious surface and road density at both the 450-m and 1000-m ecological neighborhoods (AICwts = 0.44, 0.32, and 0.24, respectively, Table 1, Step 3). These three covariates were all highly correlated with each other (0.82 - 0.99). Therefore, we report model coefficients (Table 4) and density estimates from the model including percent impervious surface for two reasons: this model had the lowest AIC, and impervious surface values include roads, and this is therefore the most inclusive covariate capturing the development gradient in this area.

Bobcat detection probability increased in areas with low relative to high recreation (p.reclevel = 2.79 [SE = 0.35]). Probability of use decreased with increasing elevation (p.elev = -2.43 [SE = 0.35]), and also decreased with increasing percent impervious surface (p.imperv = -0.60 [SE = 0.10]). Baseline detection probability was estimated to be 0.006 [SE = 0.003], which is low but precedented in other bobcat research using SCR (Greenspan et al. 2020), and reasonable given the large number of sampling occasions used in our models. The spatial scale parameter was estimated to be 1.06 km [SE = 0.03].

Our best-supported model included a positive relationship between density and increasing percent impervious surface (D.imperv = 0.51 [SE = 0.12]), in contrast to the negative relationship between increasing percent impervious surface and probability of use (Figure 2).

17

Per-pixel density estimates ranged from 0.10 - 1.14 bobcats/km^2. Across the entire state

space abundance was estimated to be 254.12 bobcats, with a state space average of 19.92

bobcats/100 km^2 (95% CI = 11.09 - 40.04). Average densities across the three study area regions

were 30.68 [SD = 18.36], 14.76 [SD = 10.32], and 11.46 [SD = 2.13] bobcats/100km^2 for urban,

WUI, and wildland, respectively (Supplemental Figure S4).

Discussion

Bobcats, because of their use of habitat across the development gradient, are a species

well-suited to explore carnivore responses to urbanized landscapes (Crooks 2002, Riley et al.

2006, Lewis et al. 2015). Although previous research has focused on bobcat responses to

landscape features and habitat quality, concurrent evaluations of these responses at both the

individual and population scales have been limited. Using an integrated spatial capture-recapture

+ resource selection function (SCR-RSF) framework, we found opposing relationships at

different scales of space use, with bobcats appearing to select against developed areas within

their home ranges but experiencing increased population densities with increasing development.

Our results align with published research demonstrating that landscape development affects

bobcat space use, and further reveal differences between individual and population level impacts.

This contrasting multi-scale response provides one potential explanation for the disparate

findings across published studies evaluating the relationships among bobcat movement, habitat

use, and density in urban and developed areas.

Individual-level space use

Individual bobcat habitat use was negatively associated with development intensity, as

measured by percent impervious surface, consistent with previous bobcat studies (Riley et al.

2010, Šálek et al. 2014, Young et al. 2019a). Bobcats preferred natural areas and largely avoided

18

developed areas at the finer scale of individual movement within the home range, i.e., second order. Other research has noted that bobcat fidelity to natural landscape features can occur at the scale of a single shrub or a narrow riparian corridor (Serieys et al. 2021). Though individual bobcats avoided development, we also found a positive association between habitat use and lower elevations. In San Diego County, development is generally greatest at lower elevations along the western coastline, decreasing in intensity as elevation increases eastward. This interplay creates a constraint on lower elevation natural habitats that are likely most suitable for bobcats in this region. In addition, we found that increased recreational activity had a strong negative effect on bobcat detection probability. This may be linked directly to behavioral responses to disturbance from recreation activities and the presence of humans (George and Crooks 2006, Reed and Merenlender 2011), which has been found to be consistent for bobcats across a human footprint gradient (Reilly et al. 2022). Research on Eurasian lynx (*Lynx lynx*) response to outdoor recreation showed that this avoidance occurred only at the local scale but did not affect space use at the home range scale (Thorsen 2022). A negative response to human factors (e.g., footprint, presence) may be driven by associated spatiotemporal differences in prey resources. For example, there is evidence of temporal shifts in prey species activity in response to increased human disturbance (Gaynor et al. 2018), and some evidence that certain prey species become more or less abundant in human-impacted landscapes (Dunagan et al. 2019). However, previous research suggests that food availability may not always be a primary factor affecting bobcat space use (Benson et al. 2006).

Density and population-level space use

Although the resource selection component of our analysis indicated bobcats avoid areas with increased development, our results also indicate that, at the population level, densities

increased as the percentage of impervious surface increased on the landscape. In addition, we found that home ranges tended to have greater overlap in the more heavily developed regions of the study area, though the limited sample size of collared individuals across the development gradient and dearth of collared females relative to males precludes population-level inference on home range overlap with telemetry data alone. Elevated bobcat densities in developed landscapes may result from habitat patches in these areas being more isolated from contiguous undeveloped habitat and constrained by movement barriers like highways, which can limit dispersal ability and cause home range pile-up (Riley et al. 2006, Poessel et al. 2014). The fence effect, the hypothesis underlying home range pile-up (Krebs et al. 1969), suggests that densities will be temporarily higher in isolated regions due to the initial restriction of movement, and eventually decline as resources become limited and immigration and emigration fail to occur over time. Lewis et al. (2015) found higher bobcat densities in wildland areas relative to the wildland urban interface in Boulder, CO, USA, and suggested the lack of evidence for home range pile-up may be due to the temporal lag of the fence effect, where populations had already experienced declines adjacent to urban areas. The extent to which the fence effect or home range pile-up affects mammalian carnivores in developed landscapes likely varies as a function of ecological, structural, and social differences among urban areas. For example, the degree of permeability of the "fence" likely varies in different systems with differing degrees of development (Lewis et al. 2015). Urbanization can also encompass components beyond structural or built metrics, including modifications to abiotic factors such as impacts to air, soil, and water quality, or biotic factors associated with intensity of human use, such as resource availability, or local wildlife community composition (Moll 2019). Higher bobcat densities could also be related to increased resources in developed areas, such as higher prey densities, given that these spaces can provide

lush vegetation to support prey populations. Additional research in southern California did not find variation in prey density as a function of development (Dunagan et al. 2019), but differences between developed areas in Los Angeles and San Diego may drive different patterns in prey density. Social factors including land-use histories and cultural attitudes are also important attributes of urbanization that vary over space and time (Magle et al. 2019, Schell et al. 2020), and a more holistic consideration of factors associated with urbanization may ultimately help resolve these among-city differences in mammalian carnivore response to urbanization (Magle et al. 2019). Lack of agreement among studies may also arise because of differences in methodological approach, scale of analyses, or a limited exploration into the factors that influence habitat use and home range at the level of the individual and the factors that exert influence at the population level. Further exploration into the linkages between these two scales is also warranted, as highlighted by the contrasting response to development at multiple scales by bobcats in San Diego County.

The bobcat range in North America is extensive, and across this distribution densities vary widely. Population densities reported in the literature range from $1 - 103$ bobcats/100 km^2 (Jacques et al. 2019, Young et al. 2019b, Lavariega et al. 2022) with differences broadly driven by variation in habitat quality, prey availability, and climate (Carbone and Gittelman 2002, Benson et al. 2006, Thornton and Pekins 2015, Lavariega et al. 2022). Developed landscapes introduce additional variation in habitat quality and the community composition of predators, competitors, and prey. Further, these landscapes introduce built features that can function as movement barriers. Bobcat density estimates in our study area were similar but trended lower than those reported for other urbanized regions of southern California, specifically in Los Angeles, Orange, and Ventura counties (Table 3). Generally, population and housing densities in

the most developed areas of San Diego County were similar to areas around Los Angeles, where a majority of bobcat research has been done in southern California. While the average bobcat density across our San Diego study area was relatively low at 19.92 bobcats/100 km^2, in the urban region of our study area densities were higher (up to 40 bobcats/100 km^2) and comparable to findings from other urban bobcat research in southern California (Ruell et al. 2009, Riley et al. 2010, Alonso et al. 2015). Looking beyond southern California for further context (Table 3), we found that bobcat density estimates reported in and around other urbanized regions of the U.S. differed substantially, ranging from 15-16 bobcats/100 km^2 in the wildland urban interface (WUI) in Colorado (Lewis et al. 2015) to 103-128 bobcats/100 km^2 in the Dallas-Fort Worth area of Texas (Young et al. 2019b). Research estimating bobcat population density in the eastern portion of the U.S. has focused primarily on wildland populations, but a study located in a densely populated region of Rhode Island characterized by high road density used genetic techniques to estimate an effective population size between 44-329 individuals in a 242,745 ha study area, which suggested low densities between 1.81 – 13.55 bobcats/100 km^2 at this eastern site (Mayer et al. 2022). Bobcat densities generally increase with increasing temperature (Thornton and Pekins 2015, Lavariega et al. 2022), which may in part explain the lower densities reported for bobcats at the WUI in Colorado and Rhode Island relative to the higher urban bobcat densities reported in Texas and southern California. Additionally, differences in social and ecological patterns that drive land-use change, development, habitat structure, and resource availability at the regional, among-city, and within-city scales can all influence wildlife diversity and abundance across urban settings (Magle et al. 2019, Schell et al. 2020, Fidino et al. 2021), and future research can target the drivers of variation in bobcat abundance and density across cities.

In addition to the influence of habitat pattern and structure, some of the differences in reported densities both within southern California and among urban areas outside the region could be attributable to different methodological approaches for data collection and analysis. For example, (Lembeck and Gould 1979) reported bobcat densities of 115-153/100 km^2 in rural San Diego County, just to the south of our inland study areas. However, these estimates were based on VHF telemetry data and coarse scale home range estimations. In this study, we used an approach that explicitly estimates density within a defined area, relative to studies that used coarse calculations, i.e., dividing available habitat by average home range size to estimate potential density. Similarly, home range estimation techniques have the potential to produce results that do not adequately represent space use in urban environments, where individuals are likely to be exhibiting fine scale movement and selection not captured by coarser representations of home range such as minimum convex polygon or fixed kernel density home range estimation methods (Serieys et al. 2021). It should also be noted that information on a limited number of home ranges can make it difficult to understand population level space use. By using the SCR-RSF approach, we were able to more fully explore the relationship between space use and population density because this approach integrates individual and population-level scales of space use (Royle et al. 2013b). Specifically, the SCR-RSF framework allowed us to examine individual-level habitat selection and space use, informing population density through the placement and overlap of home ranges among individuals.

Bobcat ecology and conservation across the development gradient

Although development pressure in and around urban areas is prevalent across bobcats' range, in some urbanized areas, like San Diego, bobcat populations appear relatively stable at moderate to high densities. The contrasting multi-scale response to development shown by

bobcats in this system could be a mechanism contributing to the local stability of higher population densities in areas characterized by greater development. Whether bobcat populations in San Diego or other urban areas will ultimately decline as a result of home range pile-up or experience lasting fence effects from development at the wildlife urban interface in the future is uncertain. What our study demonstrates is that the extant population of bobcats in San Diego is responding to the built environment in contrasting ways, and the multi-scale nature of this response may explain some of the variability reported in studies of urban bobcat populations. This observed variability in bobcat response to urbanization may also be a result of differences in habitat quality, resource availability, fragmentation, and connectivity among protected or undeveloped areas within the urban matrix. Despite their tolerance for urbanization and associated higher densities, bobcats in San Diego, like many other urbanized areas, face future risks, such as changes in habitat quality from climate change, disease outbreaks exacerbated by elevated wildlife population density, vulnerability to increasing wildfire intensity and frequency, or time lagged effects of new barriers to connectivity across the landscape. Using this robust multi-scale approach in future cross-city collaborations to consider what factors of landscape development and habitat structure affect space use and density could help identify how to best design habitat conservation plans for territorial urban wildlife species like the bobcat. Understanding the links between individual space use and population-level processes can inform important preemptive or reactive conservation action including identifying corridors, prioritizing restoration, and preserving contiguous suitable habitat. An expansion of multi-site and multi-scale analyses that incorporate behavioral differences in movement and space use will be needed to advance our understanding of wildlife responses to both dynamic built environments and dynamic natural landscapes.

Declaration of competing interest

The authors have no personal or financial competing interests to declare.

Acknowledgments

References

Alonso, R. S., B. T. McClintock, L. M. Lyren, E. E. Boydston, and K. R. Crooks. 2015. Mark-recapture and mark-resight methods for estimating abundance with remote cameras: a carnivore case study. PLOS ONE 10:e0123032.

Angel, S. 2012. Planet of cities. Lincoln Institute of Land Policy Cambridge, MA.

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. The Journal of Wildlife Management 74:1175–1178.

Augustine, B. C., J. A. Royle, M. J. Kelly, C. B. Satter, R. S. Alonso, E. E. Boydston, and K. R. Crooks. 2018. Spatial capture–recapture with partial identity: An application to camera traps. The Annals of Applied Statistics 12.

Benson, J. F., M. J. Chamberlain, and B. D. Leopold. 2006. Regulation of space use in a solitary felid: population density or prey availability? Animal Behaviour 71:685–693.

Bino, G., A. Dolev, D. Yosha, A. Guter, R. King, D. Saltz, and S. Kark. 2010. Abrupt spatial and numerical responses of overabundant foxes to a reduction in anthropogenic resources. Journal of Applied Ecology 47:1262–1271.

Bolger, D. T., T. A. Morrison, B. Vance, D. Lee, and H. Farid. 2012. A computer-assisted system for photographic mark-recapture analysis: *Software for photographic mark-recapture*. Methods in Ecology and Evolution 3:813–822.

Borchers, D. L., and M. G. Efford. 2008. Spatially explicit maximum likelihood methods for capture-recapture studies. Biometrics 64:377–385.

Calenge, C. 2006. The package adehabitat for the R software: tool for the analysis of space and habitat use by animals. Ecological Modelling 197:1035.

Carbone, C., and J. L. Gittleman. 2002. A common rule for the scaling of carnivore density. Science 295:2273–2276.

Converse, S. J., B. Mcclintock, and P. Conn. 2022. Special Feature: Linking capture–recapture and movement. Ecology 103.

Crooks, K. R. 2002. Relative sensitivities of mammalian carnivores to habitat fragmentation. Conservation Biology 16:488–502.

Crooks, K. R., C. L. Burdett, D. M. Theobald, C. Rondinini, and L. Boitani. 2011. Global patterns of fragmentation and connectivity of mammalian carnivore habitat. Philosophical Transactions of the Royal Society B: Biological Sciences 366:2642–2651.

Dunagan, S. P., T. J. Karels, J. G. Moriarty, J. L. Brown, and S. P. D. Riley. 2019. Bobcat and rabbit habitat use in an urban landscape. Journal of Mammalogy 100:401–409.

Efford, M. G., and G. Mowat. 2014. Compensatory heterogeneity in spatially explicit capture–recapture data. Ecology 95:1341–1348.

Fidino, M., T. Gallo, E. W. Lehrer, M. H. Murray, C. A. M. Kay, H. A. Sander, B. MacDougall, C. M. Salsbury, T. J. Ryan, J. L. Angstmann, J. Amy Belaire, B. Dugelby, C. J. Schell, T. Stankowich, M. Amaya, D. Drake, S. H. Hursh, A. A. Ahlers, J. Williamson, L. M. Hartley, A. J. Zellmer, K. Simon, and S. B. Magle. 2021. Landscape-scale differences among cities alter common species' responses to urbanization. Ecological Applications 31.

Gaynor, K. M., C. E. Hojnowski, N. H. Carter, and J. S. Brashares. 2018. The influence of human disturbance on wildlife nocturnality. Science 360:1232–1235.

George, S. L., and K. R. Crooks. 2006. Recreation and large mammal activity in an urban nature reserve. Biological Conservation 133:107–117.

Getz, W. M., and C. C. Wilmers. 2004. A local nearest-neighbor convex-hull construction of home ranges and utilization distributions. Ecography 27:489–505.

Glennie, R., S. T. Buckland, R. Langrock, T. Gerrodette, L. T. Ballance, S. J. Chivers, and M. D. Scott. 2021. Incorporating animal movement into distance sampling. Journal of the American Statistical Association 116:107–115.

Greenspan, E., S. Anile, and C. K. Nielsen. 2020. Density of wild felids in Sonora, Mexico: a comparison of spatially explicit capture-recapture methods. European Journal of Wildlife Research 66:60.

Greer, K. A. 2004. Habitat conservation planning in San Diego County, California: lessons learned after five years of implementation. Environmental Practice 6:230–239.

Gustafson, K. D., R. B. Gagne, T. W. Vickers, S. P. D. Riley, C. C. Wilmers, V. C. Bleich, B. M. Pierce, M. Kenyon, T. L. Drazenovich, J. A. Sikich, W. M. Boyce, and H. B. Ernest. 2019. Genetic source–sink dynamics among naturally structured and anthropogenically fragmented puma populations. Conservation Genetics 20:215–227.

Hanski, I. 2011. Habitat loss, the dynamics of biodiversity, and a perspective on conservation. AMBIO 40:248–255.

Heilbrun, R. D., N. J. Silvy, M. E. Tewes, and M. J. Peterson. 2006. Using automatically triggered cameras to individually identify bobcats. Wildlife Society Bulletin 31:748–755.

Hijmans, R. J., and J. van Etten. 2012. raster: Geographic analysis and modeling with raster data.

Horn, P. E., M. J. R. Pereira, T. C. Trigo, E. Eizirik, and F. P. Tirelli. 2020. Margay (Leopardus wiedii) in the southernmost Atlantic Forest: Density and activity patterns under different levels of anthropogenic disturbance. PLOS ONE 15:e0232013.

Howe, E. J., M. E. Obbard, and C. J. Kyle. 2013. Combining data from 43 standardized surveys

to estimate densities of female American black bears by spatially explicit capture–recapture. Population Ecology 55:595–607.

Jacques, C. N., R. W. Klaver, T. C. Swearingen, E. D. Davis, C. R. Anderson, J. A. Jenks, C. S. Deperno, and R. D. Bluett. 2019. Estimating density and detection of bobcats in fragmented midwestern landscapes using spatial capture–recapture data from camera traps. Wildlife Society Bulletin 43:256–264.

Jennings, M. K., K. A. Zeller, and R. L. Lewison. 2020. Supporting adaptive connectivity in dynamic landscapes. Land 9:295.

Kendall, K. C., T. A. Graves, J. A. Royle, A. C. Macleod, K. S. McKelvey, J. Boulanger, and J. S. Waller. 2019. Using bear rub data and spatial capture-recapture models to estimate trend in a brown bear population. Scientific Reports 9:16804.

Krebs, C. J., B. L. Keller, and R. H. Tamarin. 1969. Microtus population biology: Demographic changes in fluctuating populations of M. ochrogaster and M. pennsylvanicus in southern Indiana. Ecology 50:587–607.

Lavariega, M. C., M. Briones-Salas, A. G. Monroy-Gamboa, and D. Ramos-Méndez. 2022. Density and activity patterns of bobcat in its southernmost distribution. Animal Biodiversity and Conservation 45:145–160.

Leighton, G. R. M., J. M. Bishop, J. Merondun, D. J. Winterton, M. J. O'Riain, and L. E. K. Serieys. 2021. Hiding in plain sight: risk mitigation by a cryptic carnivore foraging at the urban edge. Animal Conservation 25:244-258.

Lembeck, M., and G. Gould. 1979. Dynamics of harvested and unharvested bobcat populations in California. Pages 16–18 Bobcat Research Conference Proceedings, Front Royal, Va.

Lewis, J. S., K. A. Logan, M. W. Alldredge, L. L. Bailey, S. VandeWoude, and K. R. Crooks. 2015. The effects of urbanization on population density, occupancy, and detection probability of wild felids. Ecological Applications 25:1880–1895.

Lewis, J. S., J. L. Rachlow, E. O. Garton, and L. A. Vierling. 2007. Effects of habitat on GPS collar performance: using data screening to reduce location error: GPS collar performance. Journal of Applied Ecology 44:663–671.

Linden, D. W., A. P. K. Sirén, and P. J. Pekins. 2018. Integrating telemetry data into spatial capture–recapture modifies inferences on multi-scale resource selection. Ecosphere 9.

Lombardi, J. V., C. E. Comer, D. G. Scognamillo, and W. C. Conway. 2017. Coyote, fox, and bobcat response to anthropogenic and natural landscape features in a small urban area. Urban Ecosystems 20:1239–1248.

Lyren, L., G. Turschak, E. Ambat, C. Haas, J. Tracey, E. Boydston, S. Hathaway, R. Fisher, and K. Crooks. 2006. Carnivore activity and movement in a southern California protected area, the North/Central Irvine Ranch. Sacramento: US Geological Survey, Western

Ecological Research Center.

Magle, S. B., M. Fidino, E. W. Lehrer, T. Gallo, M. P. Mulligan, M. J. Ríos, A. A. Ahlers, J. Angstmann, A. Belaire, B. Dugelby, A. Gramza, L. Hartley, B. MacDougall, T. Ryan, C. Salsbury, H. Sander, C. Schell, K. Simon, S. St Onge, and D. Drake. 2019. Advancing urban wildlife research through a multi-city collaboration. Frontiers in Ecology and the Environment 17:232–239.

Manly, B. F., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Introduction to resource selection studies. Resource selection by animals: statistical design and analysis for field studies pp.1–15.

Mayer, A. E., T. J. McGreevy Jr, C. Brown, L. S. Ganoe, and B. D. Gerber. 2022. Transient persistence of bobcat (Lynx rufus) occurrence throughout a human-dominated landscape. Population Ecology.

McClintock, B. T., P. B. Conn, R. S. Alonso, and K. R. Crooks. 2013. Integrated modeling of bilateral photo-identification data in mark–recapture analyses. Ecology 94:1464–1471.

McGarigal, K., H. Y. Wan, K. A. Zeller, B. C. Timm, and S. A. Cushman. 2016. Multi-scale habitat selection modeling: a review and outlook. Landscape Ecology 31:1161–1175.

Moll, R. J., J. D. Cepek, P. D. Lorch, P. M. Dennis, E. Tans, T. Robison, J. J. Millspaugh, and R. A. Montgomery. 2019. What does urbanization actually mean? A framework for urban metrics in wildlife research. Journal of Applied Ecology 56:1289–1300.

Morin, D. J., C. B. Yackulic, J. E. Diffendorfer, D. B. Lesmeister, C. K. Nielsen, J. Reid, and E. M. Schauber. 2020. Is your ad hoc model selection strategy affecting your multimodel inference? Ecosphere 11.

Nickel, B. A., J. P. Suraci, M. L. Allen, and C. C. Wilmers. 2020. Human presence and human footprint have non-equivalent effects on wildlife spatiotemporal habitat use. Biological Conservation 241:108383.

Ordeñana, M. A., K. R. Crooks, E. E. Boydston, R. N. Fisher, L. M. Lyren, S. Siudyla, C. D. Haas, S. Harris, S. A. Hathaway, G. M. Turschak, A. K. Miles, and D. H. Van Vuren. 2010. Effects of urbanization on carnivore species distribution and richness. Journal of Mammalogy 91:1322–1331.

Parsons, A. W., C. T. Rota, T. Forrester, M. C. Baker-Whatton, W. J. McShea, S. G. Schuttler, J. J. Millspaugh, and R. Kays. 2019. Urbanization focuses carnivore activity in remaining natural habitats, increasing species interactions. Journal of Applied Ecology 56:1894–1904.

Paterson, J. T., K. Proffitt, B. Jimenez, J. Rotella, and R. Garrott. 2019. Simulation-based validation of spatial capture-recapture models: A case study using mountain lions. PLOS ONE 14:e0215458.

Poessel, S. A., C. L. Burdett, E. E. Boydston, L. M. Lyren, R. S. Alonso, R. N. Fisher, and K. R. Crooks. 2014. Roads influence movement and home ranges of a fragmentation-sensitive carnivore, the bobcat, in an urban landscape. Biological Conservation 180:224–232.

R Core Team. 2021. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Randa, L. A., and J. A. Yunger. 2006. Carnivore occurrence along an urban–rural gradient: A landscape-level analysis. Journal of Mammalogy 87:1154–1164.

Reed, S. E., and A. M. Merenlender. 2011. Effects of management of domestic dogs and recreation on carnivores in protected areas in northern California: Managing dogs in protected areas. Conservation Biology 25:504–513.

Reilly, C. M., J. P. Suraci, J. A. Smith, Y. Wang, and C. C. Wilmers. 2022. Mesopredators retain their fear of humans across a development gradient. Behavioral Ecology 33:428-435.

Riley, S. P., B. L. Cypher, and S. D. Gehrt. 2010. Urban carnivores. JHU Press.

Riley, S. P. D., R. M. Sauvajot, T. K. Fuller, E. C. York, D. A. Kamradt, C. Bromley, and R. K. Wayne. 2003. Effects of urbanization and habitat fragmentation on bobcats and coyotes in southern California. Conservation Biology 17:566–576.

Riley, S. P. D., J. P. Pollinger, R. M. Sauvajot, E. C. York, C. Bromley, T. K. Fuller, and R. K. Wayne. 2006. A southern California freeway is a physical and social barrier to gene flow in carnivores. Molecular Ecology 15:1733–1741.

Royle, J. A., R. B. Chandler, R. Sollmann, and B. Gardner. 2013a. Spatial capture-recapture. Academic Press.

Royle, J. A., R. B. Chandler, C. C. Sun, and A. K. Fuller. 2013b. Integrating resource selection information with spatial capture-recapture. Methods in Ecology and Evolution 4:520–530.

Royle, J. A., and K. V. Young. 2008. A hierarchical model for spatial capture–recapture data. Ecology 89:2281–2289.

Ruell, E. W., S. P. D. Riley, M. R. Douglas, J. P. Pollinger, and K. R. Crooks. 2009. Estimating bobcat population sizes and densities in a fragmented urban landscape using noninvasive capture–recapture sampling. Journal of Mammalogy 90:129–135.

Šálek, M., L. Drahníková, and E. Tkadlec. 2014. Changes in home range sizes and population densities of carnivore species along the natural to urban habitat gradient: Carnivores along the natural-urban habitat gradient. Mammal Review 45:1–14.

Sanderson, E. W., J. Walston, and J. G. Robinson. 2018. From bottleneck to breakthrough: Urbanization and the future of biodiversity conservation. BioScience 68:412–426.

Santini, L., M. González-Suárez, D. Russo, A. Gonzalez-Voyer, A. Hardenberg, and L. Ancillotto. 2019. One strategy does not fit all: determinants of urban adaptation in mammals. Ecology Letters 22:365–376.

Scharf, H. R., and F. E. Buderman. 2020. Animal movement models for multiple individuals. WIREs Computational Statistics 12.

Schell, C. J., K. Dyson, T. L. Fuentes, S. Des Roches, N. C. Harris, D. S. Miller, C. A. Woelfle-Erskine, and M. R. Lambert. 2020. The ecological and evolutionary consequences of systemic racism in urban environments. Science 369:eaay4497.

Schell, C. J., L. A. Stanton, J. K. Young, L. M. Angeloni, J. E. Lambert, S. W. Breck, and M. H. Murray. 2021. The evolutionary consequences of human–wildlife conflict in cities. Evolutionary Applications 14:178–197.

Serieys, L. E. K., A. Lea, J. P. Pollinger, S. P. D. Riley, and R. K. Wayne. 2015. Disease and freeways drive genetic change in urban bobcat populations. Evolutionary Applications 8:75–92.

Serieys, L. E. K., A. J. Lea, M. Epeldegui, T. C. Armenta, J. Moriarty, S. VandeWoude, S. Carver, J. Foley, R. K. Wayne, S. P. D. Riley, and C. H. Uittenbogaart. 2018. Urbanization and anticoagulant poisons promote immune dysfunction in bobcats. Proceedings of the Royal Society B: Biological Sciences 285:20172533.

Serieys, L. E. K., M. S. Rogan, S. S. Matsushima, and C. C. Wilmers. 2021. Road-crossings, vegetative cover, land use and poisons interact to influence corridor effectiveness. Biological Conservation 253:108930.

Smith, J. G., M. K. Jennings, E. E. Boydston, K. R. Crooks, H. B. Ernest, S. P. D. Riley, L. E. K. Serieys, S. Sleater-Squires, and R. L. Lewison. 2020. Carnivore population structure across an urbanization gradient: a regional genetic analysis of bobcats in southern California. Landscape Ecology 35:659–674.

Sun, C. C., A. K. Fuller, and J. A. Royle. 2014. Trap Configuration and spacing influences parameter estimates in spatial capture-recapture models. PLoS ONE 9:e88025.

Suraci, J. P., K. M. Gaynor, M. L. Allen, P. Alexander, J. S. Brashares, S. Cendejas-Zarelli, K. Crooks, L. M. Elbroch, T. Forrester, A. M. Green, J. Haight, N. C. Harris, M. Hebblewhite, F. Isbell, B. Johnston, R. Kays, P. E. Lendrum, J. S. Lewis, A. McInturff, W. McShea, T. W. Murphy, M. S. Palmer, A. Parsons, M. A. Parsons, M. E. Pendergast, C. Pekins, L. R. Prugh, K. A. Sager-Fradkin, S. Schuttler, Ç. H. Şekercioğlu, B. Shepherd, L. Whipple, J. Whittington, G. Wittemyer, and C. C. Wilmers. 2021. Disturbance type and species life history predict mammal responses to humans. Global Change Biology 27:3718–3731.

Sutherland, C., A. K. Fuller, J. A. Royle, M. P. Hare, and S. Madden. 2018. Large-scale variation in density of an aquatic ecosystem indicator species. Scientific Reports 8:8958.

Sutherland, C., J. A. Royle, and D. W. Linden. 2019. oSCR: a spatial capture–recapture R package for inference about spatial ecological processes. Ecography 42:1459–1469.

Thornton, D. H., and C. E. Pekins. 2015. Spatially explicit capture–recapture analysis of bobcat (Lynx rufus) density: implications for mesocarnivore monitoring. Wildlife Research 42:394.

Thorsen, N. H. 2022. Smartphone app reveals that lynx avoid human recreationists on local scale, but not home range scale. Scientific Reports 12:1–13.

Tobler, M. W., and G. V. N. Powell. 2013. Estimating jaguar densities with camera traps: Problems with current designs and recommendations for future studies. Biological Conservation 159:109–118.

Tracey, J. A., J. Zhu, E. Boydston, L. Lyren, R. N. Fisher, and K. R. Crooks. 2013. Mapping behavioral landscapes for animal movement: a finite mixture modeling approach. Ecological Applications 23:654–669.

UN DESA. 2014. World urbanization prospects, the 2011 revision.

Venter, O., E. W. Sanderson, A. Magrach, J. R. Allan, J. Beher, K. R. Jones, H. P. Possingham, W. F. Laurance, P. Wood, B. M. Fekete, M. A. Levy, and J. E. M. Watson. 2016. Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. Nature Communications 7:12558.

Young, J., J. Golla, J. Draper, D. Broman, T. Blankenship, and R. Heilbrun. 2019a. Space use and movement of urban bobcats. Animals 9:275.

Young, J. K., J. M. Golla, D. Broman, T. Blankenship, and R. Heilbrun. 2019b. Estimating density of an elusive carnivore in urban areas: use of spatially explicit capture-recapture models for city-dwelling bobcats. Urban Ecosystems 22:507–512.

Tables

Table 1. San Diego bobcat SCR-RSF model selection results, with column 'np' indicating the number of parameters in each competing model. Step 1 identified the best supported encounter model incorporating trap-specific covariates influencing bobcat detection probability. No covariates were added to the sigma parameter. Step 2 identified the best supported encounter model incorporating RSF covariates influencing bobcat probability of space use using the best supported model from the previous step. Step 3 identified the best supported model describing spatial heterogeneity in density using the best supported encounter model selected in the previous model selection steps.

Selection Step	Density Model	Encounter Model	np	AIC	deltaAIC	AICwt	AICwt+	LogLik
	D(.)	p(rec level)	4	3490.99	0.00	1.00	1.00	1741.50
	D(.)	p(camera type)	4	3520.74	29.75	0.00	1.00	1756.37
1	D(.)	p(season)	4	3527.48	36.49	0.00	1.00	1759.74
	D(.)	p(.)	3	3528.61	37.61	0.00	1.00	1761.30
	D(.)	p(site type)	4	3529.88	38.89	0.00	1.00	1760.94
	D(.)	p(elev + imperv + rec level)	6	3438.94	0.00	0.90	0.90	1713.47
	D(.)	p(water dist + elev + rec level)	6	3443.35	4.41	0.10	1.00	1715.67
	D(.)	p(elev + road465 + rec level)	6	3452.60	13.66	0.00	1.00	1720.30
	D(.)	p(elev + road1000 + rec level)	6	3456.35	17.41	0.00	1.00	1722.18
2	D(.)	p(water dist + road1000 + rec level)	6	3461.33	22.39	0.00	1.00	1724.66
	D(.)	p(water dist + road465 + rec level)	6	3463.44	24.50	0.00	1.00	1725.72
	D(.)	p(water dist + rec level)	5	3464.26	25.32	0.00	1.00	1727.13
	D(.)	p(water dist + imperv + rec level)	6	3465.26	26.32	0.00	1.00	1726.63

D(.)	p(elev + rec level)	5	3465.38	26.44	0.00	1.00	1727.69
D(.)	p(imperv + rec level)	5	3487.41	48.47	0.00	1.00	1738.71
D(.)	p(road1000 + rec level)	5	3489.32	50.37	0.00	1.00	1739.66
D(.)	p(rec level)	4	3491.00	52.05	0.00	1.00	1741.50
D(.)	p(road465 + rec level)	5	3491.26	52.32	0.00	1.00	1740.63
D(imperv)	p(elev + imperv + rec level)	7	3427.85	0.00	0.44	0.44	1706.93
D(road465)	p(elev + imperv + rec level)	7	3428.49	0.64	0.32	0.76	1707.24
D(road1000)	p(elev + imperv + rec level)	7	3429.10	1.25	0.24	1.00	1707.55
D(.)	p(elev + imperv + rec level)	6	3438.94	11.09	0.00	1.00	1713.47
D(elev)	p(elev + imperv + rec level)	7	3439.57	11.72	0.00	1.00	1712.79
D(water dist)	p(elev + imperv + rec level)	7	3440.85	13.00	0.00	1.00	1713.43

3

Table 2. Maximum-likelihood parameter estimates and standard errors from the best supported model for bobcat density and space use

Model	Parameter	Estimate	SE
Density	D.intercept	-3.40	0.17
	D.imperv	0.51	0.12
Encounter	p0.intercept	-5.10	0.49
	p.rec level	2.79	0.35
	p.elev	-2.43	0.35
	p.imperv	-0.60	0.10
	sigma.intercept	0.06	0.03

Table 3. Comparison of density estimates from urban bobcat studies within the USA.

Year of study	Study Area	State	Density (bobcats/100 km^2)	Reference
1979	San Diego County (rural county only)	CA	115-153	Lembeck and Gould 1979
2014	Dallas-Ft. Worth	TX	103-128	Young et al. 2019b*
2013	Nacogdoches	TX	61	Lombardi et al. 2017*
2006	San Joaquin Hills, Orange County	CA	30-62	Alonso et al. 2015*
2004	Santa Monica Mountains NRA	CA	24-42	Ruell et al. 2009
2002-2008	Orange County	CA	23	Riley et al. 2010
2004 - 2009	Ventura County (post-mange epizootic)	CA	21	Riley et al. 2010
2010	Boulder (Front Range)	CO	20-24	Lewis et al. 2015*
2009	Montrose and Ridgway (Western Front)	CO	15-16	Lewis et al. 2015*
2012	San Diego County	CA	11 - 40	This study*
2018 – 2020	Washington, Kent, and Providence Counties	RI	2 – 14	Mayer et al. 2022

∗ indicates studies that used SCR or occupancy approaches

Figures
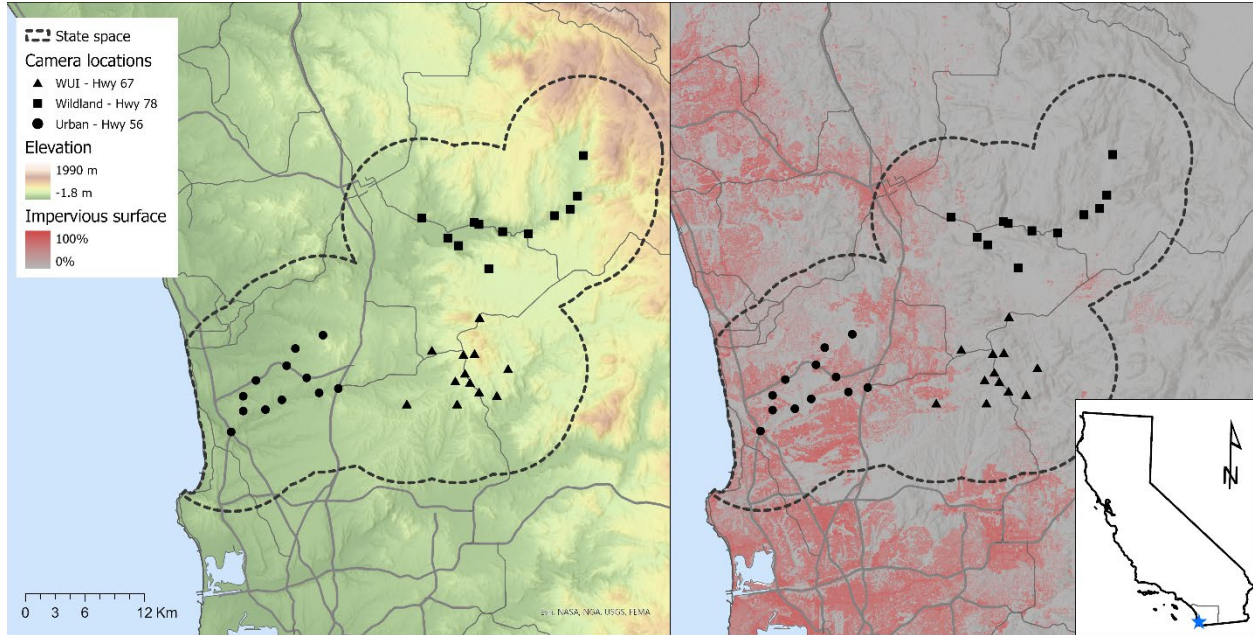
Figure 1. Study area map showing the 36 camera trap sampling sites covering a gradient of elevation (left panel) and development (right panel). Traps are identified as being placed in the urban (circles), wildland urban interface (triangles), or wildland (squares) study area regions. 8 km buffered outline around sampling sites represents the 1,275.50 km^2 state space specified for the SCR-RSF analysis.
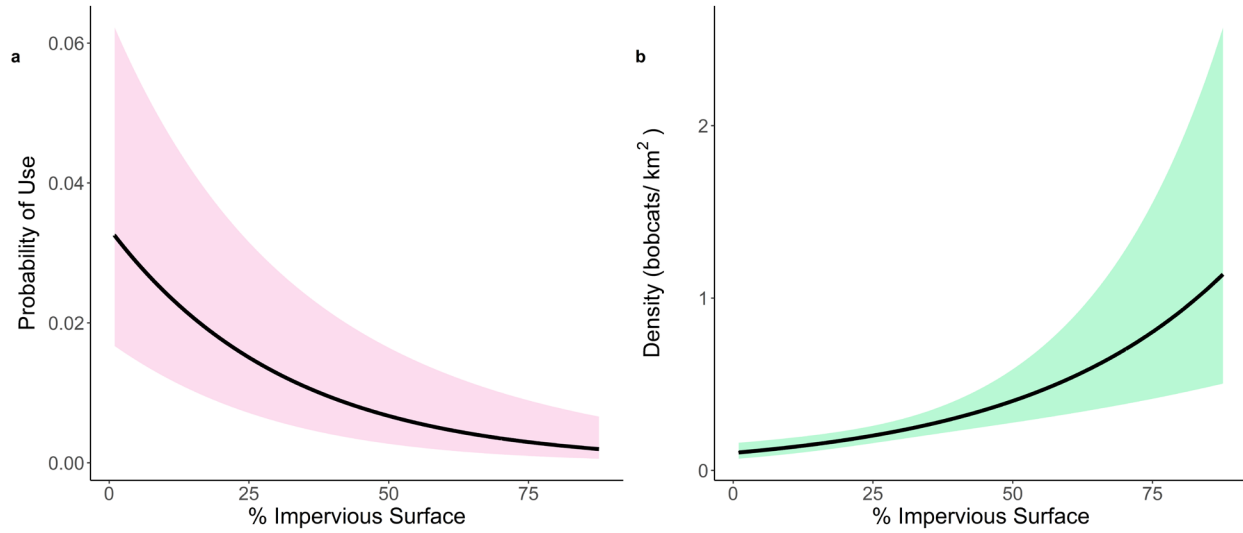
Figure 2. Best-supported model predictions of a) relative probability of use and b) density (bobcats/km^2) as a function of percent impervious surface, shown across the range of percent impervious surface values in the study area
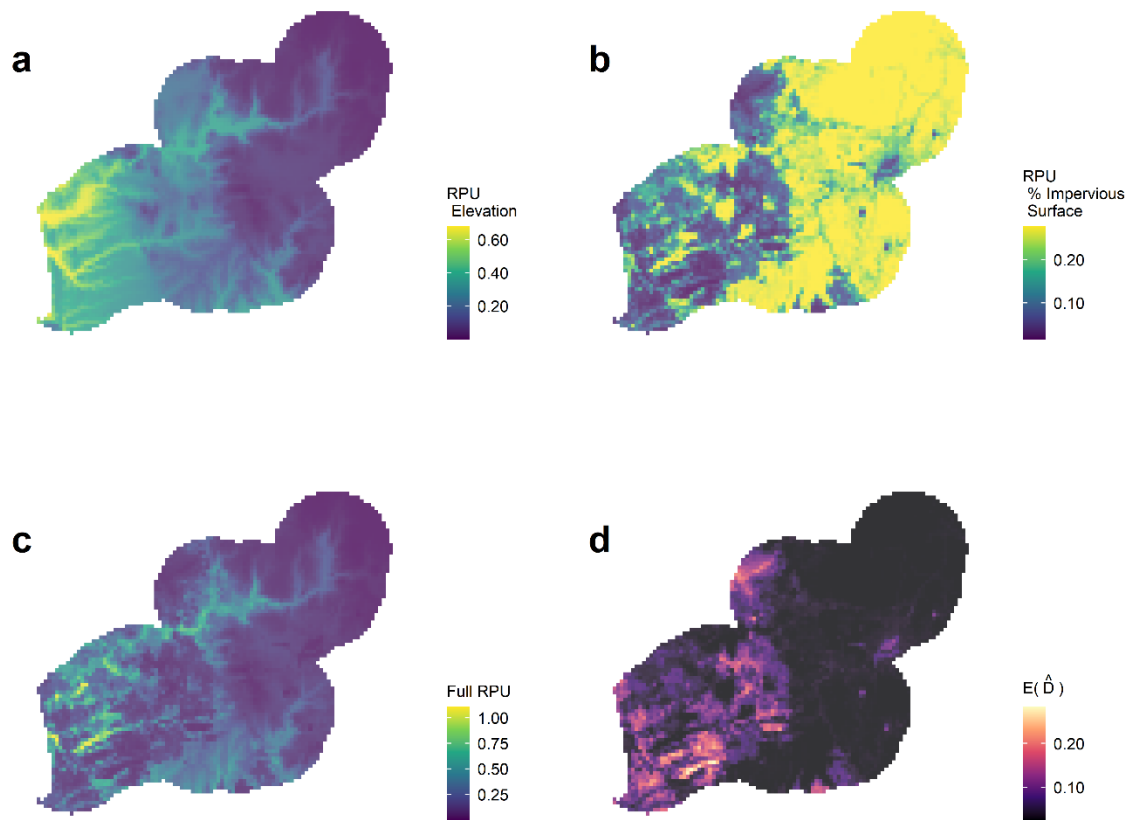
Figure 3. Best-supported model predictions projected across the 1,275.50 km^2 study area showing a) relative probability of use (RPU) given elevation, b) relative probability of use given percent impervious surface, c) total relative probability of use given both elevation and percent impervious surface. Panel d) shows variation in expected density (E($\widehat{D}$)) in bobcats per pixel (0.25 km^2) as a function of percent impervious surface pixel values.
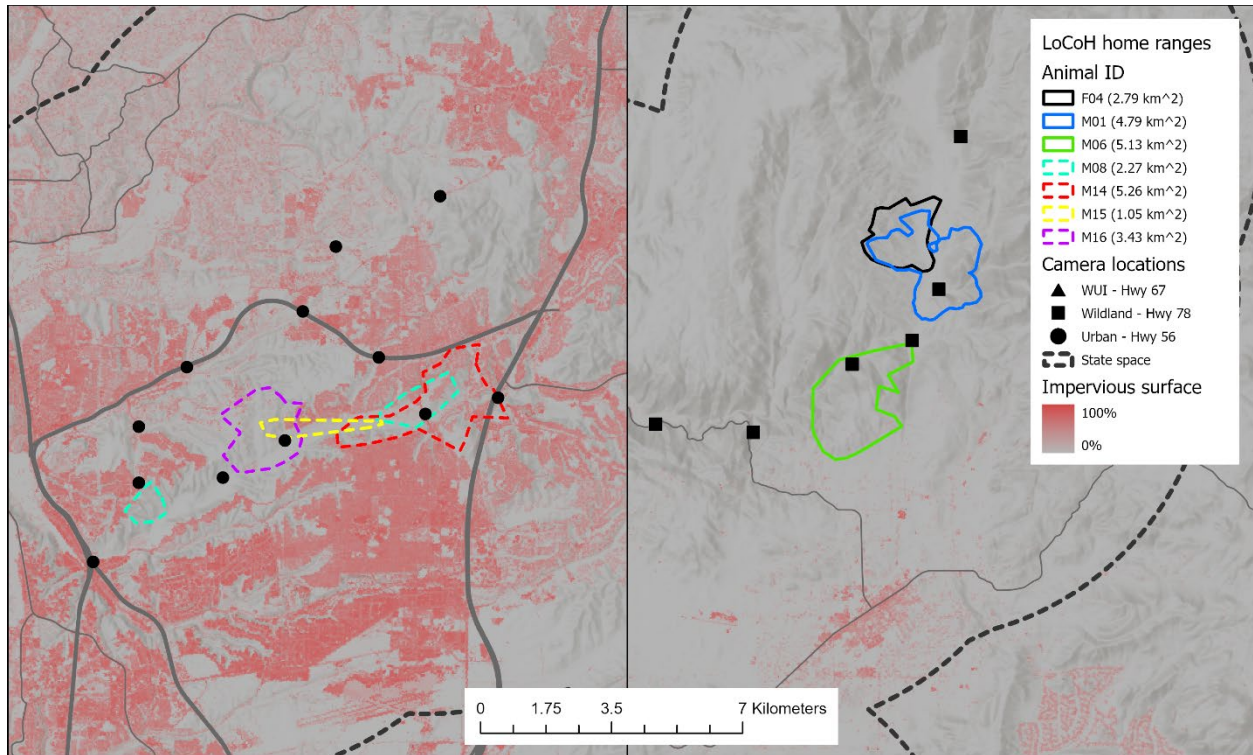
Figure 4. Bobcat local convex hull (LoCoH) home ranges in the urban (left panel) and wildland (right panel) regions of the San Diego County study area relative to development, represented by percent impervious surface.

Supplemental Material

Supplemental Table S1. San Diego bobcat SCR-RSF model selection results for the right-sided dataset, with column 'np' indicating the number of parameters in each competing model. Step 1 identified the best supported encounter model incorporating trap-specific covariates influencing bobcat detection probability. No covariates were added to the sigma parameter. Step 2 identified the best supported encounter model incorporating RSF covariates influencing bobcat probability of space use using the best supported model from the previous step. Step 3 identified the best supported model describing spatial heterogeneity in density using the best supported encounter model selected in the previous model selection steps.

Selection Step	Density Model	Encounter Model	np	AIC	deltaAIC	AICwt	AICwt+	LogLik
	D(.)	p(rec level)	4	3611.72	0.00	1.00	1.00	1801.86
	D(.)	p(.)	3	3653.58	41.86	0.00	1.00	1823.79
1	D(.)	p(camera type)	4	3654.51	42.79	0.00	1.00	1823.26
	D(.)	p(site type)	4	3655.55	43.83	0.00	1.00	1823.78
	D(.)	p(season)	4	3655.57	43.85	0.00	1.00	1823.79
	D(.)	p(elev + imperv + rec level)	6	3551.88	0.00	0.98	0.98	1769.94
2	D(.)	p(water dist + elev + rec level)	6	3559.52	7.64	0.02	1.00	1773.76
	D(.)	p(elev + road465 + rec level)	6	3572.72	20.84	0.00	1.00	1780.36
	D(.)	p(water dist + imperv + rec level)	6	3573.68	21.80	0.00	1.00	1780.84

D(.)	p(elev + road1000 + rec level)	6	3577.43	25.55	0.00	1.00	1782.72
D(.)	p(water dist + rec level)	5	3577.65	25.77	0.00	1.00	1783.83
D(.)	p(water dist + road1000 + rec level)	6	3578.76	26.88	0.00	1.00	1783.38
D(.)	p(water dist + road465 + rec level)	6	3579.60	27.71	0.00	1.00	1783.80
D(.)	p(elev + rec level)	5	3585.69	33.81	0.00	1.00	1787.84
D(.)	p(imperv + rec level)	5	3598.71	46.83	0.00	1.00	1794.36
D(.)	p(rec level)	4	3611.72	59.84	0.00	1.00	1801.86
D(.)	p(road1000 + rec level)	5	3613.06	61.18	0.00	1.00	1801.53
D(.)	p(road465 + rec level)	5	3613.72	61.84	0.00	1.00	1801.86
3							
D(water dist)*	p(elev + imperv + rec level)	7	3549.08	0.00	0.40	0.40	1767.54
D(imperv)	p(elev + imperv + rec level)	7	3550.31	1.23	0.22	0.62	1768.16
D(road465)	p(elev + imperv + rec level)	7	3551.41	2.32	0.13	0.75	1768.70
D(road1000)	p(elev + imperv + rec level)	7	3551.54	2.45	0.12	0.86	1768.77

D(.)	p(elev + imperv + rec level)	6	3551.88	2.80	0.10	0.96	1769.94
D(elev)	p(elev + imperv + rec level)	7	3553.88	4.80	0.04	1.00	1769.94

*D(water dist) was inconsistent across left and right sides (See Supplemental Table S2), and was therefore removed from consideration

Supplemental Table S2. Density covariate relationships across left- and right-sided density models. Coefficients where the direction of the relationship were inconsistent across left- and right-sided models were also uninformative, where the 85% confidence interval of the coefficient crossed 0, and are shown in italics.

Side	Density Model	Coefficient	SE	Upper 85% CI	Lower 85% CI	Informative?
	D(elev)	*-0.61*	*0.51*	*0.13*	*-1.34*	*No*
	D(imperv)	0.51	0.12	0.68	0.33	Yes
Left	D(road1000)	0.44	0.13	0.64	0.25	Yes
	D(road465)	0.48	0.15	0.69	0.27	Yes
	D(water dist)	*-0.20*	*0.75*	*0.87*	*-1.28*	*No*
	D(elev)	*0.02*	*0.51*	*0.75*	*-0.72*	*No*
	D(imperv)	0.27	0.13	0.44	0.09	Yes
Right	D(road1000)	0.20	0.13	0.39	0.00	Yes
	D(road465)	0.21	0.13	0.42	0.00	Yes
	D(water dist)	*0.63*	*0.18*	*1.70*	*-0.45*	*No*

Supplemental Table S3. Maximum-likelihood parameter estimates and standard errors from the best supported model for bobcat density and space use for the right-sided bobcat dataset

Model	Parameter	Estimate	SE
Density	D.intercept	-3.40	0.17
	D.imperv	0.51	0.12
Encounter	p0.intercept	-5.10	0.49
	p.rec level	2.79	0.35
	p.elev	-2.43	0.35
	p.imperv	-0.60	0.10
	sigma.intercept	0.06	0.03

Supplemental Table S4. Additional right-sided dataset best-supported model results

Result	Value
Baseline detection	0.004 (SE = 0.002)
Sigma	1.18 km (SE = 0.03)
Per-pixel density estimate range	0.03 - 0.11 bobcats/0.25 km2 pixel
State space abundance estimate	207.10 bobcats
Average state space density	16.24 bobcats/100 km^2 (95% CI = 10.38 - 28.52)
Urban density	20.7 bobcats/100 km^2 (SD = 6.56)
WUI density	14.14 bobcats/100 km^2 (SD = 4.05)
Wildland density	12.74 bobcats/100 km^2 (SD = 1.13)

Supplemental Table S5. Local convex hull (LoCoH) home range sizes and % overlap with other collared individuals in the Urban and Wildland regions of the study area.

Animal ID	95% LoCoH HR Area (km^2)	% overlap	Site
F04*	2.79	17.7 - 60.7*	Wildland
M01*	4.79	5.0 - 35.3*	Wildland
M03*	16.49	1.4 - 3*	Wildland
M06	5.13	0	Wildland
M08	2.27	51.8	Urban
M14	5.26	3.26 - 22.36	Urban
M15	1.05	16.4 - 38.7	Urban
M16	3.43	11.8	Urban

*indicates male-female overlap

Supplemental Table S6. Capture recapture (CR) dataset attributes

CR Attribute	Left-side	Right-side
Traps with cat detections	26	27
Individuals detected	73	74
Individuals with recaptures	38	39
Individuals with spatial recaptures	7	10
Total detections	304	293
Total recaptures	82	85
Total spatial recaptures	11	12

Supplemental Figure S1. Images taken at two different camera sites of the same bobcat individual. Colored circles identify 3 distinct markings used to confirm individual identification.

Supplemental Figure S2. Best supported model predictions from the right-sided dataset projected across the study area showing a) relative probability of use (RPU) given elevation, b) relative probability of use given percent impervious surface, c) total relative probability of use given both elevation and percent impervious surface. Panel d) shows variation in expected density (E($\widehat{D}$)) in bobcats per pixel (0.25 km^2) as a function of percent impervious surface pixel values.
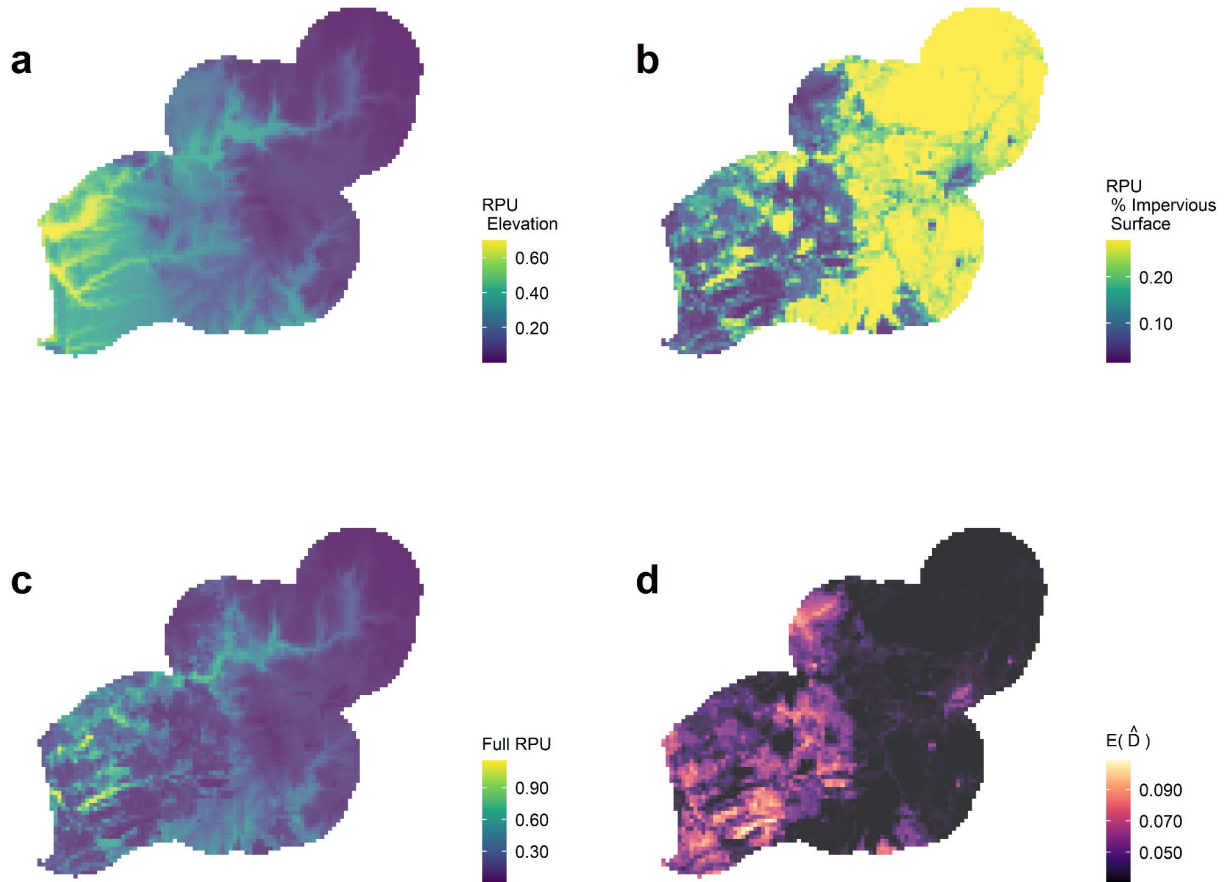
Supplemental Figure S3. Relative probability of use and density (bobcats/km^2) as a function of percent impervious surface for the right-sided dataset.
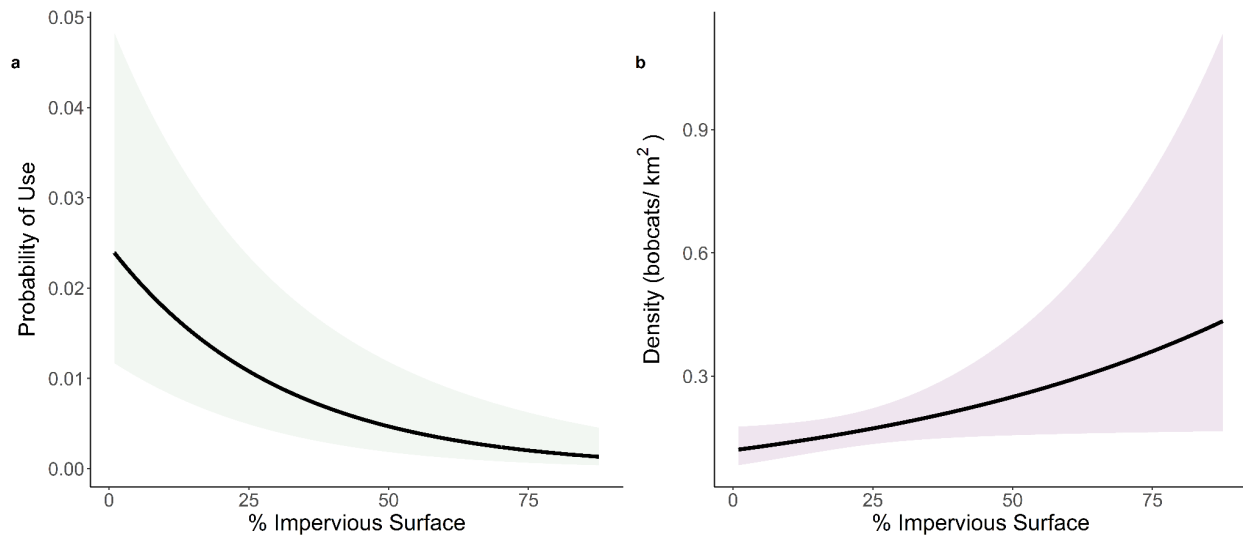
Supplemental Figure S4. Buffers used to assess region-specific variation in density across the study area. Traps are identified as being placed in the urban (circles), wildland urban interface (triangles), or wildland (squares) study area regions.
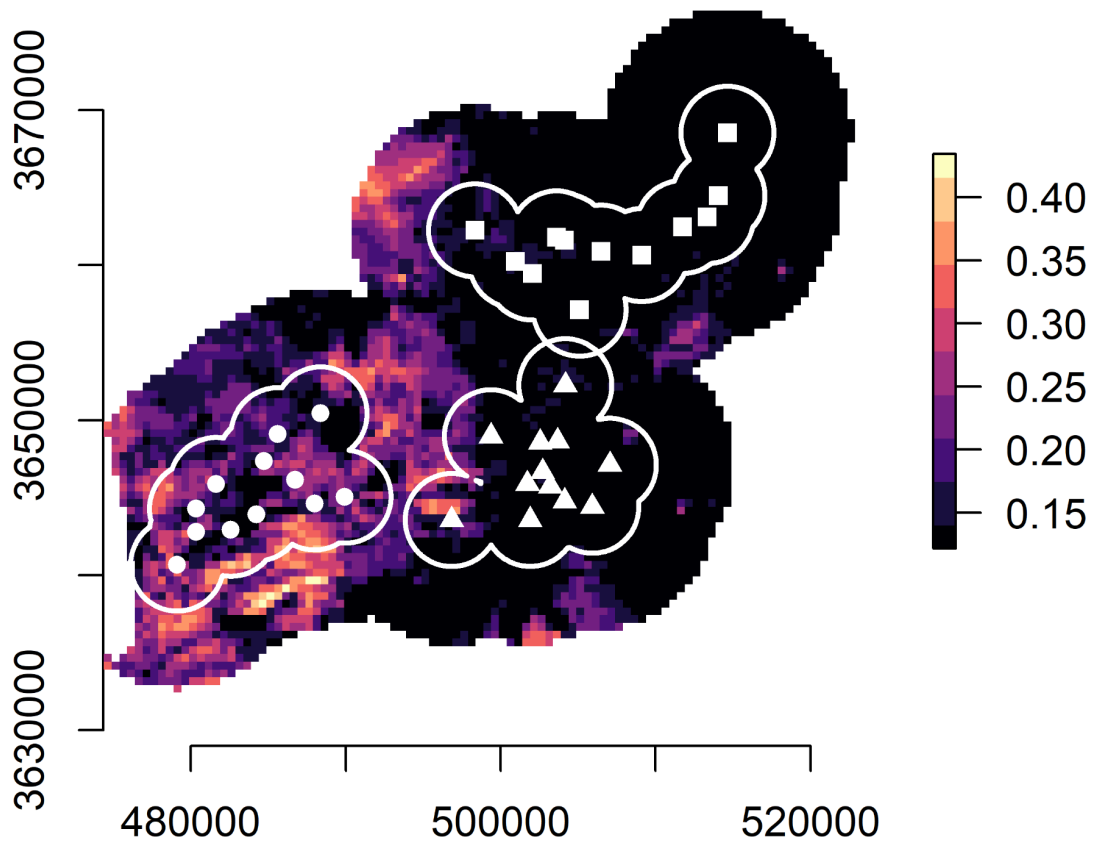
CHAPTER 2

Evaluating spatiotemporal variation in post-translocation survival of Sonoran pronghorn

Abstract

In the context of the global impacts of land modification and climate change, active management and interventions are needed to resist biodiversity loss. Wildlife translocations and reintroductions are a common tool used in species recovery, and survival post-translocation is an essential component of effective translocation and reintroduction programs. Mortality risk for translocated animals can be influenced by environmental and intrinsic factors following translocation, resulting in patterns of survival that are dynamic in space and time. The Sonoran pronghorn (*Antilocapra americana sonoriensis*), a Federally Endangered, desert-adapted ungulate, has been the focus of a large-scale reintroduction effort in southwestern Arizona, USA, following a significant drought-driven population decline in 2002. We evaluated Sonoran pronghorn survival and mortality risk following translocation as a function of dynamic environmental conditions, time since translocation, and individual space use. We used telemetry data from 405 translocated pronghorn in a time-to-event modeling framework, spanning 18 years of reintroduction efforts to consider what factors influenced mortality risk and survival at the scale of the population and individual. At the population scale, we found that long-term drought conditions had a significant negative effect on Sonoran pronghorn survival outside of summer months (Oct - Apr). In the early summer (May - Jun) and summer monsoon seasons (Jul - Sept), mortality risk was lower as a function of time since translocation, suggesting that experience on the landscape may mitigate harsh summer conditions. At the individual scale, we found that mortality risk was higher in summer months for pronghorn with more limited access to managed water, and pronghorn in areas with a greater human footprint were at higher risk of mortality

year-round. Habitat features within individual areas of use were unrelated to time since translocation and highly variable among individuals. Considering factors affecting spatiotemporal variation in mortality risk at multiple scales can inform translocation strategies to ensure that Sonoran pronghorn reintroduction and recovery efforts remain successful in an increasingly impacted and dynamic landscape.

Introduction

Anthropogenic activity is accelerating animal biodiversity loss, leading to local or complete extinctions of species across a diverse range of taxa (Dirzo & Raven, 2003; Dirzo *et al.*, 2014). Globally, populations of large-bodied terrestrial mammals have experienced widespread declines specifically attributed to habitat loss and degradation coupled with overharvesting (Laliberte & Ripple, 2004; Estes *et al.*, 2011; Ripple *et al.*, 2016). The ongoing impacts of climate change also play a role in the decline of terrestrial mammal populations. For example, increasing temperatures and decreasing precipitation have negatively impacted population growth and persistence for multiple ungulate species in North American deserts (Epps *et al.*, 2004; Gedir *et al.*, 2015).

Desert ecosystems present unique challenges for wildlife conservation. Human-driven threats including climate change and land modification can be especially detrimental to wildlife populations in desert environments, where resources are scarce and ephemeral in space and time and animals are often navigating life at the edge of their physiological limits (Vale & Brito, 2015; Zhang *et al.*, 2023). Wildlife conservation efforts in desert landscapes often employ active management and intervention strategies to prevent or reverse defaunation, in some cases with acknowledgment that a return to historic conditions is impractical, if not impossible (Wilson, Krausman & Morgart, 2010; Averill-Murray *et al.*, 2012). Active management can serve to

increase species' resilience, ultimately providing opportunity to adapt as changes occur. Specific strategies can include managing landscapes to increase permeability for mobile species (Zeller *et al.*, 2021), supplying supplemental water or forage (Wilson *et al.*, 2010; Rich *et al.*, 2019), and implementing captive breeding, reintroduction, and translocation of particularly vulnerable species to safeguard population persistence (Mawdsley, O'malley & Ojima, 2009; Seddon *et al.*, 2014).

Wildlife translocations can be used as a conservation tool to re-establish or reinforce declining populations, restore ecosystem function, and mitigate human-wildlife conflict (Armstrong & Seddon, 2008; IUCN/SSC, 2013). Conservation translocations have been influential for increasing or restoring threatened wildlife populations (Seddon, Armstrong & Maloney, 2007; Morris *et al.*, 2021), and have played a role in rescuing several species from extirpation or extinction (Hoffmann *et al.*, 2015; Cheng *et al.*, 2021). While there are documented successes, translocation efforts may miss the mark of predefined conservation objectives when mortality of translocated individuals is high (Berger-Tal, Blumstein & Swaisgood, 2020; Gross, Wilson & Wolak, 2023). Identifying locally relevant spatiotemporal factors affecting post-translocation mortality can inform management strategies that increase likelihood of reintroduction success.

The factors that underlie variation in mortality risk for translocated wildlife may act at the scale of the population, affecting all translocated individuals and resulting in patterns of mortality driven by seasonal or among-year environmental change (Facka *et al.*, 2010; Conner *et al.*, 2018; Lewis *et al.*, 2022). North American desert ecosystems experience dramatic seasonal variation in temperature and precipitation, and limited rain and high heat in summer months are a key driver of patterns of survival for desert wildlife populations (Bright & Hervert, 2005;

Heffelfinger *et al.*, 2018; Bean *et al.*, 2023). In addition to more predictable seasonal constraints, drought conditions across all seasons are becoming more prevalent, though drought severity is irregular among years due to increasing variability of precipitation (Munson *et al.*, 2012). Over short and long time periods, drought can influence survival by limiting available surface water, decreasing nutritional and water content of vegetation, and reducing available prey populations (White, Vanderbilt White & Ralls, 1996; Heffelfinger *et al.*, 2018).

In addition to population scale patterns, spatiotemporal variation in mortality risk for translocated wildlife has been identified at finer scales, from subpopulations and reintroduction areas (Conner *et al.*, 2018) to the scale of individual behavior and space use (Smith, Erb & Pauli, 2022; Eacker, Jakes & Jones, 2023; Pero *et al.*, 2023). Spatial variation in reintroduction areas can result in heterogeneous baseline habitat resources, levels of human impact, or predator and competitor densities (Linklater & Swaisgood, 2008; Grant, Johnson & Thiessen, 2019). Further, mortality risk for translocated animals can vary through time as individuals learn to effectively navigate new landscapes (Armstrong *et al.*, 2017; Pero *et al.*, 2023). Translocated individuals must contend with the trade-offs of exploring a new environment and effectively exploiting available resources while avoiding risks (Berger-Tal & Saltz, 2014). Predictability, patchiness, and the ability to move freely across the landscape to access resources all influence resulting space use patterns (Abrahms *et al.*, 2021). The timescale over which more optimal resource tracking emerges post-reintroduction has proven to be highly variable, occurring within the first year following translocation (Ebenhoch *et al.*, 2019) or over multiple generations (Jesmer *et al.*, 2018). The link between translocation, space use, and mortality risk may be particularly important in extreme and dynamic desert environments, where sufficient spatial knowledge can affect the ability to locate patchy, scarce, and ephemeral resources like forage and water.

The Sonoran pronghorn (*Antilocapra americana sonoriensis*) is a federally endangered, desert-adapted subspecies of American pronghorn (*Antilocapra americana*) that is the focus of an ongoing and expanding reintroduction program in the United States. Found only in the Sonoran Desert, this subspecies occurs in southwestern Arizona, USA, and the northwestern portion of Sonora, MX (U.S. Fish and Wildlife Service, 2016). In northern pronghorn populations winter severity is considered the most important factor driving patterns of annual survival (Jones *et al.*, 2020; Eacker *et al.*, 2023). For pronghorn populations at the southern edge of their range, including Sonoran pronghorn populations, seasonal precipitation and drought severity have been identified as the climatic factors that influence survival and population persistence (Bright & Hervert, 2005; Bean *et al.*, 2023). Previous research on mortality of Sonoran pronghorn adults and fawns found that average annual mortality was typically 20%, though in 2002 during an extreme long-term drought event the U.S. population experienced 83% mortality, dropping to just 21 individuals (Bright & Hervert, 2005). The high mortality that occurred in 2002 motivated the establishment of a reintroduction program to preclude local extinction of Sonoran pronghorn in the USA.

The reintroduction program to-date has been successful in reinforcing and reestablishing Sonoran pronghorn within a portion of their historical range, but these populations face considerable future uncertainty. Temperatures are increasing across the region, and patterns of precipitation throughout the year will become more dynamic and unpredictable (Munson *et al.*, 2012). The mechanisms through which drought and precipitation patterns influence Sonoran pronghorn survival are not well understood (Bean *et al.*, 2023), and the extent to which environmental factors influence mortality risk within and among years is of interest to managers involved in Sonoran pronghorn recovery efforts (U.S. Fish and Wildlife Service, 2016). Further,

previous research on Sonoran pronghorn mortality risk and survival occurred prior to the

establishment of the reintroduction program (Bright & Hervert, 2005), and thus evaluating

patterns of post-translocation mortality risk for this species would be valuable.

Here, we evaluate Sonoran pronghorn mortality risk and survival following translocation,

considering how factors at multiple scales shape the pronghorn survival landscape. Our aim was

to identify factors associated with spatiotemporal variability in mortality risk with the goal of

informing and supporting translocation strategies. We used mortality event and space use data

from 405 translocated pronghorn in a time-to-event modeling framework, spanning 18 years of

reintroduction efforts to consider how Sonoran pronghorn mortality risk varies as a function of

climatic conditions, time since translocation, forage availability, habitat structure, access to

managed water sources, and human development.

Methods

Study Area and translocation program background

The study area encompassed a portion of the Sonoran Desert situated in southwestern

Arizona, USA, and was bounded by the current range of Sonoran Pronghorn in the United States

(Fig. 1). This area comprised two legally distinct management units: The Cabeza Prieta

Management Unit (CPMU; 8,161 km^2) and the Arizona Reintroduction Management Unit

(AZMU; 19,179 km^2). Sonoran pronghorn occurring in the CPMU are listed as endangered

under the Endangered Species Act (ESA, 1973), while pronghorn in the AZMU are considered

part of a non-essential experimental population designated under section 10(j) of the ESA.

Following the 2002 population crash of Sonoran Pronghorn in the USA, a captive breeding and

translocation program was established in 2003 in the CPMU using a source population of six

individuals donated from Mexico, and the Sonoran Pronghorn Recovery Team (SPRT) began

releasing captive bred individuals to supplement wild populations in the CPMU in 2005. A second captive breeding pen was established in 2011 in the AZMU, with releases re-establishing Sonoran pronghorn within this management unit in 2013. Each management unit contains multiple reintroduction areas where captive bred pronghorn are released annually between December and March.

Climate within the study area is characterized by intense heat (mean summer maximum daily temperature of 40°C) and low rainfall (annual precipitation range of 10 - 30 cm), with a bimodal rainfall season that typically brings patchy monsoonal rains in summer and widespread rainfall in winter (Bright & Hervert, 2005). Seasons can be broken down into a cool, wet fall and winter (Oct - Jan), a warm spring with variable precipitation (Feb - Apr), the hot and dry early summer (May - Jun), and the hot and wet summer monsoon season (Jul - Sept; Hanson & Hanson, 2015). Broadly, vegetation subdivisions range from the Lower Colorado River Valley subdivision in the west portion of the study area moving eastward into the Arizona Upland subdivision (Dimmitt, 2015). Vegetation associations within the study area most commonly used by pronghorn include creosote (*Larrea tridentata*) - bursage (*Ambrosia spp.*) and palo verde (*Parkinsonia spp.*) - chain fruit cholla (*Cylindropunita fulgida*), and pronghorn use of these communities varies seasonally (Hervert *et al.*, 2005). Elevation across the study area ranges from 18 to 1481 m, and topography is characterized by wide alluvial valleys interspersed with fault-block mountains (Bright & Hervert, 2005). Sonoran pronghorn prefer flat terrain or gentle slopes, typically avoiding rugged terrain and slopes greater than 20% (Hervert *et al.*, 2005; O'Brien *et al.*, 2005).

To benefit desert wildlife, including Sonoran pronghorn, state and federal wildlife management agencies (Arizona Game and Fish Department, U.S. Fish and Wildlife Service) maintain numerous artificial and enhanced water sources dispersed throughout the region, as well as several irrigated patches of desert habitat managed as forage enhancement plots. While much of the current Sonoran pronghorn range occurs on undeveloped public land, human impacts throughout the study area include recreation, migrant, and military activity, fences, roads and road traffic, residential and commercial development, agricultural development, and USA - Mexico border infrastructure.

Collar data collection and processing

Translocation occurred during winter and spring months from 17 November through 2 March. Translocated Sonoran pronghorn were fitted with a VHF (Model 500, Telonics, Inc., Mesa, AZ, USA) or GPS (Survey-1D Globalstar GPS, Vectronics Aerospace Inc., Coralville, IA, USA) collar prior to release. Location collection intervals for GPS collars ranged from 1 to 24 h ($\bar{x}$ = 12). VHF collars were monitored with telemetry flights and ground tracking efforts. Mortalities were investigated as soon as possible after detection to determine cause of death and collect the collar. For mortalities where a precise date of death could not be determined, we set the estimated mortality date as 24 h after the last known confirmed time alive based on collar monitoring. Maximum time between date last confirmed alive and the detection of a mortality was 272 days ($\bar{x}$ = 41 days).

To process GPS collar data, we filtered locations to remove all 2-D fixes as well as any 3-D fix with a dilution of precision (DOP) > 5 (Lewis *et al.*, 2007). Due to variation in data archiving procedures across years, some GPS collar data collected between 2017 - 2023 lacked accuracy metadata for filtering. For GPS collar data collected between 2017 - 2023 with

available accuracy information, 1.3% of the dataset met the criteria of 2-D fix and/or DOP > 5, but a visual inspection did not reveal spatial patterning of filtered points relative to unfiltered points. Therefore, we retained all data from GPS collars that lacked satellite and DOP information, acknowledging that up to 1.3% of these points could fall above our thresholds for GPS data filtering but with the assumption that this choice was unlikely to introduce spatial bias in results.

To inform mortality risk analyses that considered multiple scales, we used GPS locations to define a population-wide spatial extent as well as time-varying individual space use areas. We defined the spatial scale of the population with a 100% minimum convex polygon (MCP) around all filtered GPS locations. We defined individual space use areas by creating 100% MCPs using 30-day intervals of GPS locations through time for each GPS-collared pronghorn. Because GPS data were predominantly collected at coarse intervals (1 location/24h), we used 100% MCPs to ensure that we sufficiently captured the area that was available for use by an individual pronghorn within a 30-day interval.

Environmental and habitat variables

We considered seven climatic and habitat variables in our mortality risk analyses: precipitation, short and long-term drought, forage availability, habitat complexity, managed water access, and anthropogenic footprint. Climate and habitat variables were quantified at either the population or individual space use scale. All spatial data were processed in Google Earth Engine (Gorelick *et al.*, 2017) and R v 4.3.0 (R Core Team, 2023).

We quantified climatic variables, precipitation and drought, at the population scale. For precipitation, we calculated daily cumulative precipitation (mm) values derived from the daily Parameter-elevation Regressions on Independent Slopes Model gridded climate image collection

(PRISM/AN81d, 4-km resolution, Daly, Smith & Olson, 2015) by summing precipitation values

for all pixels contained within the study area from the preceding 30 days. To quantify study area-

wide drought conditions, we used the Standardized Precipitation-Evapotranspiration Index

(SPEI), which considers precipitation and temperature data to calculate an index of drought

across variable timescales (Vicente-Serrano, Beguería & López-Moreno, 2010). More positive

values indicate wetter conditions where precipitation is greater than potential evapotranspiration,

while more negative values indicate dry conditions where potential evapotranspiration outpaces

precipitation. We used daily SPEI data calculated with the Gridded Surface Meteorological

Dataset image collection (GRIDMET/DROUGHT, 4-km resolution, Abatzoglou, 2013) at the

90-day and 1-year timescale to represent shorter and longer-term drought conditions.

We quantified forage availability, habitat complexity, managed water access, and human

footprint at the individual scale using the 30-day individual space use areas constructed with

Sonoran pronghorn GPS data. For all environmental metrics at the individual scale, we masked

pixels with > 20% slope to remove areas from consideration that were likely inaccessible to

Sonoran pronghorn (O'Brien *et al.*, 2005).

To approximate forage availability, we derived a dynamic metric that considered both

forage quality (greenness) and forage amount (biomass) within a 30-day interval using methods

adapted from Ortega et al. (2024). This measure was a product of vegetation greenness from the

Soil Adjusted Vegetation Index (SAVI) and biomass of annual and perennial grasses and forbs.

SAVI was derived from a Moderate Resolution Imaging Spectroradiometer time-series image

collection (MODIS/MOD13Q1, 16-day temporal resolution, 250 m^2 spatial resolution) by taking

the equation for Normalized Difference Vegetation Index (NDVI) and applying a correction

factor of L = 0.5 according to the following equation: (NIR – Red) * (1 + L) / (NIR + Red + L).

SAVI is a commonly used metric in sparsely vegetated environments, as it accounts for the influence of soil brightness (Huete, 1988; Bunting, Munson & Bradford, 2019). Biomass was acquired from the Rangeland Analysis Platform (Jones *et al.*, 2021; 16-day temporal resolution, 30 m^2 spatial resolution). The biomass image collection included annual and perennial forbs, grasses, and cropland cover types measured in lbs/acre. We did not mask cropland cover types because Sonoran pronghorn occasionally use available alfalfa pivots (SPRT personal communication). We aggregated the biomass image collection to the same resolution as the SAVI image collection before taking the product of SAVI and biomass to approximate high quality forage availability, also termed residual forage (Ortega *et al.*, 2024), in lbs/acre for the individual 30-day space use areas.

We measured habitat complexity by calculating image entropy, a measure of complexity of image texture, within a 500-m moving window using the glcmtexture() function in Google Earth Engine on a composite SAVI image (Sentinel-2, 10-m spatial resolution) from 2017 to 2023 (Farwell *et al.*, 2021; Smith *et al.*, 2022). We defined managed water access using a 250 m x 250 m resolution raster quantifying distance to managed water sites located within the study area, taking the average distance to water within the 30-day space use areas of each individual pronghorn. Human footprint was measured using the Global Human Modification (GHM) dataset, which provided an index (0 - 1) of human modification at 1 km^2 spatial resolution that considered the combined influence of five major categories of anthropogenic stressors: human settlement, agriculture, linear transportation features, mining and energy production development, and electrical infrastructure (Kennedy *et al.*, 2019). We averaged the GHM index across all pixels within each individual space use area.

Time-to-event data for mortality risk analyses

We partitioned mortality risk analyses into two main components: a population scale analysis incorporating VHF and GPS-collared translocated pronghorn, and an individual space use scale analysis using the GPS-collared subset of translocated pronghorn. At the population scale, we considered the influence of climatic factors and time since translocation on mortality risk. At the individual space use scale, we considered the influence of among-individual variation in available habitat features in space use areas on mortality risk, accounting for within-individual variability in available habitat features through time. We conducted all analyses in R v 4.3.0 (R Core Team 2023) using the survival package (Therneau, 2023).

For both the population and individual scale mortality risk analyses, we used the counting process formulation of the Cox proportional hazard model, which specifies a semiparametric modeling framework suitable for evaluating the effect of time-varying and time-independent covariates on mortality risk. This approach does not directly estimate the baseline hazard, allowing flexibility to estimate mortality risk without making assumptions about the underlying distribution of mortality (Therneau & Grambsch, 2000). We used an annual recurrent design, defining the recurrent origin as 1 December to accommodate variation in release dates for translocated pronghorn. The recurrent time scale assumes consistent within-year effects of age, year, and study site on mortality risk (Fieberg & DelGiudice, 2009). Previous research has suggested seasonal variability in factors relevant to pronghorn mortality (Bright and Hervert 2005), and we expected that the proportional hazard assumption of consistent within-year effects would likely be violated with a recurrent design. Therefore, we allowed estimated coefficients to vary seasonally by stratifying analyses into seasonal segments defined as Fall and Winter (October - January), Spring (February - April), Early Summer (May - June), and Summer Monsoon (July - September) according to Hanson and Hanson (2015). Because individuals

collared for > 1 year could contribute multiple years of monitoring data with a recurrent origin design, we clustered our data by individual ID to estimate robust standard errors using the cluster() specification in all analyses.

Population-scale mortality risk

We used the full dataset of translocated pronghorn (VHF and GPS-collared) to evaluate the influence of short-term drought, long-term drought, precipitation, and time since translocation on mortality risk. Individuals entered the risk set on the date of release to the wild and were right-censored when collar function ceased or if the individual survived the annual monitoring period. Because we were interested in understanding the relationship between time since translocation and mortality risk, we also censored individuals with VHF data that extended beyond three years of monitoring to preclude the effects of reaching old age (>8 years, SPRT personal communication) on mortality risk. We assumed that right-censoring was unrelated to survival and that individual fates were independent. We removed individuals from the dataset where the cause of mortality was capture myopathy. This included any individual that died within 7 days of release, regardless of proximate stated cause of mortality (e.g., predation, O'Gara, 2004).

At each event time (i.e., mortality event), the Cox model considers the covariate values for all individuals available in the risk set immediately preceding the event to assign a risk score to each individual that will best predict the mortality outcome. Therefore, we formatted all covariates to update just before each event time. We used the Efron approximation to account for ties (i.e., mortalities that occurred on the same day) in the dataset (Therneau and Grambsch 2000). We standardized all covariates before model implementation by subtracting each covariate value by the mean and dividing by the standard deviation. Preliminary models

indicated no significant differences in mortality risk between males and females, therefore we proceeded with model development using all available pronghorn in a single model selection framework.

To describe variation in mortality risk we developed four univariate candidate models, as well as three multivariate models that paired each climatic covariate (1-year drought, 90-day drought, 30-day precipitation) with time since translocation (Table 1). We used an AIC-based model selection approach, where a model was considered supported if it ranked within 2 ΔAIC of the lowest AIC model.

Individual-scale mortality risk

We used a GPS-collared subset of translocated pronghorn to consider the influence of variation in individual space use through time on mortality risk, in particular related to changes in forage availability, habitat complexity, managed water access, and human footprint. Preparation of the individual space use scale dataset followed identical procedures to the population scale analysis with two exceptions. First, because our sample size was reduced relative to the population scale mortality risk analysis, we combined seasonal segments so that coefficients were stratified by only two seasonal categories: Fall, Winter, Spring (Oct - Apr), and Summer (May - Sept) We isolated the early summer and summer monsoon seasons from other seasons, as they are comparably more physiologically taxing and resource limited times of year. Second, we left-censored all individuals for 30 days post-release to allow GPS locations to accumulate for the estimation of individual space use areas. Then, throughout an individual's monitoring period, for any event time where that individual accumulated fewer than 15 locations in the preceding 30 days, that individual was censored from the risk set for that event time and re-entered at the next event time with enough locations for adequate space use area estimation.

We developed candidate models to consider each individual scale covariate as a multivariate addition to the best-supported model from the population scale analysis, replacing time since translocation from the best supported population scale model with each individual space use covariate (Table 2). Similar to the population scale analysis, we used an AIC-based model selection approach, where a model was considered supported if it ranked within 2 ΔAIC of the lowest AIC model.. We found similar support for two models (1-year drought + water access & 1-year drought + human footprint), and rather than use model averaging methods, we included the two supported individual space use covariates (correlation = -0.001) in a single model, which we used to evaluate the relationship between individual space use and mortality risk.

We hypothesized that time since translocation would influence mortality risk and survival, predominantly as a function of the features of the habitat used by translocated individuals through time. To explore this relationship, we modeled landscape features, including forage availability, habitat complexity, distance to water, and human footprint, as response variables and time since translocation as the predictor variable, creating separate models for each seasonal segment (Oct - Apr and May - Sept to mirror the individual scale mortality risk analyses). We used linear mixed effects models specified with the lmer() function in the lme4 package (Bates *et al.*, 2015). We log-transformed forage availability, habitat complexity, and distance to water (i.e., managed water access), and square-root transformed human footprint to meet assumptions of normality. We then standardized all covariates, subtracting by the mean and dividing by the standard deviation. We included a random term for individual ID in each model, specifying a random slope and intercept because we expected that baselines for each covariate as well as changes through time could vary by individual.

Estimating Survival

We used each best supported mortality risk model (population and individual scale) to estimate annual survival and visualize annual survival curves for multiple covariate scenarios representing the breadth of variation for factors measured at the scale of the population and among individuals. Because we used time-varying covariates and coefficients, we estimated survival by specifying relevant covariate paths through time (Therneau and Grambsch 2000).

Results

Between December 2005 and December 2023, 431 Sonoran pronghorn were translocated from captive breeding pens to release sites in southwestern Arizona (206 releases in the AZMU, 226 releases in the CPMU; 207 females, 224 males). We deployed 176 GPS collars, 254 VHF collars, and released two uncollared individuals for a total of 430 collars deployed (one male individual was initially GPS-collared and released in the CPMU, then re-released in the AZMU with a VHF collar). Individuals were monitored for an average of 694 days (1 - 3,986) before death or cessation of collar functioning. We documented 253 mortalities attributed to the following causes: capture myopathy (9), drowned in agricultural canal (13), fence entanglement (1), natural causes (1), predation (67), vehicle collision (12), and unknown causes (148). In 2023, 6 GPS-collared individuals (3 females, 3 males) were released in northwestern Sonora, Mexico on the Reserva de la Biosfera El Pinacate y Gran Desierto de Altar, but those individuals were not included in this analysis.

For the population scale analysis, 405 Sonoran pronghorn translocated between 2005 - 2023 met the criteria for inclusion in the risk set (i.e., not a capture myopathy and lived beyond 7 days post-release). Individuals were monitored for an average of 554 days (min = 8, max = 1,096). 156 mortalities occurred while individuals were collared and monitored, attributed to the

following causes: drowned in agricultural canal (11), predation (48), vehicle collision (11), and unknown causes (86).

The best supported model for the population scale mortality risk analysis (Table 1) included long-term (1-year time scale) drought and time since translocation (Figure 2, Table 3). A 1-standard deviation decrease in long-term drought conditions (Δ1-year SPEI = 0.75; higher SPEI values indicate wetter conditions) decreased mortality risk in the fall and winter by 46% (95% CI = 13 - 66%) and in the spring season by 50% (95% CI = 33 - 63%). A 1-standard deviation increase in time since translocation (ΔTime = 300 days) decreased mortality risk by 37% (95% CI = 7 - 58%) in the early summer season and by 46% (95% CI = 16 - 65%) during the summer monsoon season.

We used the best supported population scale model to predict annual survivorship for four hypothetical translocation cohorts (Figure 3). We created a high-drought and low-drought scenario, where for each seasonal segment we used the minimum and maximum SPEI values recorded in that season, respectively. For each drought scenario, we created hypothetical cohorts of individuals experiencing either their first or second year post-translocation (Days 1 - 365 or 366 - 730). A low-drought scenario predicted annual survivorship of 0.81 (95% CI = 0.77 - 0.85) for the first-year cohort and 0.89 (95% CI = 0.87 - 0.91) for the second-year cohort. A high-drought year led to predicted annual survivorship of 0.38 (95% CI = 0.31 - 0.46) for the first-year cohort and 0.50 (95% CI = 0.44 - 0.58) for the second-year cohort.

For the individual scale analysis, 164 Sonoran pronghorn translocated between 2008 - 2012 and 2017 - 2023 met the criteria for inclusion in the risk set (i.e., not a capture myopathy and lived beyond 7 days post-release, sufficient GPS locations accumulated during the monitoring period to estimate area used). Sixty-six mortalities were recorded in collared

71

individuals attributed to the following causes: drowned in agricultural canal (3), predation (29), vehicle collision (4), unknown causes (30). After filtering, GPS collars collected a total of 115,012 locations with an average of 688 locations per individual (min = 29, max = 1,742). Individuals were monitored for an average of 376 days (min = 34, max = 893).

For our individual scale mortality risk analysis, we found greatest support for a model describing mortality risk related to long-term drought, water access, and human footprint (Figure 4, Table 4). A 1-standard deviation decrease in long-term drought conditions (Δ1-year SPEI = 0.96) decreased mortality risk by 55% (95% CI = 27 - 72%) in fall, winter, and spring. A 1-standard deviation increase in distance to water (ΔDistance = 24.46 km) within an individual space use area increased mortality risk in summer months by 56% (95% CI = 17% - 108%). There was support for a year-round effect of human footprint, where a 1-standard deviation increase in human footprint (ΔGHM = 0.027) within a space use area increased mortality risk by 37% (95% CI = 5 - 79%) in fall, winter, and spring, and 28% (95% CI = 4 - 58%) in summer months. At this scale, using the subsetted dataset of GPS-collared pronghorn, we did not find support for a general relationship between mortality risk and time since translocation in any season.

We did not detect any meaningful relationships between the habitat features used by individuals and time since translocation (Table 5). We found substantial among-individual variation regarding the characteristics of habitat features comprising individual tracked areas following translocation.

Discussion

Sonoran pronghorn experience spatiotemporal variation in mortality risk following translocation, and we found evidence for the seasonally dynamic nature of mortality risk at both

the population and individual scale. In non-summer months (October - April), long-term drought conditions increased Sonoran pronghorn mortality risk. In summer months (May - September), increased experience on the landscape measured by time since translocation decreased mortality risk. At the individual scale, reduced water access increased mortality risk in summer months and use of landscapes with a higher human footprint increased mortality risk year-round. Given the pressures of increasingly dynamic and extreme climate conditions and expanding development within the current Sonoran pronghorn range, an understanding of factors driving mortality risk can inform strategies to maintain a successful reintroduction program and meet recovery goals for the species. Our work provides specific insights regarding factors relevant to Sonoran pronghorn translocation and suggests broader implications for the role of environmental variability and individual variation on wildlife reintroduction effectiveness as a conservation tool.

At the population scale, long-term drought conditions were associated with a higher risk of mortality for reintroduced individuals in fall, winter, and spring. In the Sonoran Desert, long-term drought conditions are becoming more prevalent, and long-term drought is correlated with reduced vegetation green-up in winter months (Khatri-Chhetri *et al.*, 2021). Drought conditions in winter push Sonoran pronghorn to use foothill habitats in order to access sufficient forage, which can increase vulnerability to predation events (Bright and Hervert 2005). Additionally, pronghorn may rely on more favorable conditions in fall, winter, and spring to recover from the predictably resource-limited conditions of summer months. Harsh environmental conditions like extreme heat and low water availability in summer likely swamp the influence of long-term drought on mortality risk during this part of the year. An evaluation of population growth in 18 southwestern pronghorn populations found that drought had the most negative impacts during

spring, which aligns with the fawning season, an especially taxing time for female pronghorn (Gedir et al. 2015). This data set did not allow for an exploration of relationships between sex, drought, and mortality risk. Evaluating the relationship between environmental stressors, reproductive phenology, and adult and fawn Sonoran pronghorn survival would be a valuable extension of our research.

Because wildlife reintroductions are high-risk and high-cost conservation efforts (Berger-tal et al. 2020), local environmental and climatic dynamics are important factors to consider when selecting seasons and years for animal release with the goal of reducing post-translocation mortality. When fall, winter, and spring are characterized by long-term drought, it is likely that Sonoran pronghorn translocation cohorts released under these conditions will experience higher mortality relative to cohorts released in wetter years. To mitigate mortality risk associated with long-term drought conditions impacting these seasons, translocations could be prioritized in years that fall above a selected drought threshold. However, an overabundance of individuals in captive breeding pens can strain resources and lead to antagonistic interactions among captive animals (SPRT personal communication). Releasing bucks annually but prioritizing doe releases during wetter years could be a potential strategy to mitigate mortality risk while ensuring the captive breeding pens function effectively.

Challenges for wildlife associated with translocation and the following acclimation period can lead to temporarily elevated mortality, and estimating the duration and intensity of post-translocation effects can inform the number of individuals to release as well as future population projections (Armstrong *et al.*, 2017). We found evidence of increased mortality risk in the first year following translocation, but this effect was seasonal and limited to summer months. In the early summer and summer monsoon seasons our population scale model

supported a relationship where increased time since translocation decreased mortality risk, with roughly one year of experience (300 days) yielding a 37% (early summer) - 46% (summer monsoon) decrease in mortality risk. We did not find support for a relationship between mortality risk and time since translocation in fall, winter, and spring, possibly because when habitat conditions are comparably better, experience does not confer specific advantages. Our results suggest that translocated pronghorn with more experience on the landscape may learn effective strategies to mitigate predictably harsh summer conditions, which we expected could occur through post-release behavioral modification (Berger-Tal and Saltz 2014).

For pronghorn in the heat of summer, important advantages of increased spatial knowledge could include the ability to locate water sites, thermal refugia, and forage, while avoiding predation risk. However, significant among-individual variation of space use over time precluded our ability to identify mechanisms that underlie the inverse relationship between time since translocation and mortality risk. The benefit of spatial knowledge of resources may be confounded by associated risks, for example when high quality forage is correlated with predation risk or human impacts (Smith *et al.*, 2019; Eacker *et al.*, 2023). Sonoran pronghorn behavioral adjustments through time could also include changes in social interactions (Poirier & Festa-Bianchet, 2018) or learned anti-predator behavior (Frair *et al.*, 2007), both of which could confer survival advantages without driving changes in coarse-scale space use patterns. Significant variability among translocated individuals in space use patterns relative to time since translocation may limit management efforts aimed at increasing post-translocation survival, and suggests that additional work exploring sources of individual variation, including personality or behavioral traits, would be useful to inform effective wildlife reintroduction efforts (Merrick & Koprowski, 2017).

Decreased water access, measured as the average distance to water within an individual 30-day space use area, increased pronghorn mortality risk in the early summer and summer monsoon seasons. Sonoran pronghorn are known to be particular about their use of developed waters, and will generally only use managed water sites that have been specifically constructed for their use, in part because of sensitivity to structural design and aversion to dense vegetation around water features (SPRT personal communication). Typically, temporary waters are placed on the landscape and pronghorn use is assessed before constructing a permanent water structure. While access to water provides a clear benefit for Sonoran pronghorn, more work is needed to determine the benefit of access to multiple water sources, the influence of water access on foraging behavior, and the relationship between water access and seasonal predation risk (Bean *et al.*, 2023). The importance of managed water access for summer survival aligns with findings from previous research and provides additional evidence that developing water sources and mitigating barriers to water access are effective recovery actions for Sonoran pronghorn (Morgart *et al.*, 2005; U.S. Fish and Wildlife Service, 2016; Bean *et al.*, 2023).

We also identified a persistent relationship between human footprint and Sonoran pronghorn mortality risk. The global human modification index used to represent human footprint in our analyses was a composite capturing multiple facets of human disturbance and development (Kennedy *et al.*, 2019). It will be important moving forward to tease apart the specific mechanisms through which human footprint increases mortality risk for translocated pronghorn. In some cases, for example when pronghorn drown in canals or are hit by vehicles, the mechanism is straightforward. Sonoran pronghorn use of agricultural landscapes has been documented and use of these areas is considered beneficial (U.S. Fish and Wildlife Service 2016), though there is evidence from northern American pronghorn populations that agricultural

landscapes may act as ecological traps (Eacker et al. 2023). Within the current Sonoran pronghorn range there is extensive proposed solar development, necessitating continued assessment of the effects of future development or landscape modification on Sonoran pronghorn space use and population dynamics.

Our work highlights the influence of multiple factors across scales that influence Sonoran pronghorn mortality risk, suggesting additional research on this topic would be beneficial to informing future effective recovery actions for the species. A greater understanding of cause-specific mortality will be an important complement to this research, as in recent years there has been an increase in mountain lion predation events on Sonoran pronghorn (SPRT, personal communication). This species is not considered a primary prey source for mountain lions (Prude, 2020), and the mechanisms driving this observed increase are unknown. Certain release sites may be located in areas with higher mountain lion use or abundance, potentially associated with mule deer population patterns (DeCesare *et al.*, 2009). Further, managed water sources could serve to subsidize mountain lion presence, as lion use of water sources occurs year-round while desert ungulates like desert bighorn and Sonoran pronghorn typically only use managed water sources during summer months or during severe droughts (Harris *et al.*, 2020). However, our finding that increased managed water access decreases mortality risk suggests that the importance of water access for pronghorn survival outweighs any water-driven predation impact. Additionally, it was not possible to assess wild pronghorn survival with our dataset, but sufficient survival of wild-born pronghorn is requisite for species recovery. Risk of mortality is high during captures of wild Sonoran pronghorn, therefore non-invasive methods like genetic capture-recapture and integrated population modeling approaches may be the most effective methods for estimating wild pronghorn survival and would allow for comparisons between

translocated and wild-born pronghorn (Woodruff *et al.*, 2016). More research is needed to understand the link between management, predator presence and abundance, and predation risk for Sonoran pronghorn.

Active management and intervention strategies are increasingly employed to assist recovery of at-risk species, and these strategies have been the foundation of the Sonoran pronghorn recovery program since the U.S. population crash in 2002. These efforts have increased the current U.S. population to over 500 individuals (SPRT personal communication), meeting recovery thresholds in a subset of areas within the current pronghorn range. In 2022, the Sonoran Pronghorn Recovery Team repatriated six pronghorn to the Reserva de la Biosfera El Pinacate y Gran Desierto de Altar in Sonora, Mexico, 20 years after the U.S. population crash of 2002. Efforts are underway to reintroduce an additional non-essential experimental population in California, USA, at the northwestern edge of the recognized historic range for Sonoran pronghorn, where pronghorn have been absent for over 80 years (Brown *et al.*, 2006). By identifying factors that influence mortality risk and survival for translocated Sonoran pronghorn, this research highlights the importance of considering contributions to risk across spatiotemporal timescales and supports effective translocation practices in current and future reintroduction areas. With anticipated climatic and landscape changes within their current range, the active approach that has been a hallmark of Sonoran pronghorn management will likely continue to be essential to achieving recovery goals and maintaining this species on the Sonoran Desert landscape.

References

Abatzoglou, J.T. (2013). Development of gridded surface meteorological data for ecological applications and modelling. *International Journal of Climatology* **33**, 121–131.

Abrahms, B., Aikens, E.O., Armstrong, J.B., Deacy, W.W., Kauffman, M.J. & Merkle, J.A. (2021). Emerging Perspectives on Resource Tracking and Animal Movement Ecology. *Trends in Ecology & Evolution* **36**, 308–320.

Armstrong, D.P., Le Coeur, C., Thorne, J.M., Panfylova, J., Lovegrove, T.G., Frost, P.G.H. & Ewen, J.G. (2017). Using Bayesian mark-recapture modelling to quantify the strength and duration of post-release effects in reintroduced populations. *Biological Conservation* **215**, 39–45.

Armstrong, D.P. & Seddon, P.J. (2008). Directions in reintroduction biology. *Trends in Ecology & Evolution* **23**, 20–25.

Averill-Murray, R.C., Darst, C.R., Field, K.J. & Allison, L.J. (2012). A New Approach to Conservation of the Mojave Desert Tortoise. *BioScience* **62**, 893–899.

Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software* **67**, 1–48.

Bean, W.T., Butterfield, H.S., Fiehler, C., Hacker, D., Howard, J.K., Namitz, R., Swanson, B. & Batter, T.J. (2023). Contrasting management paradigms for pronghorn in the arid Southwest and their northern range: a review. *The Journal of Wildlife Management* **n/a**, e22523.

Berger-Tal, O., Blumstein, D.T. & Swaisgood, R.R. (2020). Conservation translocations: a review of common difficulties and promising directions. *Animal Conservation* **23**, 121–131.

Berger-Tal, O. & Saltz, D. (2014). Using the movement patterns of reintroduced animals to improve reintroduction success. *Current Zoology* **60**, 515–526.

Bright, J.L. & Hervert, J.J. (2005). Adult and fawn mortality of Sonoran pronghorn. *Wildlife Society Bulletin* **33**, 43–50.

Brown, D.E., Cancino, J., Clark, K.B., Smith, M. & Yoakum, J. (2006). An Annotated Bibliography of References to Historical Distributions of Pronghorn in Southern and Baja California. *Bulletin, Southern California Academy of Sciences* **105**, 1–16.

Bunting, E.L., Munson, S.M. & Bradford, J.B. (2019). Assessing plant production responses to climate across water-limited regions using Google Earth Engine. *Remote Sensing of Environment* **233**, 111379.

Cheng, Z., Tian, X., Zhong, Z., Li, P., Sun, D., Bai, J., Meng, Y., Zhang, S., Zhang, Y., Wang, L. & Liu, D. (2021). Reintroduction, distribution, population dynamics and conservation of

a species formerly extinct in the wild: A review of thirty-five years of successful Milu (*Elaphurus davidianus*) reintroduction in China. *Global Ecology and Conservation* **31**, e01860.

Conner, M.M., Stephenson, T.R., German, D.W., Monteith, K.L., Few, A.P. & Bair, E.H. (2018). Survival analysis: Informing recovery of Sierra Nevada bighorn sheep. *The Journal of Wildlife Management* **82**, 1442–1458.

Daly, C., Smith, J.I. & Olson, K.V. (2015). Mapping Atmospheric Moisture Climatologies across the Conterminous United States. *PLOS ONE* **10**, e0141140.

DeCesare, N.J., Hebblewhite, M., Robinson, H.S. & Musiani, M. (2009). Endangered, apparently: the role of apparent competition in endangered species conservation: Apparent competition and endangered species. *Animal Conservation* **13**, 353–362.

Dimmitt, M.A. (2015). Biomes and Communities of the Sonoran Desert Region. In *A Natural History of the Sonoran Desert*: 27–34. Dimmitt, M.A., Comus, P.W. & Brewer, L.M. (Eds.). Oakland, CA: University of California Press.

Dirzo, R. & Raven, P.H. (2003). Global State of Biodiversity and Loss. *Annual Review of Environment and Resources* **28**, 137–167.

Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B. & Collen, B. (2014). Defaunation in the Anthropocene. *Science* **345**, 401–406.

Eacker, D.R., Jakes, A.F. & Jones, P.F. (2023). Spatiotemporal risk factors predict landscape-scale survivorship for a northern ungulate. *Ecosphere* **14**, e4341.

Ebenhoch, K., Thornton, D., Shipley, L., Manning, J.A. & White, K. (2019). Effects of post-release movements on survival of translocated sage-grouse. *The Journal of Wildlife Management* **83**, 1314–1325.

Epps, C.W., McCULLOUGH, D.R., Wehausen, J.D., Bleich, V.C. & L. Rechel, J. (2004). Effects of Climate Change on Population Persistence of Desert-Dwelling Mountain Sheep in California. *Conservation Biology* **18**, 102–113.

ESA. (1973). Endangered Species Act of 1973.

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B.C., Marquis, R.J., Oksanen, L., Oksanen, T., Paine, R.T., Pikitch, E.K., Ripple, W.J., Sandin, S.A., Scheffer, M., Schoener, T.W., Shurin, J.B., Sinclair, A.R.E., Soulé, M.E., Virtanen, R. & Wardle, D.A. (2011). Trophic Downgrading of Planet Earth. *Science* **333**, 301–306.

Facka, A.N., Roemer, G.W., Mathis, V.L., Kam, M. & Geffen, E. (2010). Drought Leads to Collapse of Black-Tailed Prairie Dog Populations Reintroduced to the Chihuahuan Desert. *The Journal of Wildlife Management* **74**, 1752–1762.

Farwell, L.S., Gudex-Cross, D., Anise, I.E., Bosch, M.J., Olah, A.M., Radeloff, V.C., Razenkova, E., Rogova, N., Silveira, E.M.O., Smith, M.M. & Pidgeon, A.M. (2021). Satellite image texture captures vegetation heterogeneity and explains patterns of bird richness. *Remote Sensing of Environment* **253**, 112175.

Fieberg, J. & DelGiudice, G.D. (2009). What time is it? Choice of time origin and scale in extended proportional hazards models. *Ecology* **90**, 1687–1697.

Frair, J.L., Merrill, E.H., Allen, J.R. & Boyce, M.S. (2007). Know Thy Enemy: Experience Affects Elk Translocation Success in Risky Landscapes. *Journal of Wildlife Management* **71**, 541–554.

Gedir, J.V., Cain, J.W., Harris, G. & Turnbull, T.T. (2015). Effects of climate change on long-term population growth of pronghorn in an arid environment. *Ecosphere* **6**, art189.

Gorelick, N., Hancher, M., Dixon, M., Ilyushchenko, S., Thau, D. & Moore, R. (2017). Google Earth Engine: Planetary-scale geospatial analysis for everyone. *Remote Sensing of Environment*, Big Remotely Sensed Data: tools, applications and experiences **202**, 18–27.

Grant, L., Johnson, C. & Thiessen, C. (2019). Evaluating the efficacy of translocation: maintaining habitat key to long-term success for an imperiled population of an at-risk species. *Biodivers Conserv* **28**, 2727–2743.

Gross, I.P., Wilson, A.E. & Wolak, M.E. (2023). The fitness consequences of wildlife conservation translocations: a meta-analysis. *Biological Reviews* **n/a**.

Hanson, R.B. & Hanson, J. (2015). Sonoran Desert natural events calendar. In *A Natural History of the Sonoran Desert*: 27–34. Phillips, L.M., S.J.,. Wentworth Comus, P.W.,. Dimmitt, M.A.,. Brewer (Ed.). Oakland, CA: University of California Press.

Harris, G.M., Stewart, D.R., Brown, D., Johnson, L., Sanderson, J., Alvidrez, A., Waddell, T. & Thompson, R. (2020). Year-round water management for desert bighorn sheep corresponds with visits by predators not bighorn sheep. *PLoS ONE* **15**, e0241131.

Heffelfinger, L.J., Stewart, K.M., Bush, A.P., Sedinger, J.S., Darby, N.W. & Bleich, V.C. (2018). Timing of precipitation in an arid environment: Effects on population performance of a large herbivore. *Ecology and Evolution* **8**, 3354–3366.

Hervert, J.J., Bright, J.L., Henry, R.S., Piest, L.A. & Brown, M.T. (2005). Home-range and habitat-use patterns of Sonoran pronghorn in Arizona. *wbul* **33**, 8–15.

Hoffmann, M., Duckworth, J. w., Holmes, K., Mallon, D.P., Rodrigues, A.S.L. & Stuart, S.N. (2015). The difference conservation makes to extinction risk of the world's ungulates. *Conservation Biology* **29**, 1303–1313.

Huete, A.R. (1988). A soil-adjusted vegetation index (SAVI). *Remote Sensing of Environment* **25**, 295–309.

IUCN/SSC. (2013). Guidelines for reintroductions and other conservation translocations.

Jesmer, B.R., Merkle, J.A., Goheen, J.R., Aikens, E.O., Beck, J.L., Courtemanch, A.B., Hurley, M.A., McWhirter, D.E., Miyasaki, H.M., Monteith, K.L. & Kauffman, Matthew.J. (2018). Is ungulate migration culturally transmitted? Evidence of social learning from translocated animals. *Science* **361**, 1023–1025.

Jones, M.O., Robinson, N.P., Naugle, D.E., Maestas, J.D., Reeves, M.C., Lankston, R.W. & Allred, B.W. (2021). Annual and 16-Day Rangeland Production Estimates for the Western United States. *Rangeland Ecology & Management* **77**, 112–117.

Jones, P.F., Jakes, A.F., Eacker, D.R. & Hebblewhite, M. (2020). Annual Pronghorn Survival of a Partially Migratory Population. *The Journal of Wildlife Management* **84**, 1114–1126.

Kennedy, C.M., Oakleaf, J.R., Theobald, D.M., Baruch-Mordo, S. & Kiesecker, J. (2019). Managing the middle: A shift in conservation priorities based on the global human modification gradient. *Global Change Biology* **25**, 811–826.

Khatri-Chhetri, P., Hendryx, S.M., Hartfield, K.A., Crimmins, M.A., Leeuwen, W.J.D. van & Kane, V.R. (2021). Assessing Vegetation Response to Multi-Scalar Drought across the Mojave, Sonoran, Chihuahuan Deserts and Apache Highlands in the Southwest United States. *Remote Sensing* **13**, 1103.

Laliberte, A.S. & Ripple, W.J. (2004). Range Contractions of North American Carnivores and Ungulates. *BioScience* **54**, 123–138.

Lewis, J.C., Jenkins, K.J., Happe, P.J., Manson, D.J. & Griffin, P.C. (2022). Post-release survival of translocated fishers: implications for translocation success. *The Journal of Wildlife Management* **86**, e22192.

Lewis, J.S., Rachlow, J.L., Garton, E.O. & Vierling, L.A. (2007). Effects of habitat on GPS collar performance: using data screening to reduce location error: GPS collar performance. *Journal of Applied Ecology* **44**, 663–671.

Linklater, W.L. & Swaisgood, R.R. (2008). Reserve Size, Conspecific Density, and Translocation Success for Black Rhinoceros. *The Journal of Wildlife Management* **72**, 1059–1068.

Mawdsley, J.R., O'malley, R. & Ojima, D.S. (2009). A Review of Climate-Change Adaptation Strategies for Wildlife Management and Biodiversity Conservation. *Conservation Biology* **23**, 1080–1089.

Merrick, M.J. & Koprowski, J.L. (2017). Should we consider individual behavior differences in applied wildlife conservation studies? *Biological Conservation* **209**, 34–44.

Morgart, J.R., Hervert, J.J., Krausman, P.R., Bright, J.L. & Henry, R.S. (2005). Sonoran pronghorn use of anthropogenic and natural water sources. *Wildlife Society Bulletin* **33**, 51–60.

Morris, S.D., Brook, B.W., Moseby, K.E. & Johnson, C.N. (2021). Factors affecting success of conservation translocations of terrestrial vertebrates: A global systematic review☆. *Global Ecology and Conservation* **28**, e01630.

Munson, S.M., Webb, R.H., Belnap, J., Andrew Hubbard, J., Swann, D.E. & Rutman, S. (2012). Forecasting climate change impacts to plant community composition in the S onoran D esert region. *Glob Change Biol* **18**, 1083–1095.

O'Brien, C.S., Rosenstock, S.S., Hervert, J.J., Bright, J.L. & Boe, S.R. (2005). Landscape-level models of potential habitat for Sonoran pronghorn. *Wildlife Society Bulletin* **33**, 24–34.

O'Gara, B.W. (2004). Mortality Factors. In *Pronghorn: Ecology and Management*: 379–408. O'Gara, J.D., B.W.,. Yoakum (Ed.). Boulder, CO: University Press of Colorado.

Ortega, A.C., Merkle, J.A., Sawyer, H., Monteith, K.L., Lionberger, P., Valdez, M. & Kauffman, M.J. (2024). A test of the frost wave hypothesis in a temperate ungulate. *Ecology* **105**, e4238.

Pero, E.M., Chitwood, M.C., Hildreth, A.M., Keller, B.J., Sumners, J.A., Hansen, L.P., Isabelle, J.L. & Millspaugh, J.J. (2023). Identifying temporal dynamics in post-release survival of a restored large ungulate. *Ecological Solutions and Evidence* **4**, e12230.

Poirier, M.-A. & Festa-Bianchet, M. (2018). Social integration and acclimation of translocated bighorn sheep (*Ovis canadensis*). *Biological Conservation* **218**, 1–9.

Prude, C.H. (2020). *Influence of Habitat Heterogeneity and Water Sources on Kill Site Locations and Puma Prey Composition*. M.S., New Mexico State University, United States -- New Mexico.

R Core Team. (2023). *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.

Rich, L.N., Beissinger, S.R., Brashares, J.S. & Furnas, B.J. (2019). Artificial water catchments influence wildlife distribution in the Mojave Desert. *Jour. Wild. Mgmt.* **83**, 855–865.

Ripple, W.J., Abernethy, K., Betts, M.G., Chapron, G., Dirzo, R., Galetti, M., Levi, T., Lindsey, P.A., Macdonald, D.W., Machovina, B., Newsome, T.M., Peres, C.A., Wallach, A.D., Wolf, C. & Young, H. (2016). Bushmeat hunting and extinction risk to the world's mammals. *Royal Society Open Science* **3**, 160498.

Seddon, P.J., Armstrong, D.P. & Maloney, R.F. (2007). Developing the Science of Reintroduction Biology. *Conservation Biology* **21**, 303–312.

Seddon, P.J., Griffiths, C.J., Soorae, P.S. & Armstrong, D.P. (2014). Reversing defaunation: Restoring species in a changing world. *Science* **345**, 406–412.

Smith, J.A., Donadio, E., Pauli, J.N., Sheriff, M.J., Bidder, O.R. & Middleton, A.D. (2019). Habitat complexity mediates the predator–prey space race. *Ecology* **100**, e02724.

Smith, M.M., Erb, J.D. & Pauli, J.N. (2022). Seasonality drives the survival landscape of a recovering forest carnivore in a changing world. *Proceedings of the Royal Society B: Biological Sciences* **289**, 20220833.

Therneau, T.M. (2023). *A Package for Survival Analysis in R*.

Therneau, T.M. & Grambsch, P.M. (2000). The Cox Model. In *Modeling Survival Data: Extending the Cox Model*, Statistics for Biology and Health: 39–77. New York, NY: Springer New York.

U.S. Fish and Wildlife Service. (2016). *Recovery Plan for the Sonoran Pronghorn (Antilocapra americana sonoriensis), Second Revision*. U.S. Fish and Wildlife Service, Albuquerque, New Mexico, USA.

Vale, C.G. & Brito, J.C. (2015). Desert-adapted species are vulnerable to climate change: Insights from the warmest region on Earth. *Global Ecology and Conservation* **4**, 369–379.

Vicente-Serrano, S.M., Beguería, S. & López-Moreno, J.I. (2010). A Multiscalar Drought Index Sensitive to Global Warming: The Standardized Precipitation Evapotranspiration Index. *Journal of Climate* **23**, 1696–1718.

White, P.J., Vanderbilt White, C.A. & Ralls, K. (1996). Functional and Numerical Responses of Kit Foxes to a Short-Term Decline in Mammalian Prey. *Journal of Mammalogy* **77**, 370–376.

Wilson, R.R., Krausman, P.R. & Morgart, J.R. (2010). Forage Enhancement Plots as a Management Tool for Sonoran Pronghorn Recovery. *Journal of Wildlife Management* **74**, 236–239.

Woodruff, S.P., Lukacs, P.M., Christianson, D. & Waits, L.P. (2016). Estimating Sonoran pronghorn abundance and survival with fecal DNA and capture–recapture methods. *Conservation Biology* **30**, 1102–1111.

Zeller, K.A., Schroeder, C.A., Wan, H.Y., Collins, G., Denryter, K., Jakes, A.F. & Cushman, S.A. (2021). Forecasting habitat and connectivity for pronghorn across the Great Basin ecoregion. *Divers Distrib* **27**, 2315–2329.

Zhang, Y., Tariq, A., Hughes, A.C., Hong, D., Wei, F., Sun, H., Sardans, J., Peñuelas, J., Perry, G., Qiao, J., Kurban, A., Jia, X., Raimondo, D., Pan, B., Yang, W., Zhang, D., Li, W., Ahmed, Z., Beierkuhnlein, C., Lazkov, G., Toderich, K., Karryeva, S., Dehkonov, D., Hisoriev, H., Dimeyeva, L., Milko, D., Soule, A., Suska-Malawska, M., Saparmuradov, J., Bekzod, A., Allin, P., Dieye, S., Cissse, B., Whibesilassie, W. & Ma, K. (2023). Challenges and solutions to biodiversity conservation in arid lands. *Science of The Total Environment* **857**, 159695.

Tables

Table 1. Candidate models to evaluate the influence of population scale time-varying climatic conditions and time since translocation on Sonoran pronghorn mortality risk. All covariates were stratified by four seasonal segments: Fall and Winter (October - January), Spring (February - April), Early Summer (May - June), and Summer Monsoon (July - September).

Model	K	AIC	ΔAIC	Weight	LL
1-year drought + time since translocation	8	1974.22	0.00	1.00	-979.11
1-year drought	4	1986.37	12.15	0.00	-989.19
90-day drought + time since translocation	8	1994.02	19.80	0.00	-989.01
time since translocation	4	2000.06	25.84	0.00	-996.03
90-day drought	4	2004.18	29.96	0.00	-998.09
30-day precipitation + time since translocation	8	2006.37	32.14	0.00	-995.18
30-day precipitation	4	2018.30	44.08	0.00	-1005.15

Table 2. Candidate models to evaluate the influence of time-varying individual space use on Sonoran pronghorn mortality risk. All covariates were stratified by two seasonal segments: Fall, Winter and Spring (October - April),and Summer (May - September).

Model	K	AIC	ΔAIC	Weight	LL
1-year drought + human footprint + water access	6	656.12	0.00	0.81	-322.06
1-year drought + water access	4	660.10	3.98	0.11	-326.05
1-year drought + human footprint	4	660.83	4.72	0.08	-326.42
1-year drought + forage availability	4	667.15	11.03	0.00	-329.57
1-year drought + habitat complexity	4	667.74	11.62	0.00	-329.87
1-year drought + time since translocation	4	668.00	11.88	0.00	-330.00

Table 3. Best-supported model results from the population scale mortality risk analysis. HR > 1 indicates increased mortality risk. 95% HR confidence intervals (CI) that overlap 0 indicate weak to no effect in a season. HR is exp(β).

Season	β 1-yr drought (95% CI)	1-yr drought HR (95% CI)	β Time Since Translocation (95% CI)	Time Since Translocation HR (95% CI)
Fall & Winter	-0.61 (-1.09 - -0.14)	0.54 (0.34 - 0.87)	0.08 (-0.34 - 0.50)	1.09 (0.71 - 1.66)
Spring	-0.70 (-1.00 - -0.40)	0.50 (0.37 - 0.67)	-0.34 (-0.70 - 0.02)	0.71 (0.50 - 1.02)
Early Summer	-0.18 (-0.46 - 0.11)	0.84 (0.63 - 1.12)	-0.47 (-0.86 - -0.07)	0.63 (0.42 - 0.93)
Summer Monsoon	0.12 (-0.28 - 0.52)	1.12 (0.75 - 1.68)	-0.61 (-1.05 - -0.17)	0.54 (0.35 - 0.84)

Table 4. Best-supported model results relating individual space use and mortality risk. HR > 1 indicates increased mortality risk. 95% HR confidence intervals (CI) that overlap 0 indicate weak to no effect in a season. HR is exp(β).

Season	β 1-yr drought (95% CI)	1-yr drought HR (95% CI)	β Distance to Water (95% CI)	Distance to Water HR (95% CI)	β Human Footprint (95% CI)	Human Footprint HR (95% CI)
Fall, Winter, & Spring	-0.79 (-1.26 - -0.32)	0.45 (0.28 - 0.73)	0.18 (-0.17 - 0.53)	1.20 (0.84 - 1.70)	0.32 (0.05 - 0.58)	1.37 (1.05 - 1.79)
Summer	-0.19 (-0.54 - 0.17)	0.83 (0.58 - 1.18)	0.44 (0.15 - 0.73)	1.56 (1.17 - 2.08)	0.25 (0.04 - 0.46)	1.28 (1.04 - 1.58)

Table 5. Linear mixed-effects model results evaluating the relationship between individual space use covariates and time since translocation. High standard deviation values for the random slope and random intercept effects relative to fixed effects coefficients indicate that high variation among individuals overwhelms population-level fixed effects. Covariates were log (habitat complexity, forage availability, distance to water) or square-root (human footprint) transformed and then standardized before model implementation, and presented model results reflect the transformed, standardized data.

		Fixed Effects		*Random Effects*		
Individual Space Use Covariate	**Season**	**Intercept (SE)**	**β Time Since Translocation (SE)**	**Intercept SD**	**Slope SD**	**Residual SD**
Habitat Complexity	Fall, Winter, & Spring	-0.08 (0.08)	-0.21 (0.06)	0.97	0.65	0.41
Habitat Complexity	Summer	0.17 (0.09)	0.11 (0.10)	0.94	1.00	0.32
Forage Availability	Fall, Winter, & Spring	0.58 (0.11)	0.48 (0.09)	1.24	1.04	0.45
Forage Availability	Summer	-0.37 (0.07)	-0.18 (0.09)	0.76	0.95	0.39
Human Footprint	Fall, Winter, & Spring	0.34 (0.24)	0.38 (0.22)	3.04	2.72	0.37
Human Footprint	Summer	0.08 (0.10)	0.09 (0.11)	1.12	1.20	0.30
Distance to Water	Fall, Winter, & Spring	0.28 (0.10)	0.12 (0.08)	1.24	0.92	0.30
Distance to Water	Summer	-0.08 (0.10)	-0.15 (0.07)	1.19	0.76	0.30

Figures
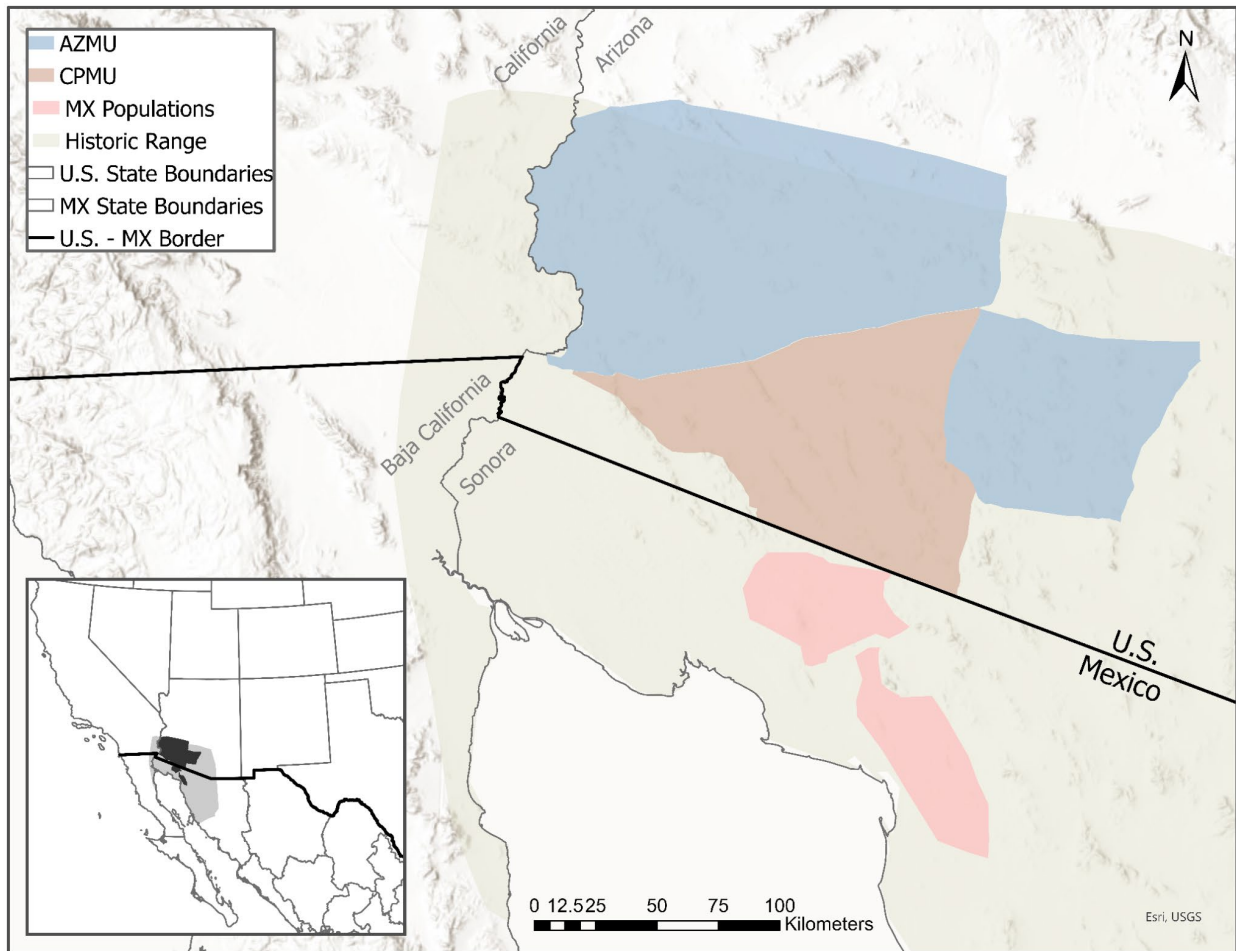
Figure 1. Current and historic range of Sonoran pronghorn in the USA and Mexico (MX). The Cabeza Prieta Management Unit (CPMU) and MX populations are federally endangered, while Sonoran pronghorn in the Arizona Management Unit (AZMU) are designated experimental under Section 10(j) of the U.S. Endangered Species Act.
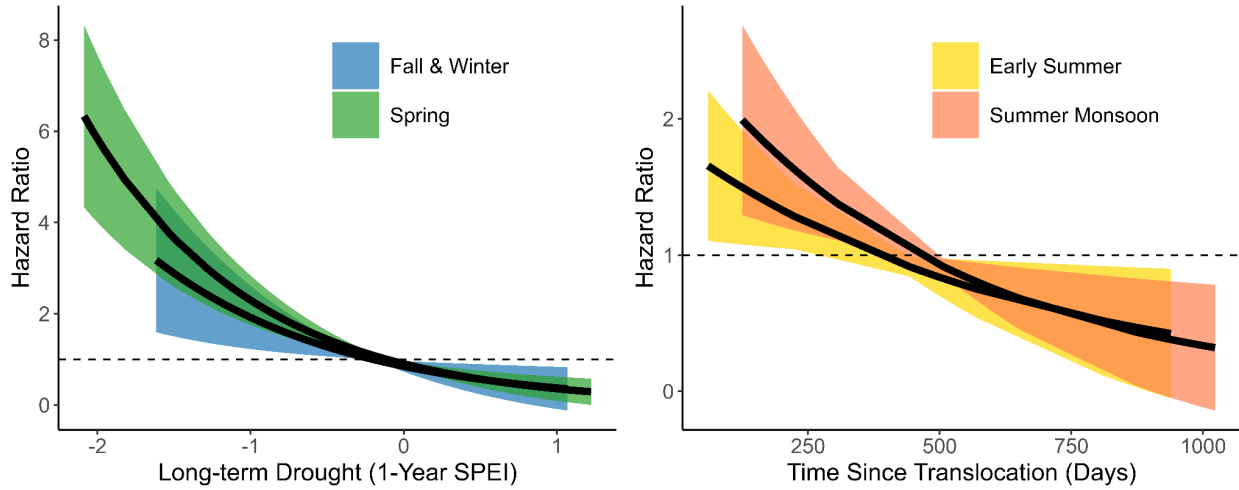
Figure 2. Predicted hazard ratios from the best-supported population scale model predicting mortality risk as a function of long-term drought in fall, winter, and spring and time since translocation in the early summer and summer monsoon seasons. Long-term drought is represented by SPEI values, where more positive values indicate wetter conditions where precipitation is greater than potential evapotranspiration, while more negative values indicate dry conditions where potential evapotranspiration outpaces precipitation. Predictions for each season were made using the range of covariate data available for that season, while holding all other covariates at their mean value for that season.
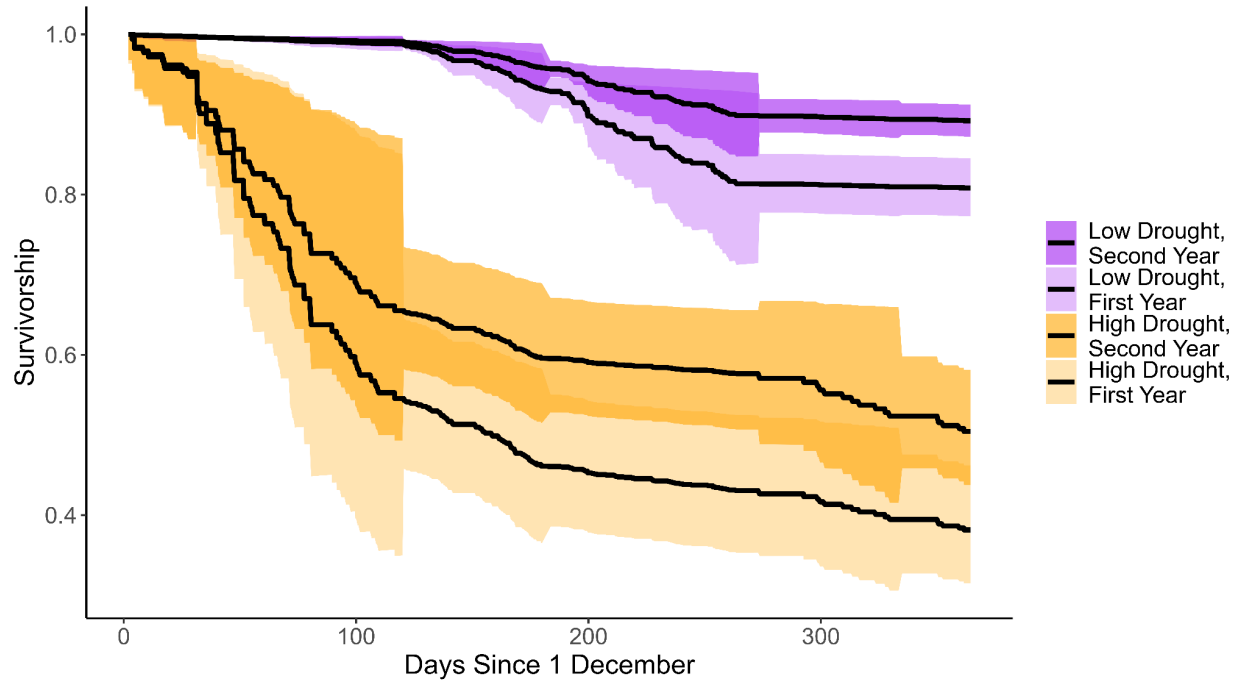
Figure 3. Predicted annual survivorship using the best supported population scale mortality risk model. Four hypothetical scenarios are presented: A low-drought (i.e. wetter conditions) year or a high-drought year, each with a cohort of individuals experiencing their first or second year post-translocation.
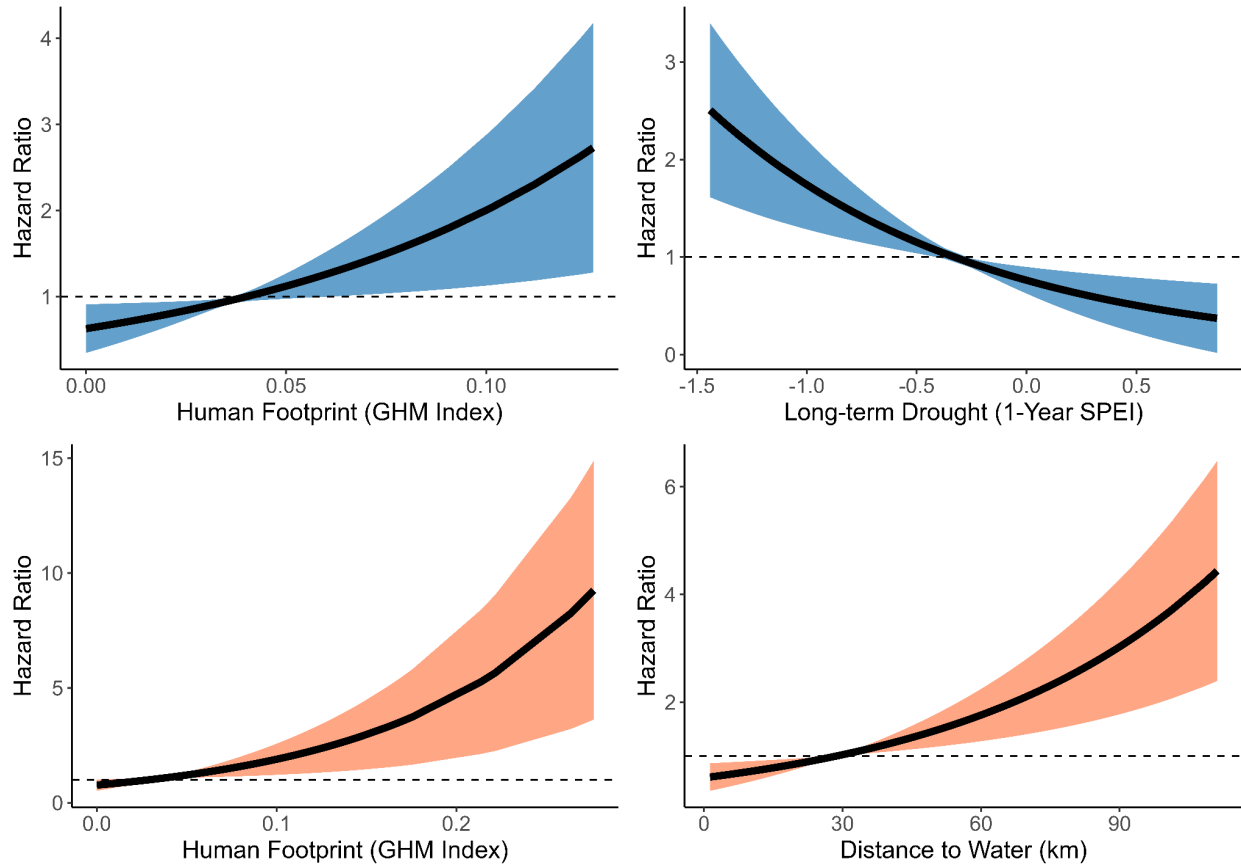
Figure 4. Predicted hazard ratios from the best-supported individual scale model showing mortality risk as a function of human footprint (top-left) and long-term drought (top-right) in fall, winter, and spring seasons and human footprint (bottom-left) and distance to water (bottom-right) in summer seasons. Predictions for each season were made using the range of covariate data available for that season, while holding all other covariates at their mean value for that season.

CHAPTER 3
Season and drought influence co-occurrence and interactions at managed water sources in the Sonoran Desert large mammal community

Abstract

Water is a key component of wildlife conservation and management in desert ecosystems. While human-modified water sites provide an essential resource to species of conservation concern, water management also has the potential to influence wildlife co-occurrence and interactions, with implications for patterns of competition and predation. This may be particularly relevant in times when species are reliant on managed water for survival, e.g., during hot, dry summers or periods of severe drought. We evaluated variation in large mammal occurrence and interspecific interactions at managed water sites across four protected areas in the Sonoran Desert, USA. As expected, occupancy at managed waters varied seasonally and was generally higher in summer months (May - September). Drought severity increased large herbivore occupancy during the monsoon, fall, and winter seasons (July - January). Although occupancy for most wildlife was higher in summer, similar seasonal patterns did not necessarily equate to high predicted co-occurrence. At a finer temporal scale we measured both potential and direct interactions, using time between detections of taxa pairs as the measure of interaction potential and physical co-occurrence as the measure of direct interaction. Potential for interactions to occur was higher in summer months (May - September). Direct interactions were higher as a function of relative abundance and high antagonism class, and also increased with drought severity in the summer monsoon (July - September) and fall-winter (Oct - Jan) seasons. Our findings indicate that at managed water sites, season and drought influence wildlife occurrence at a coarse scale, and pairwise direct interactions at a fine scale. Active water management is likely to become more prevalent as conditions in the Sonoran Desert trend hotter

and more prone to periods of severe drought. Understanding co-occurrence and the potential for wildlife interactions at water sources can ensure that managers are able to jointly consider the direct and indirect effects of this conservation and management strategy on large mammal communities.

Introduction

Spatiotemporal variation in resource availability influences wildlife at multiple scales of organization, from individual habitat use and movement (Baruch-Mordo et al. 2014) to structure of wildlife assemblages and communities (Thibault et al. 2010). Individuals will select home ranges with sufficient resources (Gedir et al. 2020, Tomaszewski et al. 2022), or track resources that are ephemeral in space and time (Baruch-Mordo et al. 2014, Aikens et al. 2017), influencing patterns of distribution and abundance at the population level (Nielsen et al. 2010, Rich et al. 2019a). Species assemblages can also be structured by variation in resource availability, as resource patchiness or scarcity can drive overlap among species, altering the potential for interspecific interactions including competition and predation (Sih 2005, Smith et al. 2019, Ferretti and Fattorini 2021). Exploitative competition can increase in intensity when resources are limited (Ferretti and Fattorini 2021). Patterns of predation will also be affected if, as a result of scarcity and limitation, prey must acquire resources in areas with increased predation risk (de Boer et al. 2010, Smith et al. 2019). The contextual importance of resources can also vary according to changing environmental conditions (Gedir et al. 2020, Martin et al. 2021), including predictable seasonal changes as well as stochastic events like severe weather (Gilbert et al. 2022b) and drought (Thibault et al. 2010, Gedir et al. 2020). For example, for much of the year herbivores adapted to live in water-limited environments can acquire sufficient water through forage consumption (Gedir et al. 2016, Kihwele et al. 2020). However, during the hottest, driest

times of year these animals must seek surface water to meet physiological water demands (Harris et al. 2020, Glass et al. 2022).

Provisioned and managed water sources are a cornerstone of wildlife conservation and management practices in desert ecosystems, and are widely distributed across the arid southwest region of the United States (Cain et al. 2008, Rich et al. 2019a, Harris et al. 2020). Managed water sites ensure that water remains available year-round to wildlife in water-limited systems (Harris et al. 2020). Managers manipulate water availability by altering natural sources of water to ensure year-round access, and by developing new water sites for wildlife using catchment systems or wells. Although water management is often designed to maintain or increase the abundance of a single species of conservation, cultural, or economic concern, e.g., desert bighorn sheep (Harris et al. 2020), numerous desert species use and benefit from managed water sources (Hall et al. 2013, Rich et al. 2019a, 2019b). Recent research in the Mojave Desert Region, USA, showed that 18 wildlife species had distributions closely tied to the occurrence of managed water catchments (Rich et al. 2019a).

While water management may be critical to desert wildlife conservation and aid in population recovery efforts in desert ecosystems (Morgart et al. 2005, Bean et al. 2023), it may also alter the strength and persistence of co-occurrence and interspecific interactions (Rocha et al. 2022), particularly during periods of low precipitation and high temperatures when water scarcity is most pronounced and species are most reliant on provisioned water (Harris et al. 2020, Terry et al. 2021, Glass et al. 2022). Provisioned water may have the indirect consequence of creating an overlapping spatial anchor for predator-prey or competitively interacting species (Sih 2005). Additionally, the availability of provisioned water has the potential to sustain species that

94

are less adapted to arid environments, allowing them to outcompete or increase predation on desert-adapted species (Hall et al. 2013, Harris et al. 2020).

In the Sonoran Desert, numerous species are reliant on actively managed water during the harsh summer months and periods of drought (Morgart et al. 2005, Bright and Hervert 2005), and an evaluation of seasonal variation in the potential for interspecific interactions at these managed sites is needed to better understand any indirect outcomes of this management strategy. Conducting analyses that consider more complete wildlife assemblages, rather than focusing on an isolated predator-prey or competitor pair when evaluating potential interactions, may better represent mechanisms governing community structure (Montgomery et al. 2019, Salvatori et al. 2022), particularly when the goal is to inform conservation action for vulnerable populations (Burgar et al. 2019). While interspecific interactions are challenging to measure directly *in situ*, spatiotemporal trends in occupancy and co-varying activity patterns are commonly used and interpreted as measures of interspecific interaction potential (Salvatori et al. 2022, Zhao et al. 2022, Gilbert et al. 2022a).

To evaluate the influence of season and drought on interspecific interactions at managed water sites, we analyzed co-occurrence at multiple temporal scales among the large mammal community of the Sonoran Desert: desert bighorn sheep (*Ovis canadensis nelsoni*), mule deer (*Odocoileus hemionus*), Coue's white-tailed deer (*Odocoileus virginianus couesi*), Sonoran pronghorn (*Antilocapra americana sonoriensis*), coyote (*Canis latrans*), gray fox (*Urocyon cinereoargenteus*), kit fox (*Vulpes macrotis*), mountain lion (*Puma concolor*), and bobcat (*Lynx rufus*). We used a long-term, multi-site, archived remote camera dataset representing 84 monitored provisioned water sources across southwestern Arizona, USA. The dataset encompassed roughly 900,000 detections of target wildlife, spanning 13 years of data collection

between 2008 and 2021. First, we asked how single-species occupancy at waters varied with season and drought conditions. Second, to explore fine-scale changes in co-occurrence, we considered the influence of season and drought conditions on time between detections and direct pairwise interactions. As the Sonoran desert becomes drier, hotter, and more climatically unpredictable (Munson et al. 2012), provisioned water will continue to be a key facet of desert wildlife management, and a more complete understanding of how this practice affects the large mammal assemblage in the region will be beneficial for informing future water management decisions that achieve desired conservation objectives.

Methods

Study Area

The Sonoran Desert Region in southwestern Arizona, USA provides a model system to evaluate the effects of season and drought on interactions at managed water sites. We focused this analysis on four federally managed and monitored areas: Kofa National Wildlife Refuge (KNWR) managed by the U.S. Fish and Wildlife Service (USFWS), Barry M Goldwater Range East (BMGRE) managed by the Department of Defense (DOD), Ajo Block managed by the Bureau of Land Management (BLM), and Organ Pipe Cactus National Monument (ORPI) managed by the National Park Service (NPS; Figure 1). Climate across the study area is characterized by extreme heat (mean maximum July temperature 33 - 39°C) and aridity (75 - 380 mm precipitation/year). Annual rainfall patterns are bimodal, with a winter rainy season and a summer monsoon season. Elevation ranges from 64 m to 1,486 m, and the landscape is characterized by wide alluvial valleys interspersed with rugged, isolated mountain ranges. Perennial water available to wildlife in the region is predominantly human-modified and actively managed. In mountainous areas, sources of water include tinajas (natural rock pools) and springs

with modifications like concrete dams and shade covers to increase water retention and reduce evaporation. In foothills and valleys, sources of water include troughs fed by wells or tanks actively filled by wildlife managers, as well as systems designed to catch water from washes that run during heavy monsoon or winter rains.

Data Collection

We collected data from 84 managed water locations across all four study areas between 2008 and 2021 using remote cameras (Bushnell Trophy Cam HD, Reconyx Hyperfire, Covert UOVISION UV565). No single area had all monitoring sites active for the full duration of the monitoring period, but most sites were actively monitored across multiple years. Images were pre-sorted by wildlife managers before archiving or were processed using a Megadetector + Timelapse workflow (Greenberg et al. 2019, Beery et al. 2019). We labeled images according to focal taxa category (desert bighorn sheep, deer, Sonoran pronghorn, coyote, fox, mountain lion, and bobcat). We combined the two deer species (Coue's white-tailed deer and mule deer) and the two fox species (gray fox and kit fox) because they fill functionally similar roles in the interacting large mammal community. We calculated total independent detections for each taxa category (Table 1), considering detections of a single taxa independent if detections occurred > 1 hour apart (Harris et al. 2015).

We measured seasonal drought at the scale of the study area. We defined seasons as early summer (May - June), summer monsoon (July - September), fall-winter (October - January), and spring (February - April; Hanson and Hanson 2015). We defined our study area for analyses by applying a 1 km buffer to a minimum convex polygon drawn around all monitored water sites. We measured drought using the 30-day Standardized Precipitation-Evapotranspiration Index (SPEI) band of the Gridded Surface Meteorological Dataset image collection

(GRIDMET/DROUGHT, 4-km resolution, Abatzoglou, 2013), taking the mean 30-day SPEI value within a monitoring season. SPEI considers precipitation and temperature data to calculate an index of drought at a specified timescale (Vicente-Serrano et al. 2010). More positive values indicate wetter conditions where precipitation is greater than potential evapotranspiration, while more negative values indicate dry conditions where potential evapotranspiration outpaces precipitation. SPEI values of -1.6 and below are considered severe drought conditions.

Seasonal occurrence of focal taxa

To evaluate seasonal patterns of large mammal occurrence at managed water sites across multiple years of sampling, we used a single species occupancy model framework. Occupancy models are hierarchical, with a component describing occupancy probability (i.e., the probability of a site being occupied by a species within a given season) and a component describing detection probability conditional on presence, to account for imperfect sampling and variation in monitoring effort (MacKenzie et al. 2017). We estimated occupancy at the seasonal scale, using the recorded presence or absence of a focal taxa for each week, or repeated 'visit', within a sampling season. We assume that occupancy is constant within a season (e.g., wildlife detected at a site in July implies presence across the summer monsoon season). To account for temporal autocorrelation from repeated sampling of sites across multiple seasons, we used the autologistic formulation of the occupancy component of the model which includes an autoregressive term that conditions occupancy probability in the current season on occupancy in the previous sampling season (Royle and Dorazio 2008). Analyses were conducted in R v 4.3.0 (R Core Team, 2023) and we used the autoOcc package for all occupancy analyses (Fidino 2024).

For each focal taxa we considered two models incorporating variables we expected to have associations with occupancy and detection probability. The first was a detection only model that included influence of season and sampling effort on detection. The second model used the same covariates in the detection component, and included covariates in the occupancy component of the model that described variation in occupancy according to spatial and temporal factors. The four spatial variables we considered were quantified within a 1 km buffer of each camera site and included temporally static metrics of topographic ruggedness, habitat complexity, and solar radiation index, as well as a dynamic metric of mean seasonal greenness (Supplemental Material S1.1). We selected these four metrics because they described different dimensions of the landscape that were uncorrelated (min correlation = 0.11, max correlation = -0.51) and expected to be meaningful for large mammals in this region. To assess temporal variation in occupancy we allowed occupancy probability to vary by seasonal category (early summer, summer monsoon, fall-winter, spring), short-term drought (seasonal mean of 30-day SPEI), and an interaction between season and short-term drought. The reference level for season was the early summer season for both detection and occupancy.

We selected a best-supported model for each focal taxa based on AIC, where models within 2Δ AIC of the lowest AIC model were considered competitive (Burnham and Anderson 2004). We used the best supported model for each taxon to predict seasonal occupancy at each site. To evaluate potential for co-occurrence, we assessed the correlation in seasonal occupancy predictions across sites for each taxa pair. We include detailed results on model selection and evaluation in the Supplemental Material.

Interactions - potential and direct

At locations with detections of two or more focal taxa, we evaluated the influence of season and drought on interaction potential and direct pairwise interactions, using time between detections of taxa pairs as the measure of potential for interaction and physical co-occurrence as the measure of direct interaction. Because Sonoran pronghorn had limited distribution across sites (detected at 6% of sites), we excluded all pairs that contained Sonoran pronghorn, which resulted in 15 taxa pairs for analysis.

We calculated site-specific time between detections for all taxa pairs within a season, yielding seasonal distributions of time between detections. Due to gaps in monitoring, we constrained calculating time between detections to those detections that fell within continuous monitoring intervals at a site, and excluded any time between detections that overlapped multiple seasons. We limited time between detections to less than or equal to one week, considering this to be the maximum time at which a pairwise detection could be biologically meaningful (Gilbert et al. 2022a). We evaluated seasonal differences in interaction potential using a Kruskal-Wallis test applied to the seasonal distributions of time between detections across taxa pairs, employing a Dunn post-hoc analysis with a Bonferroni correction for multiple comparisons to assess differences for each pairwise seasonal comparison.

For each site, we created a seasonal count of direct pairwise interactions (i.e., two different taxa recorded in the same image) across all taxa pairs. To ensure that pairwise interactions were independent, we required 1 hour to elapse after an initial direct interaction before considering the next direct interaction between a pair at a monitoring site (Harris et al. 2015).

We modeled seasonal count of direct interactions using a generalized linear model framework assuming a Poisson distribution for the response variable, the site-specific seasonal count of direct pairwise interactions. Because monitoring effort varied across sites and seasons, we used a zero-inflated Poisson (ZIP) modeling approach, where our model included a zero-inflated component to account for monitoring effort influencing the probability of excess zeroes in the interaction count dataset (Zuur et al. 2009). We developed a candidate set of ZIP models to consider the influence of season, drought, a season x drought interaction, seasonal relative abundance of the taxa pair, and antagonism level of the taxa pair on seasonal counts of direct interactions (Table 2). We defined seasonal relative abundance for a species or taxa at a site by taking the total count of independent detections divided by the total number of monitoring days. We then summed the relative abundance for both mammals comprising a taxa pair to get a relative pair abundance for each site across seasons. We classified pairs as either high (bighorn-coyote, bighorn-mountain lion, bobcat-coyote, bobcat-mountain lion, coyote-deer, coyote-fox, coyote-mountain lion, deer-mountain lion, fox-mountain lion) or low antagonism (bighorn-bobcat, bighorn-deer, bighorn-fox, bobcat-deer, bobcat-fox, deer-fox) based on the potential for a direct interaction to be costly and antagonistic for one or both taxa in the pair (Gilbert et al. 2022a). We constructed and implemented ZIP models using the glmmTMB package (Brooks et al. 2017). We selected a best supported model based on AIC, where models within 2Δ AIC of the lowest AIC model were considered competitive (Burnham and Anderson 2004). Using the best-supported model we report model coefficients and visualized predicted relationships for factors affecting direct pairwise interactions.

Results

At 84 managed water sites we accumulated a total of 100,332 remote camera monitoring days across 54 monitoring seasons (19,684 early summer, 31,330 summer monsoon, 29,505 fall-winter, 19,813 spring) between 2008 and 2021. Sites were monitored between 57 and 2,852 days and contributed to a minimum of 2 and maximum of 43 seasons of monitoring. Across all seasons, we recorded 880,136 raw detections resulting in 110,736 independent detections of the 7 focal taxa (Table 1).

Seasonal occurrence of focal taxa

We detected seasonal variation in occupancy for six of seven focal taxa (Figure 2, Supplemental Material S1.2, Tables S1.2 - S1.8, Figures S1.1 - S1.7). Coyote and fox occupancy were significantly lower in all other seasons relative to the early summer season. Bighorn sheep and deer occupancy were significantly lower in fall-winter and spring relative to early summer. Bobcat occupancy was significantly lower in the summer monsoon season relative to early summer. Mountain lion occupancy was significantly lower in spring relative to early summer. No other seasonal relationships across taxa were significant. We did not detect any seasonal relationships in occupancy for Sonoran pronghorn as the pronghorn detections across the dataset were limited.

We detected a season-specific relationship between drought and occupancy for two of seven focal taxa (Figure 3). In the summer monsoon and fall-winter seasons, both deer and bighorn sheep occupancy decreased as drought conditions decreased, though the effect for deer in the summer monsoon season was only marginally significant.

Site-specific correlation in predicted occupancy varied widely among focal taxa pairs, but appeared to be relatively stable across seasons (Figure 4). Similar seasonal patterns in occupancy did not directly translate into high seasonal correlation in predicted occupancy. For example,

bighorn and deer had similar seasonal trends in occupancy (Figures 2 & 3), but predicted

occupancy was negatively correlated at the site level across seasons, indicating spatial

partitioning between the two taxa. Taxa pairs with a high positive correlation (≥ 0.65) in site-

specific seasonal occupancy included deer-coyote, bobcat-fox, bobcat-mountain lion, and fox-

mountain lion. Taxa pairs with a high negative correlation (≤ -0.65) in site-specific seasonal

occupancy included bighorn-deer, bobcat-coyote, coyote-fox, and deer-fox. Because we had a

low number of detections for Sonoran pronghorn relative to all other taxa, we excluded this

species from our evaluation of pair-wise site-specific correlation in predicted occupancy.

Detailed information regarding single-species multi-year occupancy model results,

including model comparison information and all model coefficient estimates, associated

confidence intervals, and model interpretations and predictions, can be found in Supplemental

Material S1.1 and S1.2, Tables S1.2 - S1.8, Figures S1.1 - S1.7.

Interactions - potential and direct

We used a comparison among seasonal distributions of time between detections

combined across all focal taxa pairs as a preliminary exploration of interaction potential, to look

for temporal compression that could set up increased opportunities for direct interactions. We

detected seasonal differences in interaction potential ($\chi^2(3) = 1171.9$, $p < 0.0001$). The Dunn

post-hoc test indicated that all pairwise comparisons of the seasonal distributions of time

between detections were significantly different from each other (Table S2.2). A visual

assessment suggested that time between detections were more concentrated at lower values and

compressed towards 0 in the early summer and summer monsoon seasons relative to the fall-

winter and spring seasons for both low and high antagonism species pairs (Figure 5). Mean time

between detections across taxa pairs was 11.90 hours (SD = 20.66) in early summer, 12.44 hours

(SD = 23.73) in the summer monsoon, 16.16 hours (SD = 26.66) in the fall-winter, and 20 hours

(SD = 30.63) in the spring.

We recorded 4,712 images with >1 taxa, resulting in 537 independent direct interspecific

interactions (Table S2.1). The number of direct interactions varied by season, drought condition,

taxa pair relative abundance, and antagonism level of the taxa pair (Tables 2 & 3, Figure 6). The

number of direct interactions increased in the summer monsoon season relative to the early

summer season. The number of direct interactions decreased in the fall-winter and spring seasons

relative to the early summer season. There was no effect of drought conditions in the early

summer or spring seasons. In the summer monsoon and fall-winter seasons, wetter conditions

decreased the number of direct interactions. Increasing taxa pair relative abundance increased the

number of direct interactions. High antagonism level decreased the number of direct interactions

relative to low antagonism level. Importantly, the overall number of direct interactions in a

season was low and the predicted effects of season and drought were most notable (i.e., resulted

in an increase of 1 or more direct interactions) at high levels of taxa pair relative abundance

(Figure 6).

Discussion

In desert landscapes, water is a precious resource that influences ecological processes

across scales, from individual survival to community structure and function. Manipulating

surface water provides wildlife managers with a powerful tool that can contribute to species

recovery and support populations of conservation concern. Our research suggests that season and

drought severity influence wildlife co-occurrence and species interactions at water sites,

presenting a potentially unintended outcome of water management. Our results showed that, as

expected, occupancy at water sites increased in summer months for most taxa, and drought

severity increased herbivore occupancy in the summer monsoon and fall-winter seasons. Similar seasonal patterns of occupancy did not equate to high predicted co-occurrence for all taxa, refining expectations for overlap at water sites. At a finer temporal scale, we found that drought conditions increased direct interactions in the summer monsoon and fall-winter seasons. Increased relative abundance of the interacting taxa and high antagonism class were also important predictors of direct interactions. Considering interspecific interactions can inform water management strategies, including placement and maintenance of water sites, to achieve conservation goals and minimize unintended ecological impacts in desert ecosystems.

Occupancy analyses focused on managed water sites provide insight on expected co-occurrence of wildlife. The large mammal focal taxa we considered were detected at managed water sites in all seasons (Table 1), but estimated occupancy varied seasonally, and was generally higher in the early summer relative to other seasons (Figure 2). Our analyses indicate that wildlife occurrence at managed waters is driven by the need for water in specific seasons, though the magnitude of seasonal variation in occupancy differs across taxa (Figure 2). While our work does not provide a comparison of occupancy patterns at non-water sites, these results suggest that managed water in the Sonoran Desert Region provide a resource that is broadly important to the large mammal community in times of water scarcity, and future research on the seasonal influence of waters on distribution, survival, and reproduction would be beneficial to inform conservation and management action related to managed water.

We found evidence that drought influenced occupancy at managed water sites for desert bighorn sheep and deer in the summer monsoon and fall-winter months, where occupancy of these herbivores increased with increasing drought severity (i.e., more negative SPEI values). When habitat conditions are more favorable, arid-adapted herbivore species are able to meet

physiological water needs through forage without the need to supplement with surface water (Gedir et al. 2016). The lack of support for an effect of drought in the early summer coupled with high predicted occupancy in this season suggests that desert bighorn sheep and deer are rarely if ever able to meet water needs through forage alone during the hottest, driest times of year, regardless of drought condition. Our findings confirm previous research indicating a stronger influence of climatic conditions on water site visitation for desert bighorn sheep relative to deer (Harris et al. 2020).

Notably, similar patterns in seasonal occupancy did not necessarily translate to high correlation in predicted occurrence. For example, desert bighorn sheep and deer have similar seasonal and drought-related occupancy patterns, but seasonal predicted occurrence across sites had a strong negative correlation (< -0.65, Table 4). This indicates that spatial partitioning at this coarse scale could play a role in mitigating the potential for interactions among taxa pairs that, based on seasonal occupancy, might otherwise be expected to have a high degree of co-occurrence. Considering spatiotemporal variation in seasonal occupancy can be a useful first step for evaluating potential interspecific interaction dynamics at water sites. A valuable extension of this work would be to employ a model framework that can implicitly account for the influence of interspecific interactions on multi-species occupancy (Rota et al. 2016), as this approach could disentangle the influence of habitat requirements and interspecific avoidance or attraction on occupancy patterns.

Within the Sonoran desert large mammal community, we assessed the influence of season and drought on interspecific interactions at multiple temporal scales. When considering interaction potential measured as the time between pairwise detections of taxa, we found that the seasonal distributions of time between detections were significantly different from each other.

Interaction potential was higher in summer months (May - September), with an overall compression of time between detections, even for antagonistic pairs (Figure 5). We also identified significant seasonal variation in direct interactions, as well as an influence of drought conditions increasing direct interactions in summer monsoon and fall-winter seasons. (Figure 6). Increasing relative abundance resulted in increased direct interactions, and the influence of season and drought on interactions was most apparent (i.e., increased interactions by >1) when relative abundance was high (Table 3). Our use of relative abundance, which can vary according to actual increases in abundance as well as increases in visitation, is particularly relevant because both aspects can influence species interactions. It is important to note that relative abundance at water sites is likely influenced by drought conditions, serving as an indirect pathway through which climate affects interspecific interactions at water sites. In addition to the influence of season and drought on direct interactions that is likely mediated through abundance, there are other pathways that can contribute to the total effect of season and drought on species interactions at water sites. For example, activity patterns may shift in summer seasons to avoid extreme daytime heat, compressing mammal community visitation at water sites to a narrower portion of the diel period (Harris et al. 2015).

Despite the relatively low number of direct interactions predicted overall, even a minor increase in interaction potential can be costly, especially for species involved in high-risk antagonistic encounters. Managed waters have the potential to influence competition and predation dynamics in the Sonoran Desert large mammal community. High-antagonism pairs, which included both predator-prey and competitively interacting pairs in our dataset, exhibited fewer direct interactions than low-antagonism pairs, regardless of season and drought conditions (Table 5). This suggests that one or both taxa comprising high-antagonism pairs use behavioral

strategies to reduce interaction potential, which could include space use or activity shifts (Vanak et al. 2013, Bastille-Rousseau et al. 2016, Ferretti and Fattorini 2021). These behavioral adjustments have the potential to incur non-consumptive or indirect costs if, as a result, species have more limited access to water, limited access to resources, or adjust activity to more physiologically stressful times of day in order to avoid direct antagonistic interactions (Lima and Dill 1990). The increase in predicted interactions during drought conditions for both high- and low-antagonism pairs also indicates that fine-scale spatiotemporal partitioning at water sites becomes more challenging during periods when species are highly dependent on surface water (Harris et al. 2015).

Certain high-antagonism pairs were of specific interest. We considered mountain lion interactions to have a high degree of risk for all other large mammals in the region. Our work detected seasonal variation in mountain lion occupancy, with higher occupancy in early summer. Previous research in southwestern U.S. desert ecosystems observed a variety of seasonal patterns, in one study concluding that mountain lion visitation to water is driven by climate and prey presence (Harris et al. 2015), and in another finding that mountain lion visitation to water occurs year-round (Harris et al. 2020). While seasonal occupancy was generally highest in the early summer, predicted co-occurrence of mountain lion with primary prey species (desert bighorn sheep, deer) was slightly negative (Figure 4), suggesting that prey species to varying extents may be effectively avoiding predator encounters at the spatial point of a managed water site. We detected no direct interactions between desert bighorn sheep and mountain lions at water sites, and we detected four direct interactions between mountain lion and deer. All mountain lion-deer interactions appeared to be predation attempts, one clearly successful. Coyote-deer interactions were the most numerous direct interactions in our dataset, and we

108

documented multiple interactions that were clearly antagonistic and predatory. Interestingly, predicted occupancy of coyotes and deer had a strong positive correlation across seasons (Figure 4). Previous work has suggested that coyotes are most likely to occur in large groups in winter months, and during these times they are more likely to be successful at acquiring large prey (Bright and Hervert 2005). The inherent risk of an interaction between coyote and deer being an antagonistic, predatory encounter may have a seasonally varying component driven by the temporally varying behavioral strategies of this generalist predator (Bastille-Rousseau et al. 2016).

Challenges related to measuring interspecific interactions in natural settings are widely recognized (Caravaggi et al. 2017), particularly when relying on remote cameras, which are limited to observations at a single point in space. While this limitation is somewhat mitigated when the primary research interest lies in understanding the role of a spatially fixed resource in anchoring species interactions (Sih 2005, Smith et al. 2019), it is important to acknowledge that the influence of water sites on the Sonoran Desert large mammal community likely extends beyond a site's immediate vicinity. Our study was restricted to water sites due to the need to prioritize limited monitoring resources, and as a result, we were unable to capture the broader spatial or temporal extent of managed water influence on the large mammal community. Future work could assess interaction patterns at non-water sites, potentially incorporating other data types used to measure interactions like movement data, which may better capture the full area of influence of a managed water site (Kays et al. 2015). Additionally, water sites in the Sonoran desert region are largely motivated by game management and endangered species recovery, namely for large-bodied herbivores including desert bighorn sheep, deer, and Sonoran pronghorn. The monitored sites included in our dataset were biased towards sites managed for

desert bighorn sheep and deer, limiting our ability to include Sonoran pronghorn across scales of analysis. Because of the limited distribution of this endangered species, research on the effects of managed water on Sonoran pronghorn should target sites managed for this species' particular use.

An understanding of the context in which desert water management exerts influence on species interaction potential can inform strategies to mitigate this unintended, indirect effect. While the placement of water sites is often driven by the requirements of key species of conservation and management concern, it is critical to consider the broader ecological impacts, particularly the potential to influence species interactions. Increasing the density of water sites may provide wildlife an opportunity to avoid antagonistic interactions more effectively (Bean et al. 2023). Future research should focus on before-and-after studies to evaluate the impact of new water placements on wildlife interactions and community composition. Further, it would be useful to explore additional strategies for reducing indirect effects of water management including manipulating access to water for specific species through exclusion fencing (Hall et al. 2018) or by manipulating seasonal availability (Harris et al. 2020). Importantly, there are challenges in limiting water availability at certain sites, particularly those that rely on passive catchment systems, which are designed to fill naturally. Additional consequences of increasing direct interactions would also be valuable to explore, including potential for disease spread and restructuring of wildlife assemblages around water sites.

Interspecific interactions at managed waters can intensify in certain seasons and drought contexts, particularly during times of heightened need for surface water when these sites impose spatial constraints on wildlife. Future water management strategies in desert ecosystems will require additional consideration of the effects of human-driven development and climate change.

In the Sonoran Desert, urbanization, energy development, and border infrastructure all provide potential sources of human disturbance that could further alter occurrence and interactions at water sites. For example, fragmented habitats limit the ability to make long-range water seeking movements or access high quality forage (Sawyer et al. 2009). Research has also suggested that human disturbance can further compress species co-occurrence in space and time (Gilbert et al. 2022a), adding an additional constraint on wildlife during water limited seasons that could translate to further increases in interaction potential at managed waters. Additionally, access to managed surface water will likely increase in importance to wildlife as conditions become hotter and precipitation patterns more unpredictable. For example, increasing temperatures and prolonged droughts may increase the window of time in which multiple species require surface water for survival. As desert ecosystems continue to experience anthropogenic change, thoughtful approaches to water management that account for the influence on species interactions and other unintended effects will be valuable for ensuring that this strategy achieves desired conservation and management objectives.

References

Aikens, E. O., M. J. Kauffman, J. A. Merkle, S. P. H. Dwinnell, G. L. Fralick, and K. L. Monteith. 2017. The greenscape shapes surfing of resource waves in a large migratory herbivore. Ecology Letters 20:741–750.

Baruch-Mordo, S., K. R. Wilson, D. L. Lewis, J. Broderick, J. S. Mao, and S. W. Breck. 2014. Stochasticity in natural forage production affects use of urban areas by black bears: implications to management of human-bear conflicts. PLoS ONE 9:e85122.

Bastille-Rousseau, G., N. D. Rayl, E. H. Ellington, J. A. Schaefer, M. J. L. Peers, M. A. Mumma, S. P. Mahoney, and D. L. Murray. 2016. Temporal variation in habitat use, co-occurrence, and risk among generalist predators and a shared prey. Canadian Journal of Zoology 94:191–198.

Bean, W. T., H. S. Butterfield, C. Fiehler, D. Hacker, J. K. Howard, R. Namitz, B. Swanson, and T. J. Batter. 2023. Contrasting management paradigms for pronghorn in the arid Southwest and their northern range: a review. The Journal of Wildlife Management n/a:e22523.

Beery, S., D. Morris, and S. Yang. 2019, July 15. Efficient Pipeline for Camera Trap Image Review. arXiv.

de Boer, W. F., M. J. P. Vis, H. J. de Knegt, C. Rowles, E. M. Kohi, F. van Langevelde, M. Peel, Y. Pretorius, A. K. Skidmore, R. Slotow, S. E. van Wieren, and H. H. T. Prins. 2010. Spatial distribution of lion kills determined by the water dependency of prey species. Journal of Mammalogy 91:1280–1286.

Bright, J. L., and J. J. Hervert. 2005. Adult and fawn mortality of Sonoran pronghorn. Wildlife Society Bulletin 33:43–50.

Brooks, M., E., K. Kristensen, K. Benthem J. ,van, A. Magnusson, C. Berg W., A. Nielsen, H. Skaug J., M. Mächler, and B. Bolker M. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. The R Journal 9:378.

Bunting, E. L., S. M. Munson, and J. B. Bradford. 2019. Assessing plant production responses to climate across water-limited regions using Google Earth Engine. Remote Sensing of Environment 233:111379.

Burgar, J. M., A. C. Burton, and J. T. Fisher. 2019. The importance of considering multiple interacting species for conservation of species at risk. Conservation Biology 33:709–715.

Burnham, K. P., and D. R. Anderson. 2004. Multimodel inference: understanding aic and bic in model selection. Sociological Methods & Research 33:261–304.

Cain, J. W., P. R. Krausman, J. R. Morgart, B. D. Jansen, and M. P. Pepper. 2008. Responses of desert bighorn sheep to removal of water sources. Wildlife Monographs 171:1–32.

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.

Farr, T. G., P. A. Rosen, E. Caro, R. Crippen, R. Duren, S. Hensley, M. Kobrick, M. Paller, E. Rodriguez, L. Roth, D. Seal, S. Shaffer, J. Shimada, J. Umland, M. Werner, M. Oskin, D. Burbank, and D. Alsdorf. 2007. The Shuttle Radar Topography Mission. Reviews of Geophysics 45.

Farwell, L. S., D. Gudex-Cross, I. E. Anise, M. J. Bosch, A. M. Olah, V. C. Radeloff, E. Razenkova, N. Rogova, E. M. O. Silveira, M. M. Smith, and A. M. Pidgeon. 2021. Satellite image texture captures vegetation heterogeneity and explains patterns of bird richness. Remote Sensing of Environment 253:112175.

Ferretti, F., and N. Fattorini. 2021. Competitor densities, habitat, and weather: effects on interspecific interactions between wild deer species. Integrative Zoology 16:670–684.

Fidino, M. 2024. autoOcc: Fits Autologistic Occupancy Models, Compares Models, and Generates Model Predictions. R Package Version 0.1.1.

Gedir, J. V., J. W. Cain III, T. L. Swetnam, P. R. Krausman, and J. R. Morgart. 2020. Extreme drought and adaptive resource selection by a desert mammal. Ecosphere 11:e03175.

Gedir, J. V., J. W. C. Iii, P. R. Krausman, J. D. Allen, G. C. Duff, and J. R. Morgart. 2016. Potential foraging decisions by a desert ungulate to balance water and nutrient intake in a water-stressed environment. PLOS ONE 11:e0148795.

Gilbert, N. A., J. L. Stenglein, J. N. Pauli, and B. Zuckerberg. 2022a. Human disturbance compresses the spatiotemporal niche. Proceedings of the National Academy of Sciences 119:e2206339119.

Gilbert, N. A., J. L. Stenglein, T. R. Van Deelen, P. A. Townsend, and B. Zuckerberg. 2022b. Behavioral flexibility facilitates the use of spatial and temporal refugia during variable winter weather. Behavioral Ecology 33:446–454.

Glass, D. M., P. R. Prentice, A. D. Evans, and O. J. Schmitz. 2022. Local differences in maximum temperature determine water use among desert bighorn sheep populations. The Journal of Wildlife Management 86:e22313.

Greenberg, S., T. Godin, and J. Whittington. 2019. Design patterns for wildlife-related camera trap image analysis. Ecology and Evolution 9:13706–13730.

Hall, L. K., R. T. Larsen, R. N. Knight, K. D. Bunnell, and B. R. McMillan. 2013. Water developments and canids in two north american deserts: a test of the indirect effect of water hypothesis. PLOS ONE 8:e67800.

Hall, L. K., R. T. Larsen, R. N. Knight, and B. R. McMillan. 2018. Feral horses influence both spatial and temporal patterns of water use by native ungulates in a semi-arid environment.

Ecosphere 9.

Hanson, R.B. & Hanson, J. (2015). Sonoran Desert natural events calendar. In *A Natural History of the Sonoran Desert*: 27–34. Dimmitt, M.A., Comus, P.W. & Brewer, L.M. (Eds.). Oakland, CA: University of California Press.

Harris, G. M., D. R. Stewart, D. Brown, L. Johnson, J. Sanderson, A. Alvidrez, T. Waddell, and R. Thompson. 2020. Year-round water management for desert bighorn sheep corresponds with visits by predators not bighorn sheep. PLOS ONE 15:e0241131.

Harris, G., J. G. Sanderson, J. Erz, S. E. Lehnen, and M. J. Butler. 2015. Weather and prey predict mammals' visitation to water. PLOS ONE 10:e0141355.

Huete, A. R. 1988. A soil-adjusted vegetation index (SAVI). Remote Sensing of Environment 25:295–309.

Kays, R., M. C. Crofoot, W. Jetz, and M. Wikelski. 2015. Terrestrial animal tracking as an eye on life and planet. Science 348:aaa2478.

Keating, K. A., P. J. P. Gogan, J. M. Vore, and L. R. Irby. 2007. A simple solar radiation index for wildlife habitat studies. The Journal of Wildlife Management 71:1344–1348.

Kihwele, E. S., V. Mchomvu, N. Owen-Smith, R. S. Hetem, M. C. Hutchinson, A. B. Potter, H. Olff, and M. P. Veldhuis. 2020. Quantifying water requirements of African ungulates through a combination of functional traits. Ecological Monographs 90:e01404.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619–640.

MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. Bailey, and J. E. Hines. 2017. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Elsevier.

Martin, M. E., K. M. Moriarty, and J. N. Pauli. 2021. Landscape seasonality influences the resource selection of a snow-adapted forest carnivore, the Pacific marten. Landscape Ecology 36:1055–1069.

Montgomery, R. A., R. J. Moll, E. Say-Sallaz, M. Valeix, and L. R. Prugh. 2019. A tendency to simplify complex systems. Biological Conservation 233:1–11.

Morgart, J. R., J. J. Hervert, P. R. Krausman, J. L. Bright, and R. S. Henry. 2005. Sonoran pronghorn use of anthropogenic and natural water sources. Wildlife Society Bulletin 33:51–60.

Munson, S. M., R. H. Webb, J. Belnap, J. Andrew Hubbard, D. E. Swann, and S. Rutman. 2012. Forecasting climate change impacts to plant community composition in the Sonoran Desert region. Global Change Biology 18:1083–1095.

Nielsen, S. E., G. McDermid, G. B. Stenhouse, and M. S. Boyce. 2010. Dynamic wildlife habitat models: Seasonal foods and mortality risk predict occupancy-abundance and habitat selection in grizzly bears. Biological Conservation 143:1623–1634.

R Core Team. (2023). R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing.

Rich, L. N., S. R. Beissinger, J. S. Brashares, and B. J. Furnas. 2019a. Artificial water catchments influence wildlife distribution in the Mojave Desert. The Journal of Wildlife Management 83:855–865.

Rich, L. N., B. J. Furnas, D. S. Newton, and J. S. Brashares. 2019b. Acoustic and camera surveys inform models of current and future vertebrate distributions in a changing desert ecosystem. Diversity and Distributions 25:1441–1456.

Rocha, F., B. Bennett, and P. Monterroso. 2022. Understanding top-down and bottom-up processes in an ungulate community to define conservation priorities in a desert environment. Biodiversity and Conservation 31:2179–2203.

Rota, C. T., M. A. R. Ferreira, R. W. Kays, T. D. Forrester, E. L. Kalies, W. J. McShea, A. W. Parsons, and J. J. Millspaugh. 2016. A multispecies occupancy model for two or more interacting species. Methods in Ecology and Evolution 7:1164–1173.

Royle, J. A., and R. M. Dorazio. 2008. Hierarchical modeling and inference in ecology: The analysis of data from populations, metapopulations and communities. Elsevier.

Salvatori, M., V. Oberosler, C. Augugliaro, M. Krofel, and F. Rovero. 2022. Effects of free-ranging livestock on occurrence and interspecific interactions of a mammalian community. Ecological Applications 32:e2644.

Sawyer, H., M. J. Kauffman, R. M. Nielson, and J. S. Horne. 2009. Identifying and prioritizing ungulate migration routes for landscape-level conservation. Ecological Applications 19:2016–2025.

Sih, A. 2005. Predator-Prey Space Use as an Emergent Outcome of a Behavioral Response Race. Pages 240–255 Ecology of Predator-Prey Interactions. Oxford University Press, USA.

Smith, J. A., E. Donadio, J. N. Pauli, M. J. Sheriff, O. R. Bidder, and A. D. Middleton. 2019. Habitat complexity mediates the predator–prey space race. Ecology 100:e02724.

Smith, M. M., J. D. Erb, and J. N. Pauli. 2022. Seasonality drives the survival landscape of a recovering forest carnivore in a changing world. Proceedings of the Royal Society B: Biological Sciences 289:20220833.

Terry, P. J., A. C. Alvidrez, and C. W. Black. 2021. Factors affecting bighorn sheep activity at water developments in southwestern Arizona. The Journal of Wildlife Management:jwmg.22134.

Thibault, K. M., S. K. M. Ernest, E. P. White, J. H. Brown, and J. R. Goheen. 2010. Long-term insights into the influence of precipitation on community dynamics in desert rodents. Journal of Mammalogy 91:787–797.

Tomaszewski, E. M., M. K. Jennings, R. Botta, K. M. Curtis, and R. L. Lewison. 2022. Limited resources shape home range patterns of an insular ungulate in a semi-arid ecosystem. Journal of Arid Environments 200:104728.

Vanak, A. T., D. Fortin, M. Thaker, M. Ogden, C. Owen, S. Greatwood, and R. Slotow. 2013. Moving to stay in place: behavioral mechanisms for coexistence of African large carnivores. Ecology 94:2619–2631.

Vicente-Serrano, S. M., S. Beguería, and J. I. López-Moreno. 2010. A multiscalar drought index sensitive to global warming: the standardized precipitation evapotranspiration index. Journal of Climate 23:1696–1718.

Zhao, Q., A. K. Fuller, and J. A. Royle. 2022. Spatial dynamic N-mixture models with interspecific interactions. Methods in Ecology and Evolution 13:2209–2221.

Zuur, A. F., E. N. Ieno, N. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer, New York, NY.

Tables

Table 1. Summaries of independent detections across seasons for the seven focal taxa

Taxa	Areas Detected (of 4)	Total Sites Detected (of 84)	Independent Detections			
			Early Summer	*Summer Monsoon*	*Fall-Winter*	*Spring*
Bighorn	3	51	5,975	7,657	1,820	652
Bobcat	4	77	2,030	1,013	707	739
Coyote	4	72	10,443	5,488	6,746	4,121
Deer	4	74	16,345	18,450	12,335	3,307
Fox	4	75	4,487	3,028	3,083	934
Mountain lion	4	46	517	307	129	71
Sonoran Pronghorn	3	5	170	57	68	57

Table 2. Candidate zero-inflated Poisson models describing variation in seasonal count of direct interactions between taxa pairs. All models included a zero-inflated component where the probability of an excess zero in the dataset was allowed to vary according to total monitoring days. Season was a categorical variable where early summer was the reference level in all models. Drought was described as the seasonal mean of 30-day SPEI values. Antagonism was a categorical variable of low and high antagonism, with low being the reference level. RAI was the combined relative abundance of the taxa pair at a site within a season.

Candidate Model	#Parameters	AIC	ΔAIC	LogLik
~ season + drought + season x drought + antagonism + RAI	12	2566.77	0.00	-1271.39
~ season + drought + antagonism + RAI	7	2572.30	5.53	-1277.15
~ season + antagonism + RAI	6	2581.94	15.17	-1282.97
~ antagonism + RAI	5	2697.72	130.94	-1343.86

Table 3. Coefficient estimates with reported standard errors and 95% confidence intervals for the best-supported model describing variation in the seasonal count of direct interactions between taxa pairs.

Model Component	Term	Estimate	SE	Lwr 95% CI	Upr 95% CI	z value	p-value
Poisson	Intercept (Early Summer + Low Antagonism)	-1.52	0.14	-1.81	-1.24	-10.56	< 0.001
	Summer Monsoon	0.35	0.12	0.10	0.59	2.79	< 0.01
	Fall-Winter	-1.09	0.24	-1.57	-0.61	-4.47	< 0.001
	Spring	-1.96	0.59	-3.11	-0.81	-3.33	0.001
	Early Summer x SPEI	-0.01	0.09	-0.19	0.18	-0.07	0.944
	Combined RAI	0.45	0.02	0.40	0.49	18.38	< 0.001
	High Antagonism	-0.86	0.11	-1.09	-0.64	-7.51	< 0.001
	Summer Monsoon x SPEI	-0.33	0.12	-0.56	-0.09	-2.74	< 0.01
	Fall-Winter x SPEI	-0.69	0.27	-1.21	-0.17	-2.58	0.010
	Spring x SPEI	0.18	0.78	-1.35	1.71	0.23	0.815
Zero-Inflated	Intercept	1.39	0.22	0.95	1.83	6.20	< 0.001
	# Seasonal Monitoring Days	0.00	0.00	-0.01	0.00	-1.43	0.152

Figures
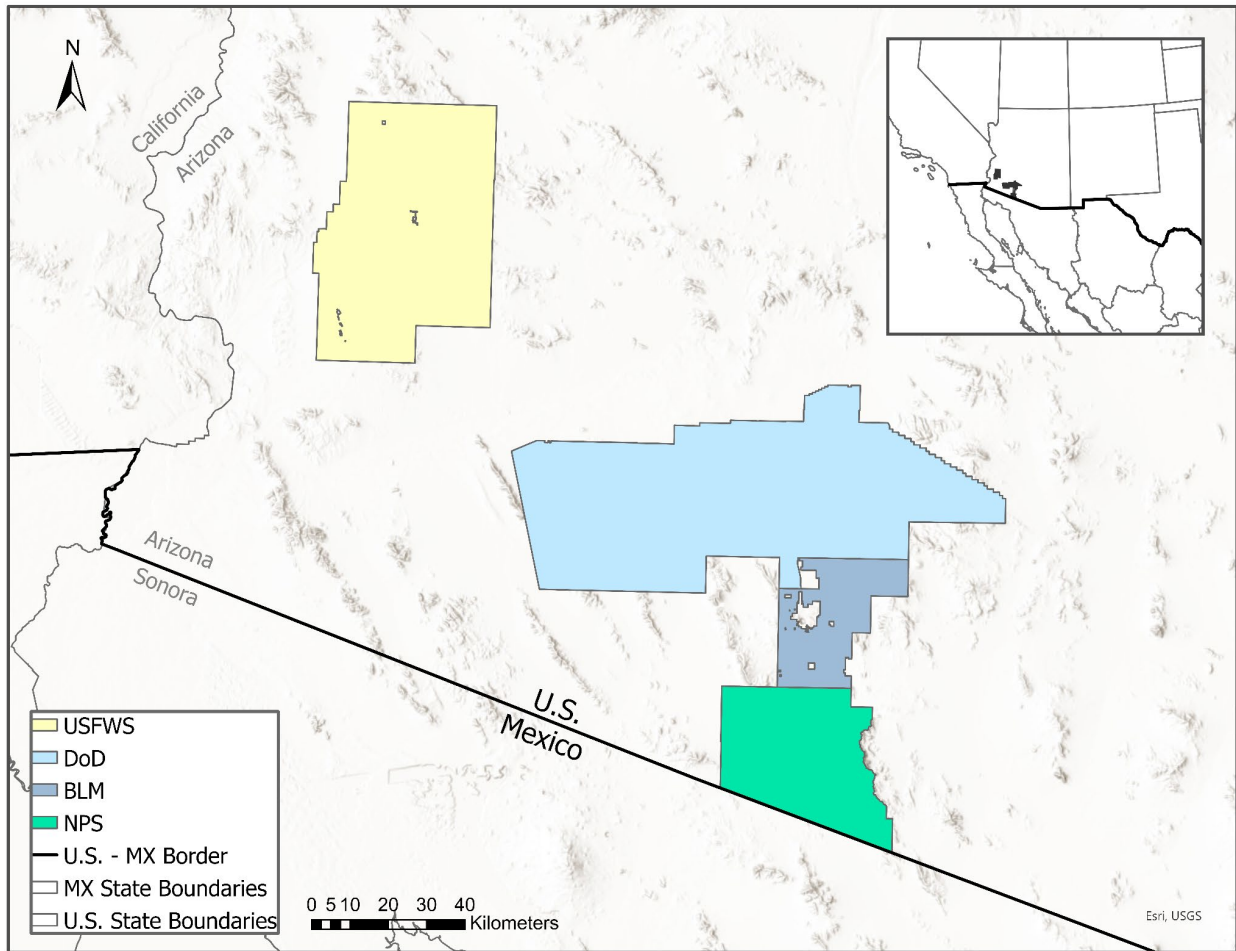
Figure 1. Map of federally managed areas with monitored water sites that contributed to this study
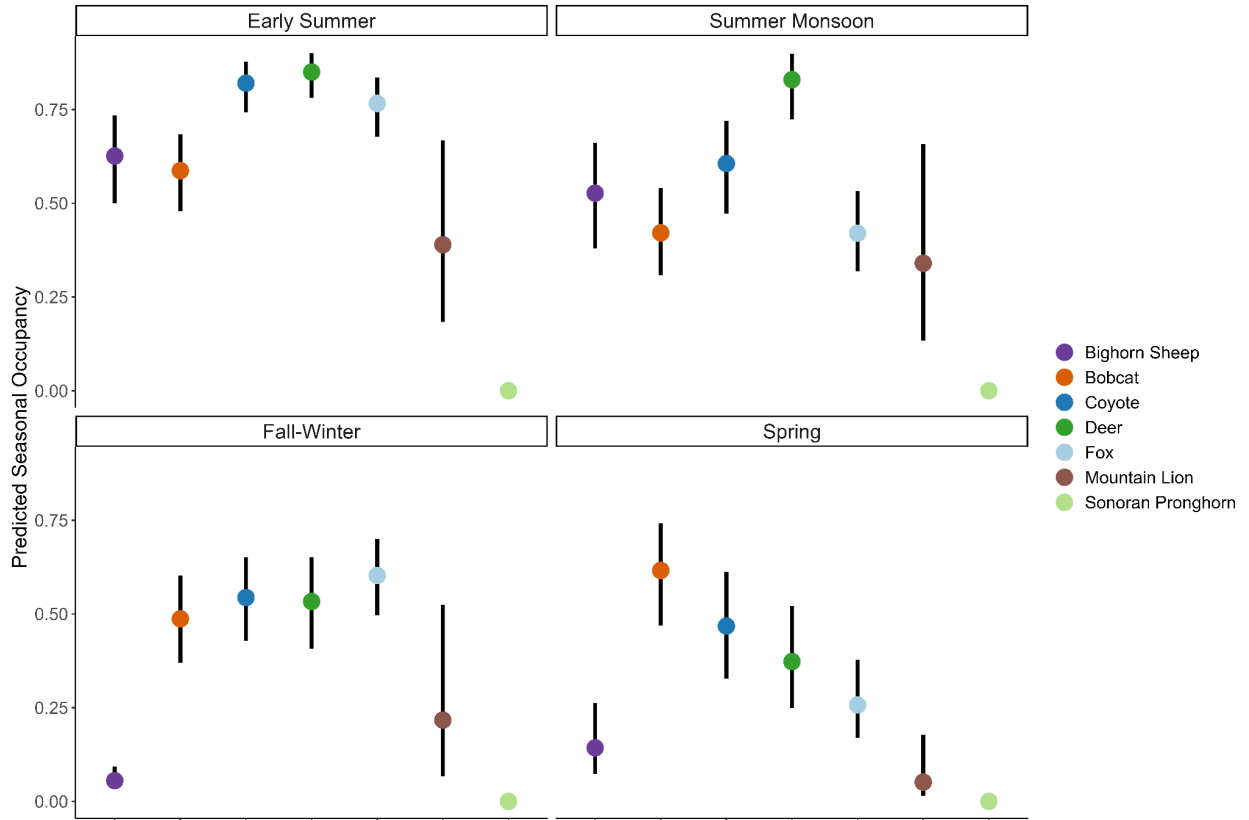
Figure 2. Predicted seasonal occupancy at managed water sites for seven focal taxa, where occupancy is allowed to vary by season, but all other values used to make predictions were held at their respective mean values.
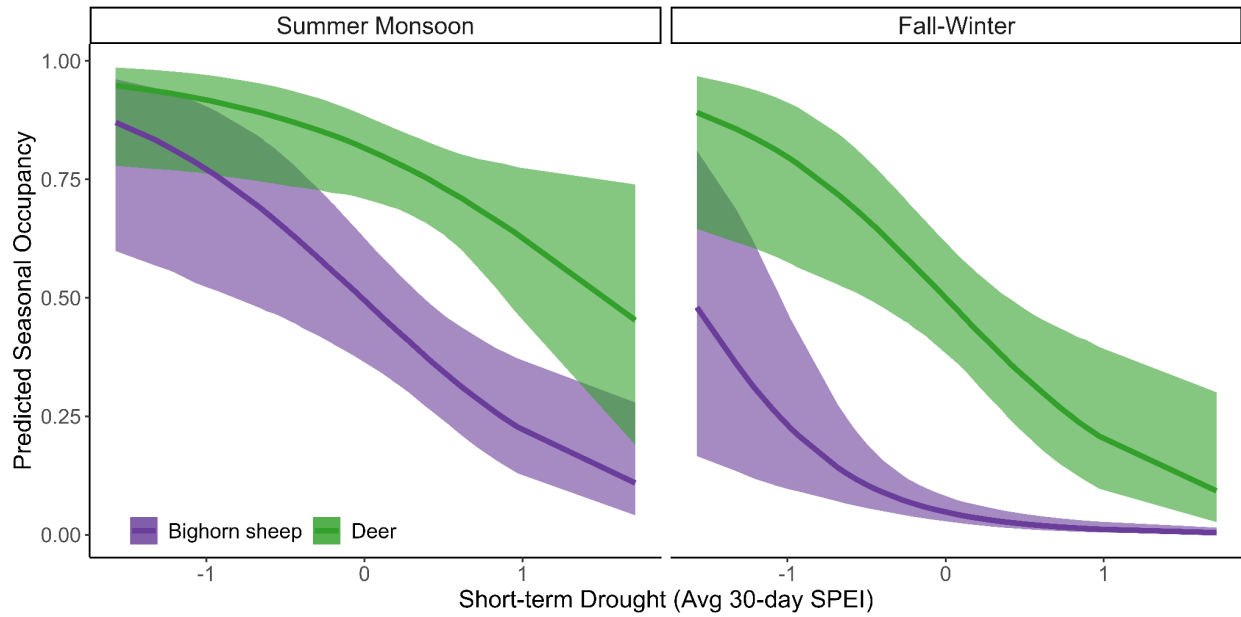
Figure 3. Predictions of seasonal occupancy as a function of short-term drought for desert bighorn sheep and deer. Drought is represented by seasonal mean 30-day SPEI values, where more positive values indicate wetter conditions where precipitation is greater than potential evapotranspiration, and more negative values indicate dry conditions where potential evapotranspiration outpaces precipitation.
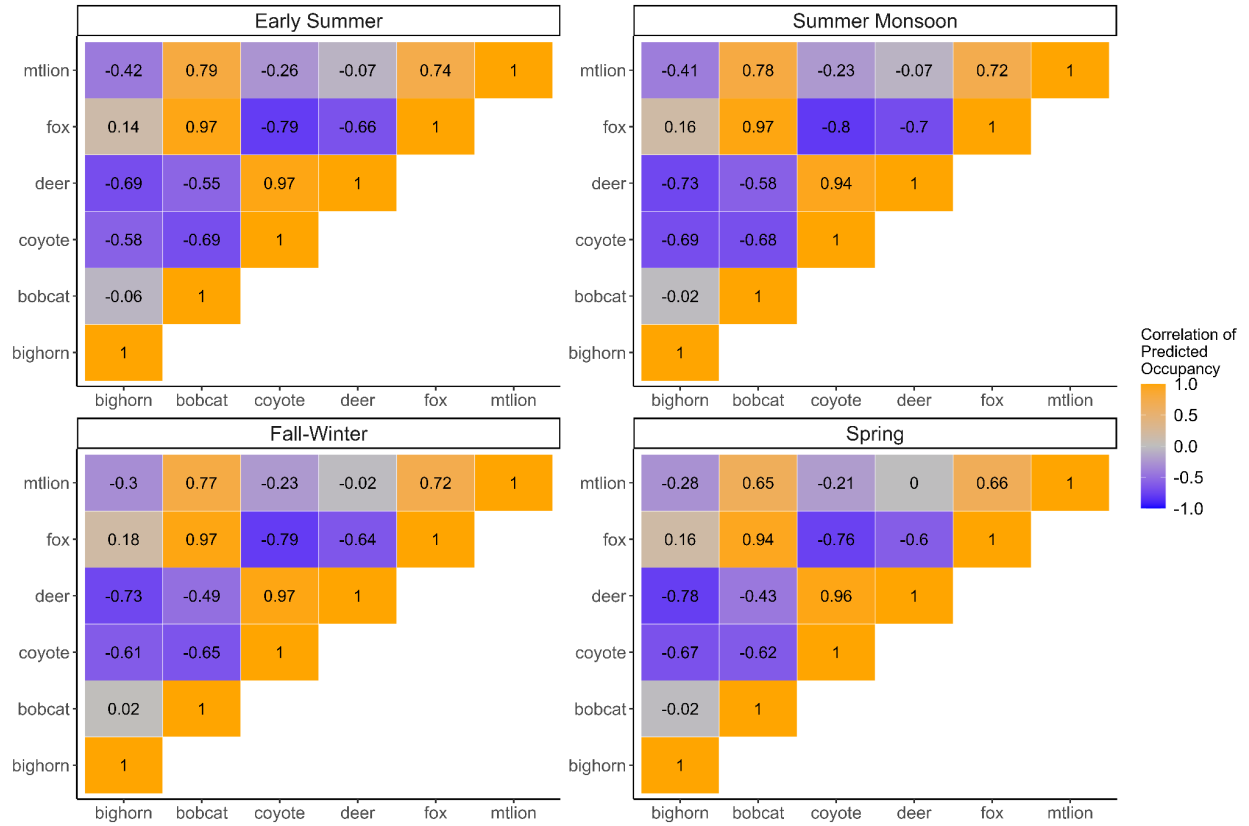
Figure 4 Pair-wise correlation of predicted seasonal occupancy across all managed water sites for six of seven focal taxa.
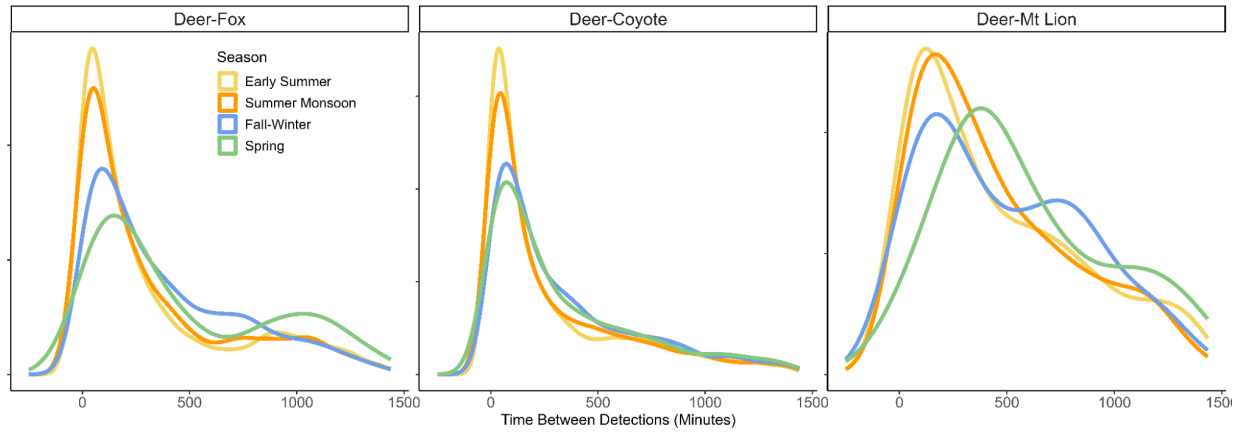
Figure 5. Example distributions of time between detections for early summer, summer monsoon, fall-winter, and spring seasons for low antagonism (deer-fox) and high antagonism (deer-coyote, deer-mountain lion) taxa pairs.
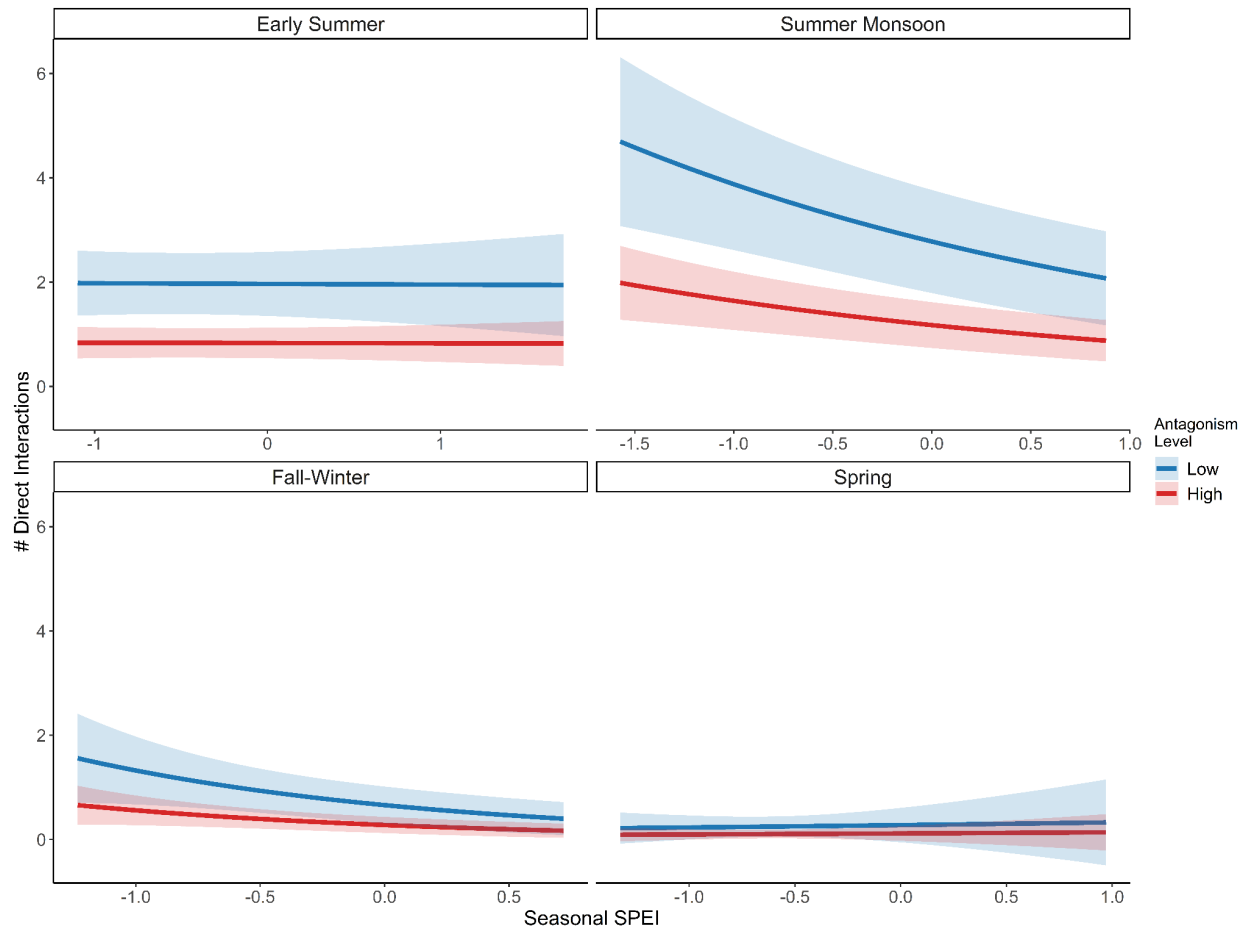
Figure 6. Influence of drought (seasonal mean 30-day SPEI) and antagonism level on the number of direct interactions predicted seasonally across all taxa pairs. Abundance was held at a single value representative of higher recorded taxa pair relative abundance for visualization to demonstrate that higher abundances are requisite for a meaningful increase in interactions. More positive SPEI values indicate wetter conditions where precipitation is greater than potential evapotranspiration, and more negative values indicate dry conditions where potential evapotranspiration outpaces precipitation.

Supplemental Material

S1 Supplemental Material for Seasonal Occurrence of Focal Taxa

S1.1 Spatial Occupancy Covariates

To define spatial characteristics at the scale of each managed water site, we measured greenness, habitat complexity, solar radiation index (SRI), and terrain ruggedness within a 1 km buffer of each monitored location. Greenness was quantified at the seasonal scale for each site using the Soil Adjusted Vegetation Index (SAVI), which is calculated using the equation for the Normalized Difference Vegetation Index (NDVI) with a correction factor (L) for soil brightness, (NIR – Red) * (1 + L) / (NIR + Red + L), and is therefore useful for assessing greenness in environments with high amounts of bare ground and sparse vegetation (Huete 1988, Bunting et al. 2019). We calculated SAVI using a correction factor of 0.5 with the NIR and Red bands from a Moderate Resolution Imaging Spectroradiometer time-series image collection (MODIS/MOD13Q1, 16-day temporal resolution, 250 m^2 spatial resolution), taking the mean of all images available within a monitoring season. We defined habitat complexity by calculating image entropy, a measure of pixel randomness used to describe image texture, on a composite SAVI image (Sentinel-2, 10-m spatial resolution) from 2017 to 2023 (Farwell et al. 2021, Smith et al. 2022). We used the glcmtexture() function in Google Earth Engine, defining a 500 m moving window for the entropy calculation across the study area and then taking the mean entropy within a 1 km buffer of the managed water site. Terrain ruggedness and SRI were quantified using a 30-m resolution digital elevation model (Farr et al. 2007). We defined terrain ruggedness as the standard deviation of elevation within the 1 km buffer of each water location. We used an established calculation to define SRI that includes information about slope, aspect, and latitude to describe the expected amount of solar radiation striking a surface at solar noon (Keating et al. 2007, Terry et al. 2021).

Table S1.1. Occupancy model selection results for all focal taxa. All models included an autologistic term in the occupancy component, where seasonal occupancy probability varies according to occupancy in the previous season.

Taxa	Detection	Occupancy	npar	AIC	ΔAIC
Bighorn	~season + effort	~season + drought + season*drought + spatialcovs	18	8605.24	0
	~season + effort	~1	7	8857.82	252.58
Bobcat	~season + effort	~season + drought + season*drought + spatialcovs	18	9832.7	0
	~season + effort	~1	7	9848.56	15.86
Coyote	~season + effort	~season + drought + season*drought + spatialcovs	18	14079.26	0
	~season + effort	~1	7	14163.77	84.51
Deer	~season + effort	~season + drought + season*drought + spatialcovs	18	14810.69	0
	~season + effort	~1	7	14891.93	81.25
Fox	~season + effort	~season + drought + season*drought + spatialcovs	18	11191.42	0
	~season + effort	~1	7	11228.09	36.67
Mt Lion	~season + effort	~season + drought + season*drought + spatialcovs	18	3539.16	0
	~season + effort	~1	7	3572.42	33.26
Pronghorn	~season + effort	~season + drought + season*drought + spatialcovs	18	310.21	0
	~season + effort	~1	7	328.53	18.32

Tables S1.2 - S1.8. Coefficient estimates with associated standard errors and 95% confidence intervals for autologistic occupancy models.

Taxa	Submodel	Parameter	Estimate	SE	Lower 95% CI	Upper 95% CI	p-value
Desert bighorn sheep	*Occupancy*	Intercept	-1.08	0.14	-1.36	-0.80	0.00
		Summer monsoon	-0.26	0.23	-0.72	0.20	0.26
		Fall-winter	-2.21	0.26	-2.72	-1.69	0.00
		Spring	-1.47	0.31	-2.08	-0.85	0.00
		Drought	0.05	0.11	-0.16	0.27	0.63
		Ruggedness	0.90	0.14	0.62	1.18	0.00
		Habitat complexity	-0.42	0.08	-0.58	-0.26	0.00
		Solar radiation index	-0.32	0.08	-0.48	-0.16	0.00
		Greenness	-0.53	0.11	-0.74	-0.33	0.00
		Summer monsoon:Drought	-0.59	0.20	-0.98	-0.19	0.00
		Fall-winter:Drought	-0.89	0.24	-1.35	-0.43	0.00
		Spring:Drought	-0.20	0.26	-0.71	0.31	0.44
		Autoregressive term	2.81	0.22	2.38	3.24	0.00
	Detection	Intercept	0.39	0.06	0.28	0.50	0.00
		Summer monsoon	-0.84	0.07	-0.98	-0.70	0.00
		Fall-winter	-1.38	0.08	-1.55	-1.21	0.00
		Spring	-1.55	0.11	-1.76	-1.35	0.00
		Seasonal effort	0.00	0.00	0.00	0.00	0.07

Taxa	Submodel	Parameter	Estimate	SE	Lower 95% CI	Upper 95% CI	p-value
Bobcat	*Occupancy*	Intercept	-1.01	0.16	-1.33	-0.68	0.00
		Summer monsoon	-0.43	0.22	-0.87	0.00	0.05
		Fall-winter	-0.26	0.21	-0.68	0.16	0.22
		Spring	0.07	0.26	-0.44	0.59	0.78
		Drought	-0.07	0.11	-0.29	0.15	0.53
		Ruggedness	0.16	0.12	-0.07	0.39	0.18
		Habitat complexity	0.15	0.07	0.01	0.29	0.04
		Solar radiation index	0.06	0.08	-0.09	0.20	0.46
		Greenness	0.22	0.08	0.06	0.38	0.01
		Summer monsoon:Drought	-0.07	0.18	-0.43	0.30	0.72
		Fall-winter:Drought	-0.32	0.21	-0.72	0.08	0.12
		Spring:Drought	-0.14	0.22	-0.57	0.29	0.52
		Autoregressive term	2.47	0.16	2.15	2.79	0.00
	Detection	Intercept	-0.20	0.05	-0.30	-0.10	0.00
		Summer monsoon	-1.21	0.08	-1.36	-1.06	0.00
		Fall-winter	-1.25	0.08	-1.41	-1.09	0.00
		Spring	-0.99	0.08	-1.15	-0.83	0.00
		Seasonal effort	0.00	0.00	0.00	0.00	0.03

Taxa	Submodel	Parameter	Estimate	SE	Lower 95% CI	Upper 95% CI	p-value
Coyote	*Occupancy*	Intercept	-0.42	0.16	-0.73	-0.12	0.01
		Summer monsoon	-0.70	0.23	-1.15	-0.24	0.00
		Fall-winter	-0.86	0.22	-1.28	-0.44	0.00
		Spring	-1.04	0.26	-1.56	-0.53	0.00
		Drought	-0.08	0.12	-0.32	0.16	0.52
		Ruggedness	-0.74	0.13	-0.99	-0.49	0.00
		Habitat complexity	0.11	0.07	-0.04	0.25	0.15
		Solar radiation index	-0.02	0.08	-0.16	0.13	0.84
		Greenness	-0.06	0.08	-0.23	0.10	0.47
		Summer monsoon:Drought	-0.26	0.20	-0.65	0.13	0.20
		Fall-winter:Drought	-0.23	0.21	-0.65	0.18	0.27
		Spring:Drought	-0.25	0.23	-0.70	0.19	0.26
		Autoregressive term	2.78	0.16	2.46	3.10	0.00
	Detection	Intercept	0.57	0.05	0.48	0.67	0.00
		Summer monsoon	-1.29	0.06	-1.41	-1.17	0.00
		Fall-winter	-0.87	0.06	-0.99	-0.75	0.00
		Spring	-0.83	0.07	-0.96	-0.69	0.00
		Seasonal effort	0.00	0.00	0.00	0.00	0.00

Taxa	Submodel	Parameter	Estimate	SE	Lower 95% CI	Upper 95% CI	p-value
Deer	*Occupancy*	Intercept	-0.40	0.15	-0.71	-0.10	0.01
		Summer monsoon	-0.10	0.25	-0.59	0.39	0.68
		Fall-winter	-1.01	0.22	-1.45	-0.57	0.00
		Spring	-1.41	0.26	-1.93	-0.89	0.00
		Drought	0.01	0.12	-0.22	0.25	0.91
		Ruggedness	-0.60	0.12	-0.83	-0.36	0.00
		Habitat complexity	0.10	0.08	-0.05	0.25	0.21
		Solar radiation index	0.02	0.08	-0.13	0.17	0.79
		Greenness	0.09	0.08	-0.07	0.25	0.27
		Summer monsoon:Drought	-0.43	0.22	-0.87	0.01	0.05
		Fall-winter:Drought	-0.60	0.23	-1.04	-0.15	0.01
		Spring:Drought	-0.15	0.22	-0.58	0.28	0.49
		Autoregressive term	2.99	0.17	2.65	3.32	0.00
	Detection	Intercept	1.08	0.05	0.98	1.18	0.00
		Summer monsoon	-0.84	0.06	-0.96	-0.72	0.00
		Fall-winter	-1.07	0.06	-1.19	-0.94	0.00
		Spring	-1.65	0.07	-1.79	-1.50	0.00
		Seasonal effort	0.00	0.00	0.00	0.00	0.02

Taxa	Submodel	Parameter	Estimate	SE	Lower 95% CI	Upper 95% CI	p-value
Fox	*Occupancy*	Intercept	-0.48	0.14	-0.75	-0.22	0.00
		Summer monsoon	-0.98	0.21	-1.40	-0.56	0.00
		Fall-winter	-0.51	0.20	-0.89	-0.13	0.01
		Spring	-1.45	0.26	-1.96	-0.95	0.00
		Drought	-0.11	0.11	-0.32	0.10	0.32
		Ruggedness	0.12	0.11	-0.09	0.34	0.26
		Habitat complexity	0.04	0.07	-0.09	0.17	0.57
		Solar radiation index	0.02	0.07	-0.12	0.16	0.79
		Greenness	0.12	0.08	-0.03	0.27	0.10
		Summer monsoon:Drought	-0.15	0.17	-0.49	0.19	0.38
		Fall-winter:Drought	-0.18	0.19	-0.55	0.20	0.35
		Spring:Drought	0.05	0.21	-0.36	0.45	0.82
		Autoregressive term	2.51	0.16	2.19	2.83	0.00
	Detection	Intercept	0.01	0.05	-0.09	0.11	0.88
		Summer monsoon	-0.95	0.07	-1.09	-0.82	0.00
		Fall-winter	-0.78	0.07	-0.92	-0.64	0.00
		Spring	-0.81	0.08	-0.98	-0.65	0.00
		Seasonal effort	0.00	0.00	0.00	0.00	0.66

Taxa	Submodel	Parameter	Estimate	SE	Lower 95% CI	Upper 95% CI	p-value
Mountain lion	Occupancy	Intercept	-2.43	0.34	-3.09	-1.77	0.00
		Summer monsoon	-0.12	0.52	-1.14	0.90	0.82
		Fall-winter	-0.47	0.53	-1.51	0.57	0.37
		Spring	-1.43	0.61	-2.62	-0.24	0.02
		Drought	-0.06	0.20	-0.46	0.34	0.76
		Ruggedness	-0.29	0.16	-0.61	0.03	0.08
		Habitat complexity	0.24	0.11	0.02	0.46	0.03
		Solar radiation index	-0.13	0.11	-0.34	0.08	0.24
		Greenness	0.74	0.14	0.47	1.01	0.00
		Summer monsoon:Drought	0.51	0.38	-0.23	1.24	0.18
		Fall-winter:Drought	0.15	0.43	-0.69	0.99	0.73
		Spring:Drought	-0.22	0.43	-1.05	0.62	0.61
		Autoregressive term	4.36	0.35	3.68	5.04	0.00
	Detection	Intercept	-1.06	0.10	-1.25	-0.87	0.00
		Summer monsoon	-1.16	0.14	-1.43	-0.88	0.00
		Fall-winter	-1.54	0.17	-1.88	-1.20	0.00
		Spring	-1.34	0.21	-1.74	-0.93	0.00
		Seasonal effort	0.00	0.00	0.00	0.00	0.47

Taxa	Submodel	Parameter	Estimate	SE	Lower 95% CI	Upper 95% CI	p-value
Sonoran pronghorn	*Occupancy*	Intercept	-8.93	1.76	-12.39	-5.48	0.00
		Summer monsoon	-0.86	1.27	-3.34	1.63	0.50
		Fall-winter	-0.20	1.20	-2.55	2.15	0.87
		Spring	-0.71	1.40	-3.45	2.03	0.61
		Drought	-0.95	0.73	-2.39	0.49	0.19
		Ruggedness	-4.48	1.74	-7.89	-1.07	0.01
		Habitat complexity	-0.35	0.35	-1.03	0.33	0.32
		Solar radiation index	-0.68	1.22	-3.08	1.72	0.58
		Greenness	-0.80	0.51	-1.80	0.21	0.12
		Summer monsoon:Drought	0.05	0.99	-1.90	1.99	0.96
		Fall-winter:Drought	-0.06	0.93	-1.89	1.76	0.94
		Spring:Drought	1.26	1.39	-1.46	3.99	0.36
		Autoregressive term	5.92	1.62	2.76	9.09	0.00
	Detection	Intercept	0.57	0.38	-0.17	1.32	0.13
		Summer monsoon	-1.39	0.53	-2.43	-0.36	0.01
		Fall-winter	-0.95	0.52	-1.97	0.06	0.07
		Spring	-0.82	0.55	-1.90	0.26	0.14
		Seasonal effort	0.00	0.00	-0.01	0.01	0.47

Figures S1.1 - S1.7 Predicted spatiotemporal occupancy relationships for the seven focal taxa
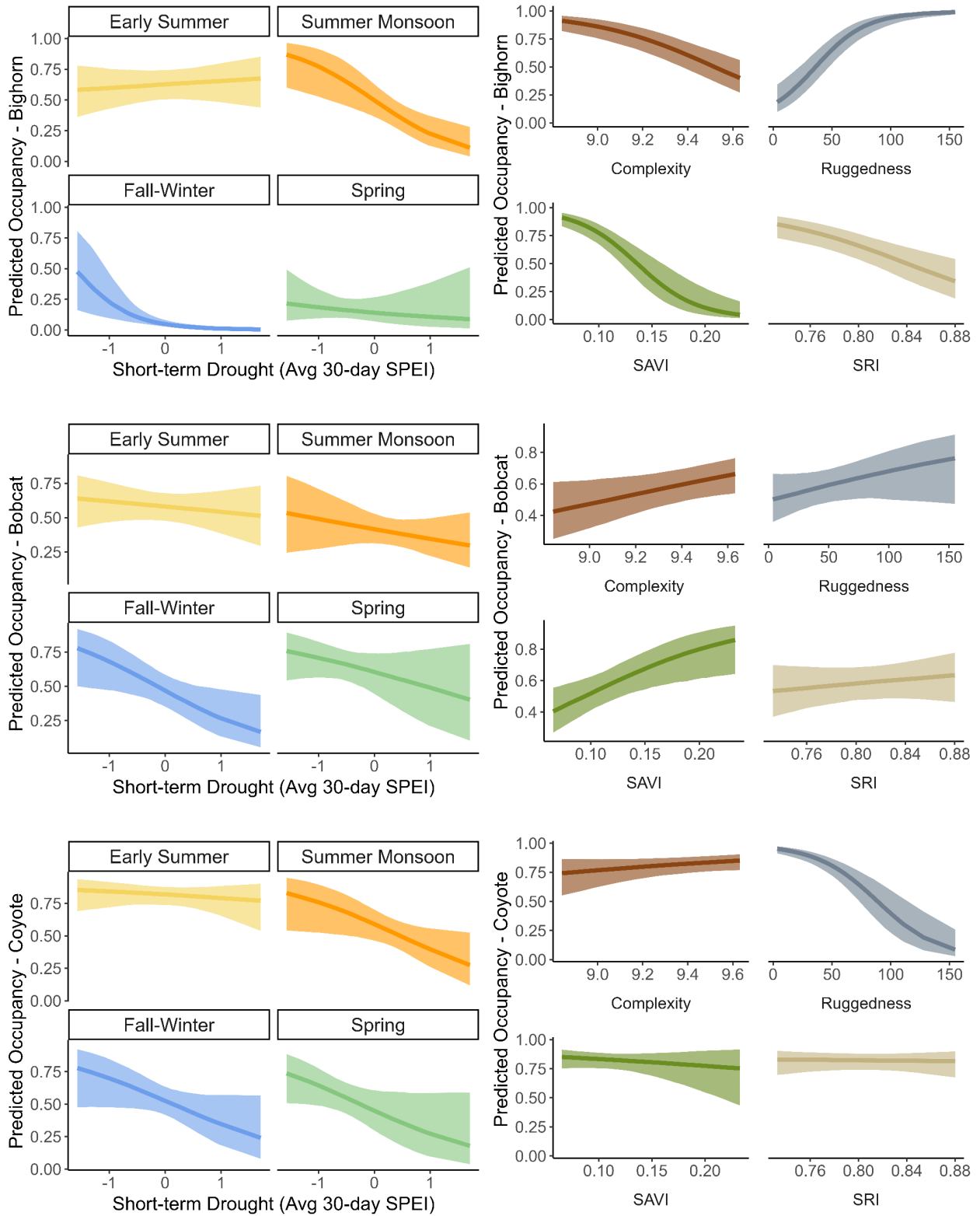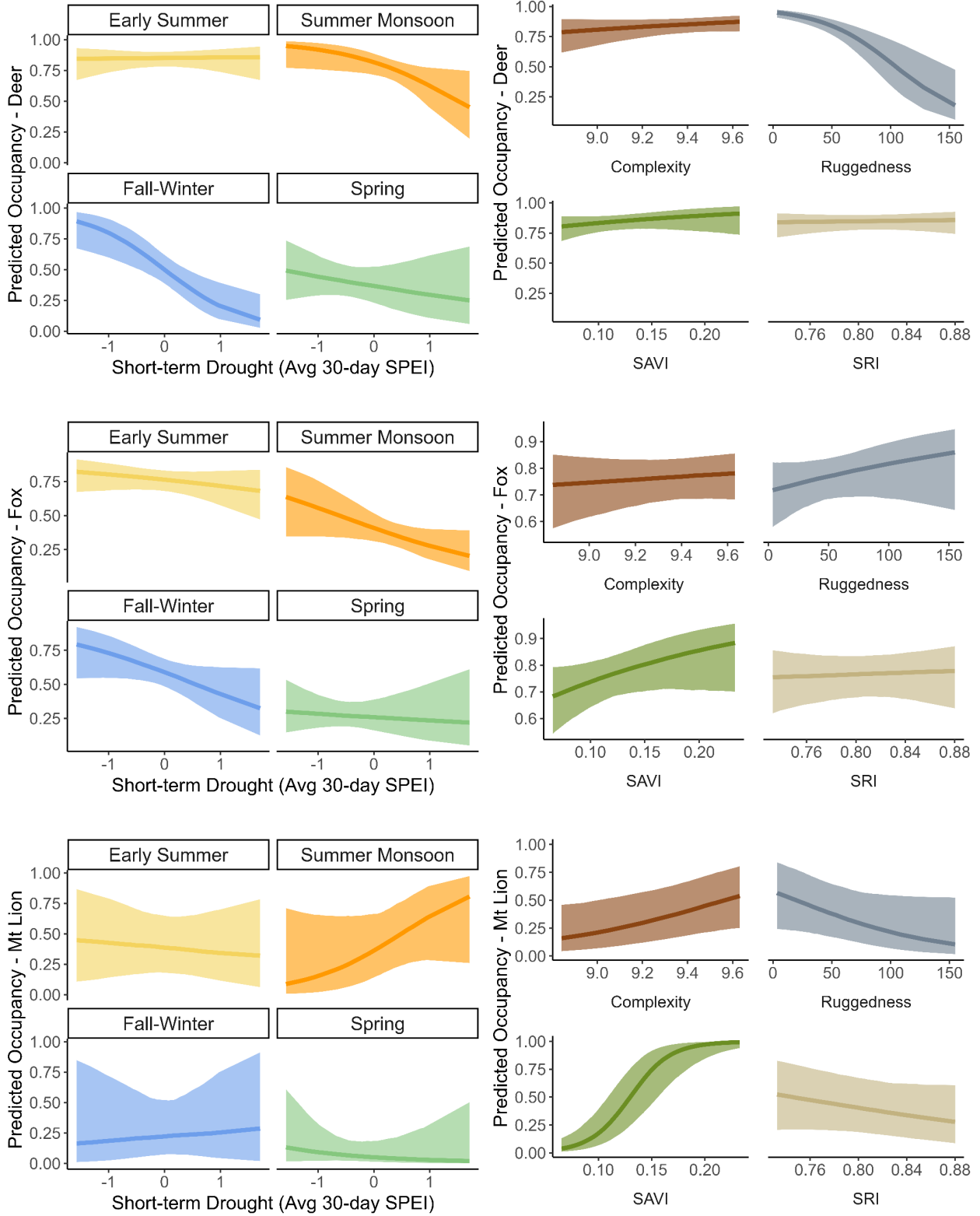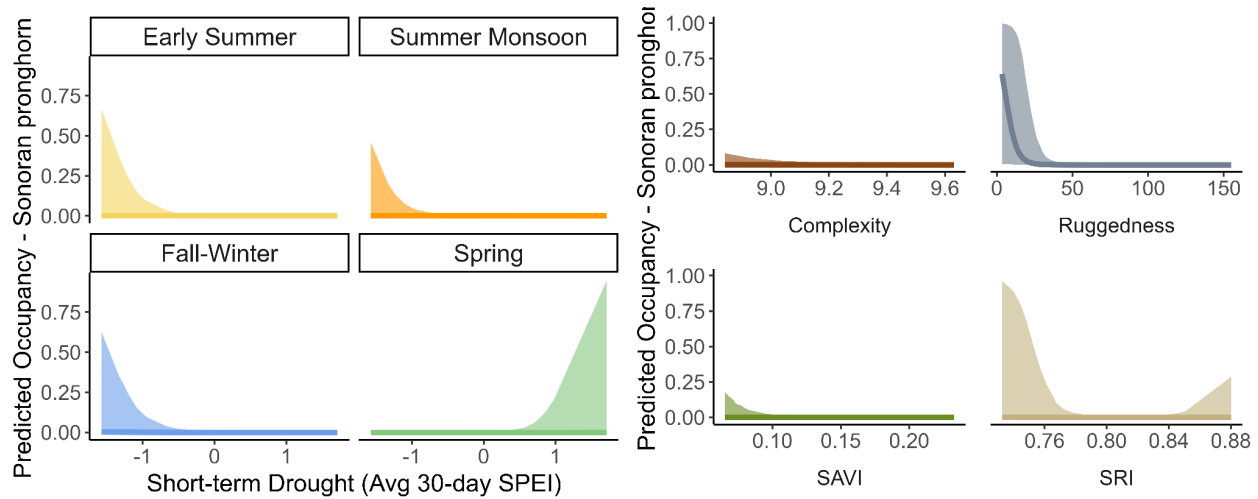
S1.2 Occupancy model descriptions for focal taxa

The detection component for each focal taxa included season as a categorical variable (early summer, summer monsoon, fall-winter, and spring) as well as a count of the total number of monitoring days in a sampling season.

For desert bighorn sheep, occupancy was significantly lower in the fall-winter and spring seasons relative to the early summer season. In the summer monsoon and fall-winter seasons, there was a significant interaction between season and drought, where with wetter conditions occupancy decreased and drier conditions occupancy increased. Occupancy decreased with increasing habitat complexity, increased with increasing ruggedness, decreased with increasing greenness, and decreased with increasing SRI. The estimate for the autoregressive term indicated that occupancy probability increased at sites where desert bighorn sheep occurred in the previous season.

For bobcats, occupancy was significantly lower in the summer monsoon season relative to the early summer season. None of the interactions with drought and season were significant. Occupancy increased with increasing habitat complexity and with increasing greenness. The estimate for the autoregressive term indicated that occupancy probability increased at sites where bobcats occurred in the previous season.

136

For coyotes, occupancy was significantly lower in all other seasons relative to the early summer season. No occupancy-drought relationships were supported. Occupancy probability decreased as ruggedness increased. The estimate for the autoregressive term indicated that occupancy probability increased at sites where coyotes occurred in the previous season.

For deer, occupancy in fall-winter and spring seasons was significantly lower relative to early summer season. In the fall-winter season, there was a significant interaction between season and drought, where with wetter conditions occupancy decreased and drier conditions occupancy increased. The same relationship with drought was marginally significant in the summer monsoon season. Occupancy probability decreased as ruggedness increased. The autoregressive term indicated that occupancy probability increased if deer were detected at a site in the previous season.

For foxes, occupancy was lower in all other seasons (summer monsoon, fall-winter, spring) relative to the early summer season. No relationship with drought was supported, and no spatial relationships were supported. The autoregressive term indicated that occupancy probability increased if foxes were detected at a site in the previous season.

For mountain lions, occupancy in spring was significantly lower relative to the early summer season. No drought relationships were supported. Occupancy probability increased with increasing habitat complexity and with increasing greenness. Occupancy probability increased if mountain lions were detected at a site in the previous season.

For Sonoran pronghorn, no seasonal or drought-related relationships were supported. Occupancy decreased with increasing ruggedness and occupancy probability increased if pronghorn were detected at a site in the previous season.

S2 Supplemental Material for Pairwise Interactions and Interaction Potential

Table S2.1. Summaries of independent direct interactions measured across seasons for 15 taxa pairs (all taxa pairs with Sonoran pronghorn were excluded from direct interaction analyses)

Taxa Pair	Areas Detected (of 4)	Total Sites Detected (of 84)	Independent Direct Interactions			
			Early Summer	*Summer Monsoon*	*Fall-Winter*	*Spring*
Bighorn-Bobcat	1	1	0	1	0	0
Bighorn-Coyote	2	5	11	4	0	1
Bighorn-Deer	2	12	14	67	9	0
Bighorn-Fox	2	5	4	1	0	0
Bighorn-Mt Lion	0	0	0	0	0	0
Bobcat-Coyote	2	7	5	7	1	1
Bobcat-Deer	3	15	20	12	0	0
Bobcat-Fox	2	4	4	1	0	0
Bobcat-Mt Lion	0	0	0	0	0	0
Coyote-Deer	4	29	109	67	22	5
Coyote-Fox	2	7	5	4	1	0
Coyote-Mt Lion	0	0	0	0	0	0
Deer-Fox	3	25	74	63	9	1
Deer-Mt lion	1	2	1	1	0	0
Fox-Mt Lion	0	0	0	0	0	0

Table S2.2 Dunn post-hoc results from Kruskal-Wallis test comparing seasonal distributions of interaction potential measured as the independent time between detections of taxa pairs.

Seasonal Comparison	Z-score	Adjusted p-value
Early Summer - Summer Monsoon	6.57	< 0.0001
Early Summer - Fall-Winter	-19.16	< 0.0001
Early Summer - Spring	-25.24	< 0.0001
Summer Monsoon - Fall-Winter	-23.10	< 0.0001
Summer Monsoon - Spring	-28.17	< 0.0001
Fall-Winter - Spring	-10.94	< 0.0001