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RESEARCH ARTICLE

Movement models and simulation reveal highway impacts and mitigation opportunities for a metapopulation-distributed species

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Abstract

Context When human-made barriers impact wildlife by limiting habitat connectivity, simulation can reveal movements lost to fragmentation, strategies to restore corridor function, and potential benefits of corridor restoration.

Objectives Guided by previous genetic research, we examined desert bighorn sheep movement near two highways that restrict gene flow and modelled their movement and habitat selection behavior. The ultimate goal was to simulate movement without highway barriers as a means to site crossing structures that mitigate fragmentation and to reveal their benefits for habitat reachability.

Methods We fit integrated step selection functions (iSSFs) to GPS data from 9 bighorn populations near highways in California. After comparing iSSF simulations to validation data, we simulated 8200 bighorn-years of movement—200 year-long tracks each for 41 individuals—on a landscape with and without highways. We derived utilization distributions (UD) from simulations to identify probable high-use locations along the highways, compare these locations to previously predicted genetic corridors and roadkill events, and estimate changes in habitat reachability and elevation without these barriers.

Results Simulation UDs correlated well with observed bighorn movements. Barrier-free simulations indicated preferred corridors across highway-blocked valleys, often at the same locations predicted by landscape genetics models (4 of 6 genetic-based corridors matched simulation-based corridors), and where bighorn roadkill events occurred (3 of 3 roadkill events occurred at simulation-predicted corridors). Relative to barrier-present simulations, barrier removal increased accessible habitat for 8 of 9 populations, with increases ranging from 7 to 138% per population. Barrier-free conditions allowed movement to higher elevations in two populations.

Conclusion Animal movement simulation can effectively assess fragmentation impacts and reveal mitigation options when other data sources are scarce. Our simulations confirm previously predicted corridors,

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provide detailed locations for targeted mitigation, and suggest certain corridors pose greater habitat-related benefits.

Keywords Connectivity model · Step selection functions · Movement ecology · Habitat fragmentation effects · Desert bighorn sheep · *Ovis canadensis nelsoni*

Introduction

Human development limits habitat access and wildlife movement worldwide, and can compromise evolved behaviors such as migration, resource tracking, and dispersal (Harris et al. 2009; Tucker et al. 2018). To protect and restore habitat connectivity at various scales, we must first identify areas that wildlife either currently use or formerly used to move between populations or habitat patches. Further examining the ecological role of these movements can assist in prioritizing which connections to protect or restore. Encouragingly, mitigation measures like wildlife crossings can improve corridor function across barriers when carefully located (Sawaya et al. 2014; Seidler et al. 2018).

Choosing mitigation sites can be straightforward with GPS collar data if the corridor is semi-functional (Sawyer et al. 2009), but may require additional data when barriers greatly restrict movement. Connectivity models derived from landscape genetics and habitat characteristics can predict the location of impacted corridors (Balkenhol et al. 2016), but the now-rare use of these corridors can limit confidence in the predicted locations. Connectivity restoration can be costly, so managers may benefit from examining multiple models and datasets for consistency among predicted corridors before taking action (Zeller et al. 2018). Inconsistency among models may reveal movements that facilitate different ecological functions. Predictions based on genetic data can highlight corridors important to effective dispersal, gene flow or colonization, but may be less effective at characterizing local movement within home ranges (Mateo-Sánchez et al. 2015). These movements may be of equal importance to conservation efforts and restoration, but require models built from data collected at finer scales and timeframes that reflect recent conditions (Epps and Keyghobadi 2015).

Animal movement data can be incorporated into connectivity models in various ways, with approaches evolving along with available wildlife movement models. Step selection functions (SSF) represent movement data as a series of discrete steps. The steps taken are compared to a sample of possible steps to infer whether an animal preferentially selects or avoids certain habitat features relative to their availability on the reachable landscape (Thurfjell et al. 2014). SSF-predictions can be converted to resistance layers for use in Circuitscape or least-cost path (LCP) modelling (Zeller et al. 2012), but SSFs can also be used to directly simulate movement. Movement simulation can predict habitat use with greater accuracy than the resistance layer approach, particularly in complex landscapes (Signer et al. 2017). Predictive accuracy may also depend on the type of movements used to fit SSFs, and some argue that directed and fast movements should be targeted for connectivity modelling (Abrahms et al. 2016). Alternatively, integrated Step Selection Functions (iSSF) offer a means to incorporate diverse movement behavior into the model itself instead of filtering data to certain movement types prior to model fitting. iSSFs combine a traditional SSF with a movement kernel that describes an animal's characteristic speed and directional persistence (Avgar et al. 2016). When covariates interact with the parameters of the movement kernel, the function allows for movement behavior that changes with local conditions. Like SSFs, iSSFs can be used to simulate movement under current or novel conditions in order to derive connectivity-related metrics (Hooker et al. 2021; Whittington et al. 2022). Both approaches may be especially valuable to site wildlife crossing structures, which are most efficient when placed near highly plausible travel routes.

We apply iSSFs and simulation to a desert bighorn sheep (*Ovis canadensis nelsoni*) metapopulation currently impacted by habitat fragmentation in Southern California. Although desert bighorn populations are naturally fragmented to some degree by open valleys and bajadas, bighorn readily move across low-lying areas to form a well-connected metapopulation (Bleich et al. 1990; Epps et al. 2007, 2018; Creech et al. 2014). Inter-population connectivity allows small populations to persist throughout desert regions through gene flow, demographic rescue, and local recolonization events (Bleich et al. 1990; Epps et al. 2010). Major highways and other human developments have limited many of these movements so that managers now recognize distinct desert bighorn metapopulation units, primarily bounded by highways. The impact on historic movements has reduced the overall connectivity of desert bighorn populations (Epps et al. 2007; Creech et al. 2014), increased loss of genetic diversity (Epps et al. 2005), and become a major focus for desert bighorn management by the California Department of Fish and Wildlife (CDFW) and U.S. National Park Service (NPS).

In addition to severing connectivity, human developments fragment habitat that likely comprised historic desert bighorn home ranges. Many populations make use of multiple habitat patches (Dekelaita et al. In review), which can facilitate the use of interspersed resources (Bleich et al. 1990). Diverse patch use can also increase the duration when high-quality resources are available (Armstrong et al. 2016)—a potentially important strategy in resource-limited environments. Elevation gradients in particular shape the timing and productivity of Mojave Desert vegetation, and as a result, high-elevation patches can act as refugia for desert bighorn (Epps et al. 2004; Creech et al. 2020). Low-elevation patches tend to have spatially and temporally heterogeneous resources that are increasingly affected by human activities and development (Parker et al. 2021). Fragmentation likely limits desert bighorn access to varied habitat and resources that were once accessible, shifting home ranges away from their optimal and historic patterns.

Bighorn still sporadically attempt to cross major highways despite the risks (Dekelaita et al. In Review), suggesting a continued drive to access fragmented habitat. With increasing funds devoted to wildlife connectivity comes the opportunity to improve bighorn movement across roadways with wildlife crossing structures. Although genetic analyses identified the population connections impacted by highways in California (Epps et al. 2007; Creech et al. 2014), models that reflect current movement behavior may better inform crossing placement and design. Simulating movement from these models might also quantify mitigation-related gains in habitat access and available resources.

Our study goals were to: (1) develop and validate iSSFs that capture key aspects of desert bighorn movement behavior, including the highway barrier effect; (2) use these models to simulate movement over a hypothetical barrier-free landscape to compare to simulations under current conditions; (3) identify likely locations for movement across the valleys where highways currently exist; and (4) quantify the gains in habitat reachability that barrier mitigation might facilitate, both in terms of area and elevation profile. This process demonstrates how a novel movement model can help locate and prioritize mitigation efforts in a barrier-impacted landscape, and offer valuable predictions that complement landscape genetics models.

Materials and methods

Study area

The study area spans lands managed by the NPS, U.S. Bureau of Land Management, and U.S. Department of Defense in San Bernardino County, California, USA. This region of the Mojave Desert supports a network of spatially distinct desert bighorn populations throughout rugged mountains separated by low creosote scrub (Bleich et al. 1990; Creech et al. 2014, 2020). Multiple mountain ranges on either side of interstate highways 15 (I-15) and 40 (I-40) are recognized habitat for desert bighorn, though not all ranges currently support reproducing populations. I-15 intersects the main routes of access to these vacant habitats from adjacent occupied areas, while I-40 intersects habitat occupied on both sides by desert bighorn. We focused on 9 desert bighorn-occupied and 3 bighorn-unoccupied mountain ranges adjacent to I-15 and I-40 on the Mojave National Preserve and adjacent lands (Fig. 1; Table 1).

Movement barriers

Both I-15 and I-40 were constructed in the mid-20th century and are major routes for interstate travel. Occasional underpasses and culverts along the highway allow for water flow and some wildlife movement under the roadway, though none were constructed specifically for wildlife. To our knowledge, desert bighorn have not been documented using these structures. Neither highway appears to act as a complete barrier to movement, but both present increased risks to bighorn that attempt to cross. During GPS-monitoring from 2013 to 2019, one collared ewe out of 52 collared adults near I-15 crossed the highway

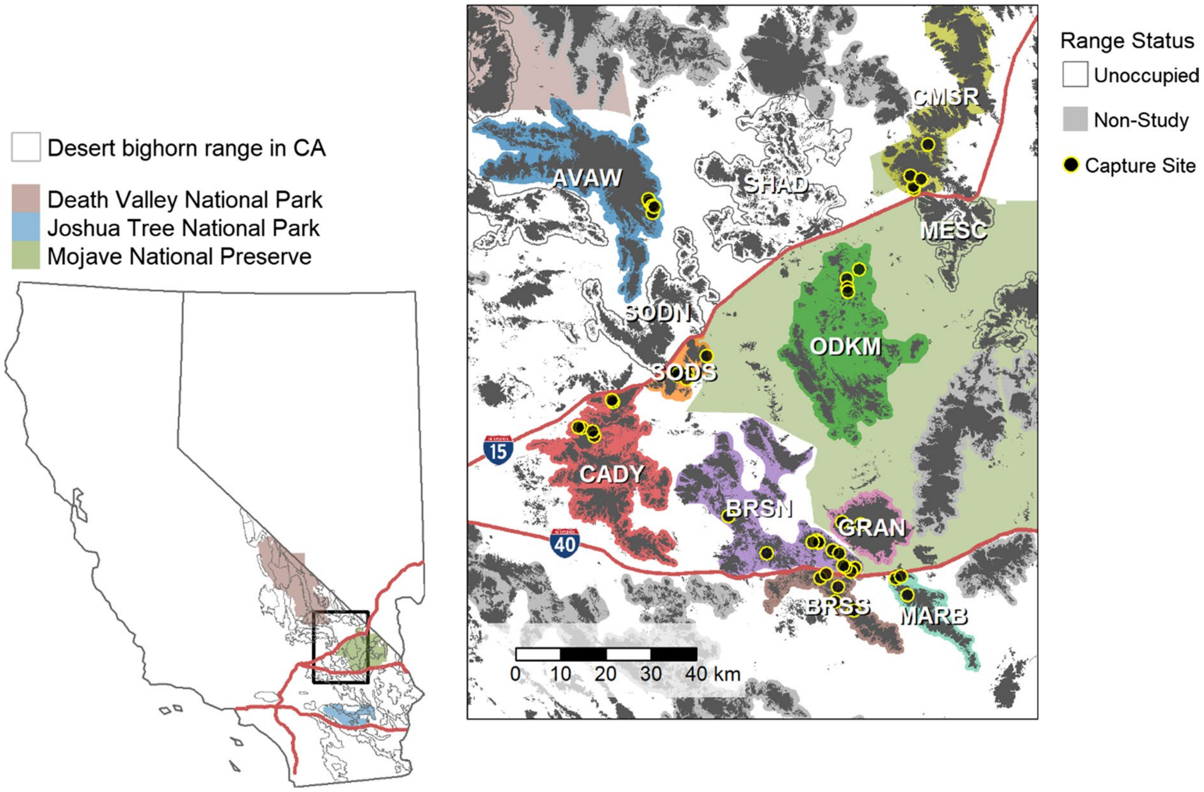

Fig. 1 Map of study area relative to known desert bighorn habitat in Southern California, and major highways (red lines) that intersect the desert bighorn metapopulation. Inset map highlights the study area extent and mountain ranges either occupied (filled polygons) or unoccupied by desert bighorn (unfilled polygons) according to state records. Dark grey polygons show distinct habitat patches (slope > 10°) that make up each range. Labels denote the 12 focal ranges of this study, and colored polygons signify ranges where GPS collars were deployed on adult desert bighorn (points)

Table 1 Summary of range and animal trajectory data included in this analysis after filtering and smoothing GPS error from tracks

Range name	Range code	Max elev (m)	n bighorn	n male	n female	Median track days	Min, max track days
Avawatz	AVAW	1872	4	3	1	832	300, 1156
North Bristol	BRSN	1234	5	3	2	701	372, 1027
South Bristol	BRSS	1062	5	4	1	411	317, 1162
Cady	CADY	1403	5	2	3	775	438, 1160
Clark/Spring	CMSR	2410	4	1	3	1044	956, 1156
Granite	GRAN	2055	5	3	2	601	262, 1149
Marble	MARB	1168	3	3	0	433	290, 1163
Old Dad/Kelso/Marl	ODKM	1505	4	3	1	1159	1028, 1159
South Soda	SODS	738	6	1	5	880	346, 1159
Total			41	23	18		

from the South Soda Mountains to the North Sodas and back again (Dekelaita et al. In review). A young, uncollared ram attempted to cross I-15 at a similar location in 2020, but was struck and killed by a vehicle. At least two collared desert bighorn out of 128 collared adults near I-40 successfully crossed (Epps et al. 2018; Dekelaita et al. In review) between the Marble and Granite Mountains. This was also the site of two bighorn roadkill events in 2019 and 2022. Despite rare examples of continued connectivity, successful movements across these valleys are likely lower than pre-highway conditions (Epps et al. 2018).

Multiple data sources indicate that past desert bighorn populations accessed habitat or interacted with populations across both highways. Genetic data suggest effective dispersal distances for bighorn include up to 16.4 km of travel across flat terrain for males and 10 km for females (Epps et al. 2007; Creech et al. 2014). Additional observed movements between ranges span 6–20 km, including movement over 5–8 km of flat terrain (Bleich et al. 1990). The ranges divided by highways within the study area are well within bighorn dispersal capabilities (Creech et al. 2014). South Soda Mountain bighorn likely accessed the North Sodas historically, which would provide potential interaction with the nearby Avawatz population. Older rams may have used the Shadow Mountains during long forays from neighboring populations (Weaver and Hall 1972). State surveys from the mid-twentieth century describe the Mescal Range and Ivanpah Mountains as transient or seasonal habitat used by Clark Mountain bighorn (Weaver and Mensch 1970). Given the topography along I-40, all study populations should be well-connected (Epps et al. 2007; Creech et al. 2014).

Desert bighorn capture and GPS collar deployment

CDFW coordinated capture of 49 adult desert bighorn (25 male, 24 female) from occupied focal habitat along I-15 and I-40 during 31 October 2018–05 November 2018. All capture procedures were reviewed and approved by the NPS Institutional Animal Care and Use Committee (PWR_MOJA_Epps.Powers_DesertBighornSheep_2016.A3). We fit each bighorn with a Sirtrack Pinnacle Pro GPS collar (Lotek Wireless Inc., Newmarket, Ontario, Canada) programmed to collect a location every hour if outside of a 1-km buffer around I-15 or I-40 and every 30 min if within the 1-km buffer. The dynamic fix schedule was intended to capture greater path detail in the event of a highway crossing. GPS data were downloaded via the Iridium satellite system and Lotek Webservice.

GPS data processing

The resulting GPS dataset was reduced to locations beginning 24 h after a capture event until the day before the estimated mortality date (or collar failure), or to the study end date (31 October 2021). We then removed individuals lacking data in all 4 seasons of the year ($n = 41$ remaining, 23 male, 18 female) and assigned each animal a range code based on where they spent a majority of their time during the study. Seasons were defined as fall (October–November), winter (December–March), spring (April–June), and summer (July–September) based on a climograph for Mojave National Preserve (Mckee et al. 2015). We filtered and smoothed each trajectory using a GPS error model and time-series kriging to reduce the influence of location error on our analysis (Online Resource 1). All smoothed trajectories retained data gaps due to missing or filtered GPS locations and total duration varied with the fate of the animal and collar (Table 1). After accounting for error, smoothed movement tracks did not cross I-15 or I-40 at any point during the study.

We then converted smoothed trajectories to steps of 1-h intervals and calculated step lengths and turn angles using the R package amt (Signer et al. 2019). We filtered out steps that occurred prior to an identified change point in step lengths relative to sun angle associated with a daily increase in movement (Online Resource 2). Finally, we divided steps into a training dataset (steps from November 2018 to October 2020) and a validation dataset (steps from November 2020 to October 2021) withheld from model fitting in order to assess predictive performance. We decided to withhold a unique period of data from the same animals as opposed to withholding entire animals from model training due the small number of unique animals per range. In doing so, we retain more variation in animal behavior in our fitted models to better capture population-level trends.

Integrated step selection analysis

We chose iSSFs as opposed to SSFs to incorporate variable movement behavior expected for desert bighorn based on past research and observations (for further iSSF descriptions see Avgar et al. 2016; Fieberg et al. 2021). An iSSF can include covariates for conditions at the start of a step that interact with the step length (*sl*), natural log of step length (*log_sl*), or cosine of turn angle (*cos_ta*), to estimate a selection-free movement kernel. The estimated coefficients for each covariate adjust the distributions for step lengths and turn angles, and thereby reflect how the covariate influences an animal's movement speed or directional persistence. Covariates associated with the start point of a step were included either to modify the movement kernel, or to modify habitat selection strength through an interaction with an end-point covariate. Covariates extracted from the end-point of a step were included in a step selection function; the associated coefficients indicate preference or avoidance of a habitat feature and determine the probability an animal moves to a location given its habitat characteristics and current location (Avgar et al. 2017). We describe the spatial and temporal covariates below and denote a covariate as associated with conditions at the start or end of a step with a "start" or "end" subscript.

Each step within a track was considered a "used" movement and was grouped with 100 random steps from the same start point to represent "available" movements. We created random steps by sampling a step length and turn angle from gamma and Von Mises distributions estimated from each individual's observed step lengths and turn angles respectively (Avgar et al. 2016). Sets of used and available steps were given a unique step id to define the strata in iSSFs fit via conditional logistic regression where used steps were given a response variable = 1, and available steps = 0 (Signer et al. 2019). We fit three models of increasing complexity, starting with a base model of topography-related covariates and expected seasonal changes in movement (terrain model). To the terrain model, we added variables related to water-use (water model) and forage availability (forage model) as described in further detail below. Covariates were assigned to each used and available step based on location and time. We then fit all three iSSFs to step data from each desert bighorn to capture variable selection patterns and diverse movement behavior.

After fitting each model to all individuals, we simulated movements for animals that had validation data in order to assess predictive performance (described below). Our study goals were to predict suitable locations for wildlife crossing structures and identify habitat across the highway that desert bighorn might regularly access. We therefore assessed model performance using simulation results averaged across individuals within each range and averaged across all individuals. The derived products focus on locations likely used by the most animals, and avoid giving too much weight to movements from a single animal or simulation. We compared the simulation-produced patterns to the validation data to determine which model best predicted observed habitat use. The selected model was then used to simulate another set of movements under the current and novel situations of highway presence and absence. We identified crossing locations and barrier impacts to habitat use using these simulation results. All data processing, model fitting, and simulations were conducted in program R (R Core Team 2020).

Terrain model covariates

The terrain model included several variables either previously identified as important habitat features for desert bighorn, or selected based on previously observed bighorn behavior in this region (Table 2). We included slope ($\text{slope}_{\text{end}}$), distance to ridges ($\text{dridge}_{\text{end}}$), and northness ($\text{northness}_{\text{end}}$) for end-point selection, which we derived from a 30 × 30 m resolution digital elevation model (accessed at: http://earthexplorer.usgs.gov/; U.S. Geological Survey 2018). We included a quadratic term for slope (degrees) to allow for selection of intermediate values (Hoglander et al. 2015; Gedir et al. 2020). We derived northness by transforming aspect so values ranged from − 1 [south] to 1 [north]: $\cos((\text{aspect} \times \pi)/180)$. We allowed selection for northness to vary by season as bighorn may switch their preference between south- and north-facing slopes (Gedir et al. 2020). Ridges were identified by first creating a topographic position index (TPI) as the difference between the elevation of a focal cell and the mean elevation of a local 5 × 5 cell neighborhood (Gallant and Wilson 2000). After

Table 2 Set of iSSF models fit and compared via simulation

Model	Covariates
Terrain	cos_ta*(sl + lsl) + season$_{\text{start}}$:(sl + lsl + cos_ta) + slope$_{\text{start}}$:(sl + lsl + cos_ta) + elevdiff$_{\text{end}}$ + elev$_{\text{start}}$:elevdiff$_{\text{end}}$ + dridge$_{\text{end}}$ + slope$_{\text{end}}$ + slope$^{2}_{\text{end}}$ + northness$_{\text{end}}$ + season$_{\text{start}}$:northness$_{\text{end}}$ + patchsize$_{\text{end}}$ + nearhwy$_{\text{start}}$:dhwy$_{\text{end}}$ + dcore$_{\text{end}}$ + season$_{\text{start}}$:dcore$_{\text{end}}$
Water	**terrain** + dwater$_{\text{end}}$ + lastwater$_{\text{start}}$:dwater$_{\text{end}}$ + AI3mo$_{\text{start}}$:dwater$_{\text{end}}$ + lastwater$_{\text{start}}$:AI3mo$_{\text{start}}$:dwater$_{\text{end}}$ + watervisit$_{\text{start}}$:sl
Forage	**terrain** + **water** + ndvi$_{\text{end}}$ + ndvi$^{2}_{\text{end}}$ + ndvi$_{\text{start}}$:(sl + lsl + cos_ta)

The terrain model includes topographic features and movement behaviors expected to influence desert bighorn movement and habitat selection. The water model includes the terrain model plus the water-related covariates shown. The forage model includes the terrain and water covariates, plus forage-related covariates shown. Start and end subscripts denote whether the variable was associated with the start or end-point of a step

visually inspecting TPI values, we selected a cutoff of TPI ≥ 6 to define ridges and calculated the Euclidean distance to the nearest ridge in meters. We expected bighorn to prefer locations close to or on ridgetops, which would be indicated by a negative coefficient on dridge$_{\text{end}}$ (Hoglander et al. 2015; Gedir et al. 2020).

Though elevation is often included in resource selection functions for bighorn (Hoglander et al. 2015; Gedir et al. 2020), in many deserts elevation is correlated with precipitation and forage availability (Epps et al. 2004). We hoped to test the effects of water and forage distribution on movement, and therefore did not include elevation directly. We did however, include the absolute difference in elevation for each step (elevdiff$_{\text{end}}$) as a covariate on end-point selection. We expected desert bighorn would limit elevation change across short distances to move efficiently across the rugged landscape, resulting in a negative coefficient on elevdiff$_{\text{end}}$. We interacted elevdiff$_{\text{end}}$ with starting elevation (elev$_{\text{start}}$) because in low areas with poor visibility and high predation risk, bighorn may seek to move quickly back to safe terrain. In this study area, sloped terrain often occurs in distinct patches that are separated by flat valleys or large, dry washes. To distinguish unique patches of sloped habitat we clustered adjacent grid cells with slope > 10° (Epps et al. 2007). We then simplified patches (Online Resources 2) and created a patch area raster (km^{2}) with non-patch areas = 0 and included the natural log of 1 + patch area as a covariate on end-point selection (patchsize$_{\text{end}}$). Desert bighorn use patches of various size, but generally spend more time in larger patches of contiguous sloped terrain (CDFW unpublished GPS data).

We interacted two covariates with all movement parameters (*sl*, *log_sl*, *cos_ta*): season$_{\text{start}}$ and slope$_{\text{start}}$, using the seasons described previously. Desert bighorn tend to travel faster and more directly when moving over flat terrain and so we expected step lengths and turn angles to differ when moving from a position of low slope compared to high slope (CDFW unpublished GPS data). We also expected that directional movement (straight-line travel) would tend to be faster than more tortuous movements, and so included an interaction between turn angle (*cos_ta*) and step length parameters (*sl*, *lsl*). We expected step lengths and turn angles to vary by season and sex; male and female bighorn exhibit unique seasonal movement behaviors due to breeding and reproduction (Dekelaita et al. In review).

Though desert bighorn use multiple habitat patches, they display home-ranging behavior, and tend to constrain their movement near a core area (Geist 1971; Bleich et al. 1990). We identified the habitat patch with the most locations for each individual and created an individual-specific Euclidean distance to core raster (dcore$_{\text{end}}$), calculated relative to the median location within the most-used habitat patch. We chose the median location because bighorn home ranges in this region are often irregularly shaped along rocky terrain. We allowed the distance to core coefficient to vary seasonally, expecting that males may prefer locations further from their core during breeding (summer and fall), while females may stay closer to their core during lambing and early gestation (spring and summer; Dekelaita et al. In review).

Lastly, we modelled the highway barrier effect with a modified distance to highway ($dhwy_{end}$) covariate. As no observed steps in our dataset crossed the highway, an indicator variable of whether a step crosses the highway could produce an unreliable barrier effect estimate (Beyer et al. 2016). Euclidean distance to a highway unrealistically assumes points of equal distance on either side of the highway present equal risk, although a highway crossing is much riskier than not crossing. To reflect this, we multiplied distance to highway by -1 if the step crossed the highway and applied a negative log transformation to the resulting value; $\mathrm{sign}(x) \times \log(|x| + 1)$ (Whittaker et al. 2005; Online Resources 2). We expected to see a steep threshold effect, where selection for a location rapidly declined at small, positive values of $dhwy_{end}$. We only included this effect if a step began within 2 km of the highway by interacting $dhwy_{end}$ with an indicator variable $nearhwy_{start}$, expecting that bighorn were unlikely to perceive and be influenced by the highway beyond this distance. We only estimated the barrier effect for animals with at least 100 observed steps that began within 2 km of the highway.

Water model covariates

Desert bighorn use variable water resources including natural springs, ephemeral tenajas, and manmade structures (e.g., guzzlers or cattle troughs). Selection strength for water sources can be variable and highly seasonal (Gedir et al. 2020). We expected the importance of water to fluctuate temporally and spatially in response to environmentally induced water stress. Maximum elevation of our bighorn-occupied mountain ranges ranged from 738 to 2410 m (Table 1), with higher elevation ranges experiencing lower temperatures and more annual precipitation. Each range contains a variable number of water sources used by desert bighorn; though the locations of major perennial sources are known, bighorn can also utilize unmapped and unpredictable water. Most precipitation occurs over winter in this region, with occasional, inconsistent late-summer monsoons. Typical peak water stress occurs in late spring to mid-summer when temperatures increase and vegetation dries out, but before late-summer monsoons. Drought conditions can extend earlier and later, particularly in recent years with more intense and long-lasting droughts (Hopkins 2018).

For the water model, we added covariates to the terrain model that reflected the best available data regarding local water availability and aridity-induced variation in water needs. We created range-specific rasters of Euclidean distance to water ($dwater_{end}$) that reflected the minimum distance to any known perennial water source within a minimum convex polygon drawn around all GPS locations from a range. Water source locations were provided by CDFW and the NPS. We assumed that water sources outside a population's typical range would not influence bighorn movement. To account for varying environmental stress on bighorn water dependency, we calculated a site-specific, 3-month moving average Aridity Index ($AI3mo_{start}$) based on Daymet Daily Surface Weather Data (FedData package in R; Thornton et al. 2020; Bocinsky 2020; Detailed methods in Online Resources 2). This index reflected varying water stress across ranges, seasons, and study years due to local precipitation and evapotranspiration rates. We allowed selection for $dwater_{end}$ to vary with aridity conditions, and the time since a water visit by interacting $dwater_{end}$ with $AI3mo_{start}$ and $lastwater_{start}$. The time since a water visit ($lastwater_{start}$) was included as the natural log of 1 + the number of days since an animal's location was within 500 m of a known water source. To deal with the period of unknown water use prior to the first observed location within 500 m of a water source, we drew a random number from a uniform distribution between 1 and 10 for the first step of the track and began the count from this random variable. Across all animals, a median ± median absolute deviation of 3.07% ± 4.32% of steps occurred before the first observed water visit, indicating that a majority of data did not depend on this random variable. The final water-related effect included in the model reflected the risks associated with visiting a water source. We interacted $watervisit_{start}$ with step length (*sl*), expecting that a desert bighorn near a water source (< 500 m) would quickly move away to avoid predators also attracted by water.

Forage model covariates

Vegetation green-up can be patchy and unpredictable in the Mojave Desert, but provides essential nutrition and water to desert bighorn. The Normalized Difference Vegetation Index (NDVI) derived from satellite imagery describes landscape greenness and is often used as a surrogate for forage biomass and quality (Pettorelli et al. 2005; Creech et al. 2016). Previous studies found NDVI values to have small but sometimes significant effects on desert bighorn habitat selection (Hoglander et al. 2015; Gedir et al. 2020). For our forage model, we added temporally variable NDVI covariates ($ndvi_{end}$, $ndvi_{start}$) to the water model to allow bighorn to select locations or adjust their movement in response to current forage conditions (Details can be found in Online Resources 2). We included a quadratic term for $ndvi_{end}$ to allow selection of intermediate levels of greenness, which may indicate actively growing, nutritious forage. High values of NDVI may also indicate dense shrub cover, which bighorn avoid (Devoe et al. 2020; Lula et al. 2020; Robinson et al. 2020). We interacted $ndvi_{start}$ with movement parameters (*sl*, *log_sl*, *cos_ta*), expecting that bighorn might increase movement speed and directional travel when starting in areas of low NDVI. Forage-responsive movement has been observed in other ungulates such as elk (Merrill et al. 2020), and may ensure adequate nutrition in periods or areas of low productivity. All continuous spatial covariates not transformed by other means described above were centered and scaled using their mean and standard deviation.

Model validation and predictive performance

Of the animals used in model fitting, 21 had data within the validation period (10 male, 11 female, November 2020–October 2021). We simulated tracks of equal length to validation data using the same start point and the estimated parameters of each of the three model variations (See simulation details in Online Resources 2). If animals had insufficient near-highway locations, we used the mean barrier coefficient from animals with adequate data. To determine the adequate data amount, we plotted the standard error of the individual barrier coefficient relative to the number of points recorded near the highway, and visually determined when standard errors leveled off (Fig. 2b). We ran 100 simulations for each model (terrain, water, and forage) and individual.

We converted all simulation results into utilization distributions (UD) similar to Signer et al. (2017) to summarize the frequency of habitat use across all simulated movements and compare predictive performance between models. Using approaches developed to assess habitat selection models, we compared UDs to withheld data (Boyce et al. 2002). For each animal and simulation, we calculated the proportion of steps that intersected each 250 m × 250 m raster cell (the largest grid size of our spatial covariates), and averaged cell values across simulations to create

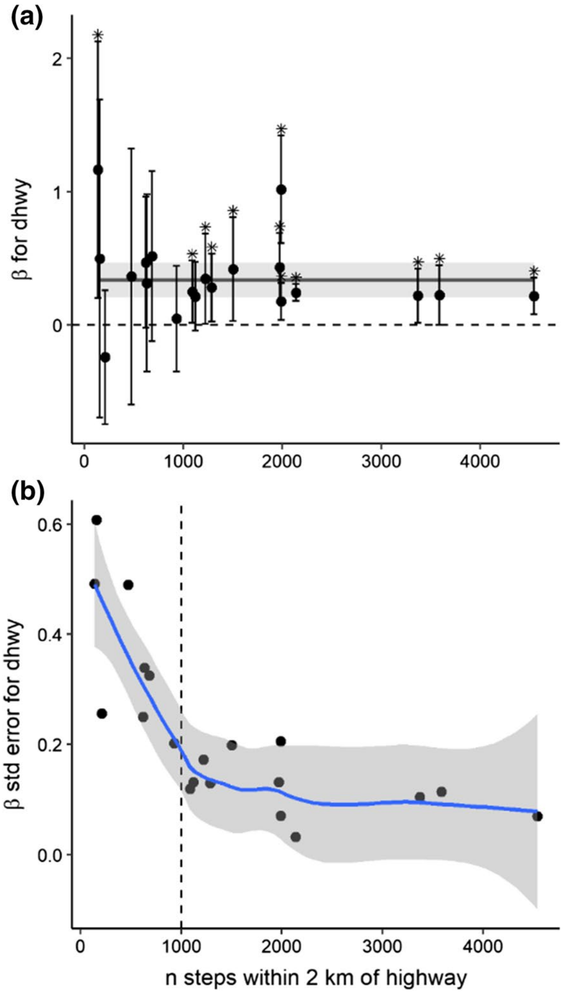

Fig. 2 **a** Coefficient estimates (points) and 95% confidence intervals (bars) for the distance to highway ($dhwy_{end}$) effect from the terrain model relative to the number of steps starting < 2 km from a highway for each desert bighorn. The dotted horizontal line at zero indicates no highway effect, points above 0 indicate preference for locations further from the highway, and significant coefficients are denoted by an asterisk. The effect was fit to 20 animals with at least 100 steps starting < 2 km from a highway. **b** Standard errors of the $dhwy_{end}$ coefficient relative to the number of steps near the highway (points) with a locally weighted smoothing curve (line and shading) plotted to aid in detecting a stabilization point (dotted line) where standard errors level off

an individual simulation UD. We then created range-averaged simulation UDs and a study-averaged simulation UD to describe broad patterns of predicted habitat use for each model. To compare these UDs to our withheld data, we binned cells into quantiles (ranks) based on their values − 10 bins for range-averaged and 20 bins for study-averaged UDs. We then used Spearman rank correlation to assess the relationship between bin rank and the proportion of withheld steps located in each bin. The quantile split did not result in perfectly equal sample sizes across bins, so we divided step proportions by the number of cells within each bin prior to calculating correlation coefficients. We considered the model that resulted in the strongest correlations to have better predictive performance, i.e., better discriminated areas of low and high use by bighorn. To visualize how UD rank scores related to observed bighorn habitat use, we plotted the density of withheld tracks (proportion of tracks per cell) by bin rank for the range- and study-averaged UDs from the selected model. We considered UD ranks with a higher density of withheld data to indicate areas with higher probability of desert bighorn use.

Predicting habitat use without highway barriers

We used the top-performing model to simulate 200 additional tracks for each individual (n = 41) for a full year (Nov 2018–Oct 2019) both with and without the barrier effect (details in Online Resources 2). This resulted in 5252 steps per simulation and 8200 simulated bighorn-years (43,066,400 steps) per barrier condition. We examined plots of the change in total habitat area with each new simulation to determine whether the value had stabilized, suggesting that we ran an adequate number of simulations (Online Resources 3). Using the same methods previously described, we converted all simulated tracks into range-averaged and study-averaged simulation UDs. The raster cells of each UD were assigned rank scores based on the bin cut-off values used in model validation. We plotted all simulation UDs using these rank scores to assist interpretation (Morris et al. 2016).

Identifying suitable locations for crossing structures

To identify locations where wildlife crossing structures would likely improve desert bighorn movement across these highways, we used the study-averaged UD raster derived from movement simulated without the barrier effect. We divided both I-15 and I-40 into 1-km segments and extracted the mean UD rank value within a 100 m buffer of each segment. The 3 highway segments with the highest mean rank were identified at each of 6 locations predicted to be former bighorn movement corridors based on landscape genetics (Creech et al. 2014). Locations with mean ranks > 15 (of 20) were considered highly probable movement corridors based on model validation results (Fig. 3c). We compared the location of these selected highway segments to recent roadkill events recorded by CDFW or partners (n = 3) and the predicted LCPs from genetic models (Creech et al. 2014).

Quantifying potential habitat gains without movement barriers

We used the range-averaged simulation UDs to calculate the amount of habitat (km^2) accessed across the highway during simulations run without a barrier effect and the ratio of this area to the habitat accessed during simulations with the barrier effect. Areas visited rarely during simulation may be highly stochastic and as a result, we saw occasional, small increases in cumulative area metrics even after 200 simulations (Online resource 3). We therefore excluded UD cells with ranks ≤ 3 (of 10) from the area and ratio calculations. We extracted elevation values for the area accessed with and without the barrier effect and compared elevation density plots for each simulation condition and range. Finally, to distinguish between frequent and infrequent predicted habitat use across the highway, we calculated the percent of accessed raster cells with simulation ranks 8–10 (frequent use) and with ranks 4–7 (infrequent use) with cutoffs based on Fig. 3b.

Results

GPS data processing

Detailed results of the error model and kriging process can be found in Online Resources 1. Smoothed tracks spanned a mean area of 175 km^2 (range: 20–664 km^2), as determined by minimum convex polygons drawn around each animal's locations. Processing resulted in a mean of 8160 observed steps per

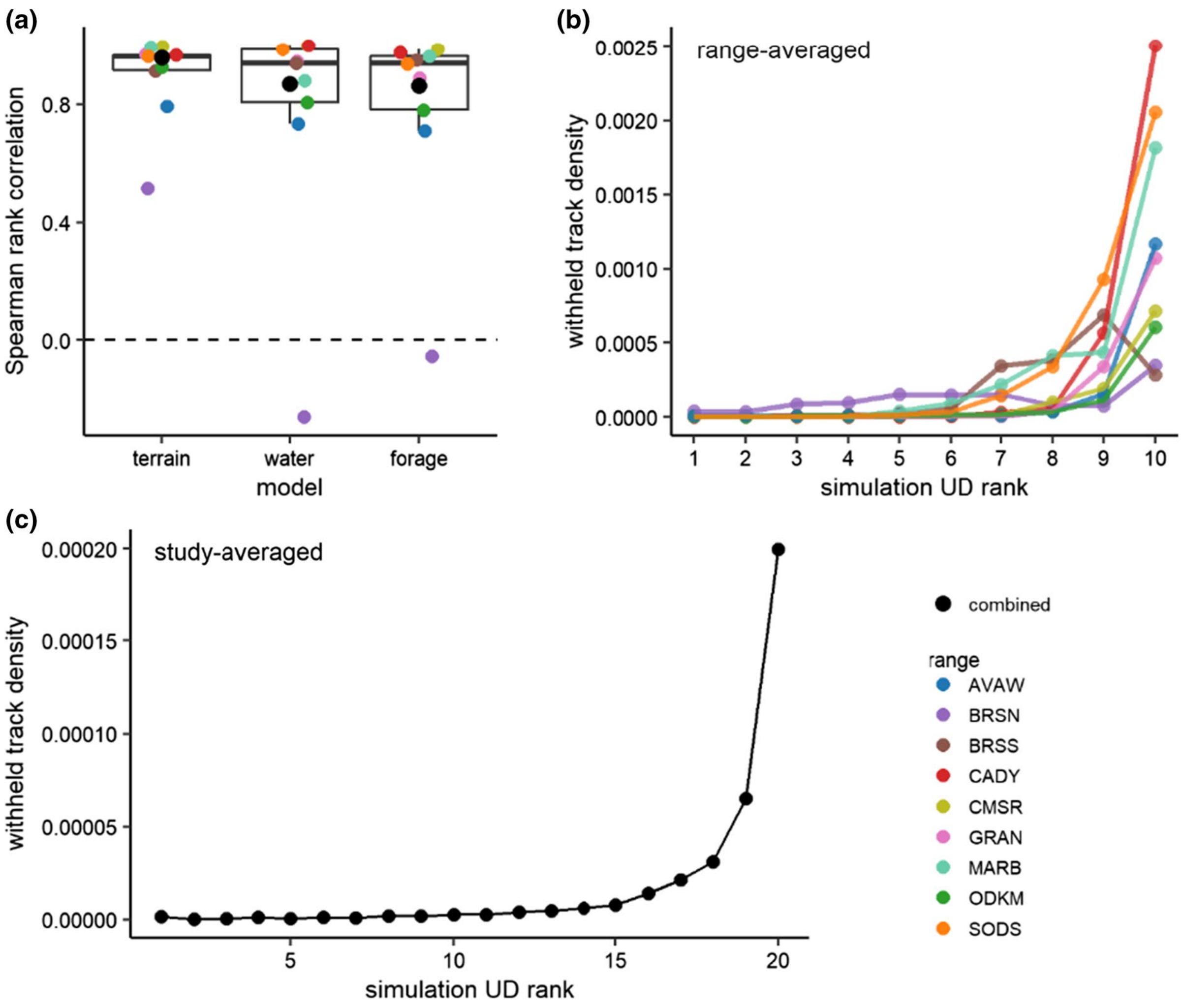

Fig. 3 **a** Spearman rank correlation coefficients calculated using the range-averaged simulation UD ranks and withheld data (colored points and boxplots) and study-averaged simulation UD ranks and withheld data (black points) for each model. Correlations show good agreement between simulated and withheld data, and indicate the terrain model best predicted habitat use across all ranges. The density of withheld data located within each simulation UD rank for the terrain model are shown in **b** for range-averaged UDs and **c** for the study-averaged UD. Upper ranks in both cases account for the majority of observed utilization, while lower ranks are associated with irregular use or brief movement through habitat

individual for model training (range: 3553–10,637) and mean of 4194 steps per individual for model validation (range: 1209–5322). The maximum step lengths travelled by each individual ranged 1484–6910 m.

Integrated step selection analysis

Plots of iSSF coefficients and other associated metrics can be found in Online Resources 3. The largest and most consistent effects on habitat selection in the terrain model indicated bighorn stay close to ridges, prefer north-facing slopes in fall and south-facing slopes in winter, prefer larger patches of sloped terrain, and avoid large changes in elevation unless moving from low elevations. Males often exhibited seasonal changes in movement and were expected to take longer steps in summer, while female step patterns were more consistent across seasons. The direction and strength of the dcore$_{end}$ effect was variable, with inconsistent seasonal shifts across individuals. The highway barrier effect was statistically significant

($p < 0.05$) in 12 out of 20 animals with at least 100 points near the highway, and indicated preference for locations further from the highway (Fig. 2a). The standard errors of the dhwy_{end} coefficient were less variable for individuals with at least 1000 steps that began within 2 km of the highway (Fig. 2b). We used the mean dhwy_{end} coefficient (0.33 ± 0.13 95% CI) estimated for animals with > 1000 steps near a highway when simulating movements with barriers for animals with fewer near-highway points. The distance to water coefficient was often significant and typically indicated avoidance of locations very far from water sources—an effect that increased with the time since an individual's last water visit. The interaction between $\text{dwater}_{\text{end}}$ and $\text{AI3mo}_{\text{start}}$ was occasionally significant, and for those individuals, increasing aridity increased the strength of selection for locations closer to water. The coefficients related to forage influences on movement were variable and significant for fewer animals than water and terrain-related covariates. The effect of $\text{ndvi}_{\text{start}}$ on step length was the only forage-related coefficient significant in most animals, but the direction of the effect was variable.

Model validation and predictive performance

Based on Spearman rank correlations, the terrain model produced simulated movements that more strongly correlated with withheld observed tracks than the water and forage model (Fig. 3a). The terrain model showed the highest correlations calculated from range-averaged UDs in 6 of 9 ranges with a median correlation coefficient of 0.964 and range of 0.515–1. The terrain model also had the highest correlation coefficient (0.959, $p < 0.001$) for the study-averaged UD (Fig. 3a). We conducted all remaining simulations using the terrain model because of this consistent performance. The withheld track density for each UD rank is shown in Fig. 3.

Predicting habitat use without highway barriers

Movements simulated without the barrier effect in place resulted in 2855 of 8200 (34.8%) year-long tracks that crossed a highway compared to 883 of 8200 (10.8%) tracks simulated with the barrier effect—a 3.2-fold decrease in predicted crossings when movements are limited by highways. We identified 3 highway segments with the highest mean simulation rank at six former bighorn movement corridors impacted by the highway (Fig. 4). At 5 of 6 sites, the top highway segments included areas of high predicted use, i.e., segments with mean UD ranks 15–20 (Table 3). At sites 2 and 6, recent roadkill events occurred along the highway within segments with mean rank values of 16, 17.2 and 18.3—all predicted to receive high amounts of use (Fig. 4, insets 2 and 6). Previously predicted LCPs passed through the highest-ranked highway segments at all sites except 2 and 4, where the simulation UD identified alternative locations as the most-likely crossing point.

Movement simulations without a barrier present increased habitat access at 8 out of 9 ranges. Simulations for bighorn in the Avawatz Mountains (AVAW) did not result in any highway crossings or habitat use across the highway, likely due to the large minimum distance of the range to I-15 (14 km). Simulated barrier-free movements at all remaining ranges accessed habitat across the highway that ranged in total area from 19 to 246 km^2. Relative to the amount of habitat accessed in simulations with the highways, this suggests an increase in available habitat ranging from 7 to 138% without barriers (Fig. 5a). The largest increase in accessible area occurred in SODS and BRSS, which included higher elevations than accessible under current conditions (Figs. 6 and 7). Of the area accessed across the highway, a majority of the habitat was used infrequently, with a mean across ranges of 92% (min = 78%, max = 100%) of simulation UD cells ranked 4–7, and mean of 8% (min = 0%, max = 22%) ranked 8–10 (Fig. 5b).

Discussion

We applied a movement and habitat-informed iSSF to simulate desert bighorn movements that are currently limited by human-made barriers, namely major highways. Our analysis supports prior conclusions that desert bighorn largely avoid crossing two major highways, and demonstrates a common consequence of human infrastructure: limited local movements and reduced habitat reachability for nearby wildlife populations. Moreover, in two cases, barriers restrict access to higher-elevation habitats predicted to maintain bighorn populations more resilient to the effects of climate change. Simulated movement under

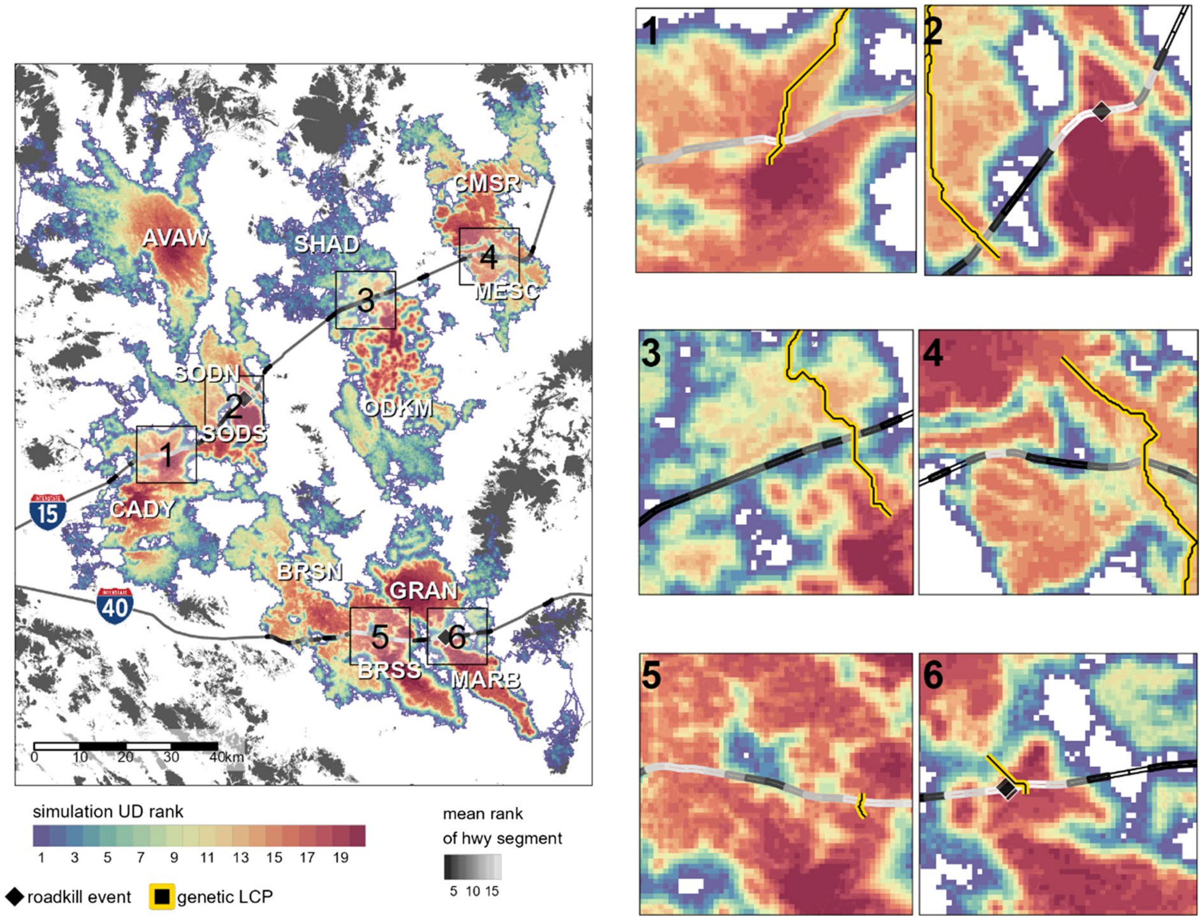

Fig. 4 Map of the study-averaged simulation UD with ranks indicating predicted levels of desert bighorn use. Ranks were based on 8200 simulated bighorn-years from selected iSSFs without a highway barrier and rank cut-off points identified during model validation (Fig. 3c). Six sites (inset plots 1–6) along I-15 and I-40 were selected based on impacted movement corridors modelled in Creech et al. (2014), plotted here as genetic least-cost paths (LCP). The mean UD rank for each 1 km segment of highway is shown as a gradient from dark to light (low to high rank) with recent desert bighorn roadkill events plotted at sites 2 and 6

barrier-free conditions identified specific locations along I-15 and I-40 to target mitigations that improve habitat access and metapopulation connectivity. Data-driven movement simulations thus offer potential for robust new insights in connectivity conservation, even in well-studied systems.

Table 3 Simulation UD values for highway segments crossed most during simulations without barriers at each corridor site (Fig. 4) along I-15 and I-40

Site	Top 3 segment mean UD rank
1	18, 15.5, 15.5
2	19.5, 18.7, 17
3	10, 6.25, 6
4	15.5, 11.2, 9.75
5	16, 16, 15.8
6	18.3, 17.5, 17.2

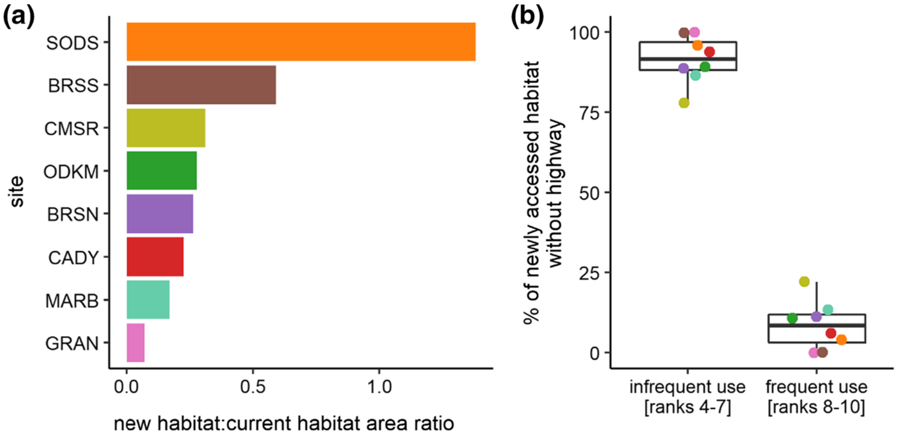

Fig. 5 **a** Ratio of habitat accessed across the highway during barrier-free simulations to all habitat accessed during barrier-present simulations. Ratios were calculated using range-averaged simulation UDs after removing cells ranked 1–3 to omit areas accessed rarely during simulation. **b** Percentage of habitat accessed across the highway that fell within ranks indicating infrequent versus frequent use

Movement simulation offers complementarity and flexibility to connectivity research

Our simulation results largely agreed with past landscape genetics models that predicted the identity and location of impacted bighorn corridors (Epps et al. 2005, 2007; Creech et al. 2014). While connectivity models based on landscape genetics reflect longer time scales and may not capture some types of movement (Anderson et al. 2010; Epps and Keyghobadi 2015), we found strong agreement between genetic and movement-based corridor predictions. Desert bighorn tend to move toward visible and open habitat (Berger et al. 2022). In doing so, they likely do move along the most efficient routes between discrete patches, as is assumed in LCP models. Movement simulations did, however, identify an alternative highest-ranked crossing location for two corridors (Fig. 5, inset 2 and 4). These crossing locations appear to be the most convenient, instead of the most efficient, given the iSSF-approach predicted that animals spent more time in near-highway habitat away from the LCP. Notably, the segments of both highways crossed most during simulations were also the sites of documented vehicle collisions with non-study bighorn. While both approaches appear robust for this system, movement simulation may be preferred when barriers are long established, or when animals are unlikely to perceive the surrounding landscape conditions. This approach can also be useful when genetic data may be inappropriate for testing effects of recent barriers because of population translocations, large effective population sizes, or other issues.

Movement simulation offers a unique benefit to connectivity research—the capacity to predict habitat use as a consequence of a realistic and dynamic movement process. In connectivity modelling, the user often predefines start and end-points that represent core or important habitat patches, or at the other extreme, estimates connectivity for a random collection of start and end-points (Cushman et al. 2013; Dickson et al. 2019). The ease of travel between these start and end-points is then estimated under assumptions that are often convenient but unlikely, such as perfect knowledge of the landscape and consistent movement throughout the process (Unnithan Kumar et al. 2022). Our simulation approach allowed movement characteristics and selection to vary with current conditions and included realistic limitations on movement. We made no a priori assumptions about where an animal would travel, allowing the model to inform whether and how often a location was used. Without the need to delineate habitat patches or assume simple movement rules, iSSF simulation can further assess how various movement behaviors, landscape changes, or habitat preferences shape habitat use.

Evidence of selection does not guarantee coefficients will improve spatial prediction

Even without the influence of water and forage, our final model simulated habitat-informed movements that reflected observed patterns of bighorn habitat use. We do not suggest, however, that these resources are not drivers of bighorn movement and distribution. In fact, many of the estimated covariates associated with these resources showed a significant effect

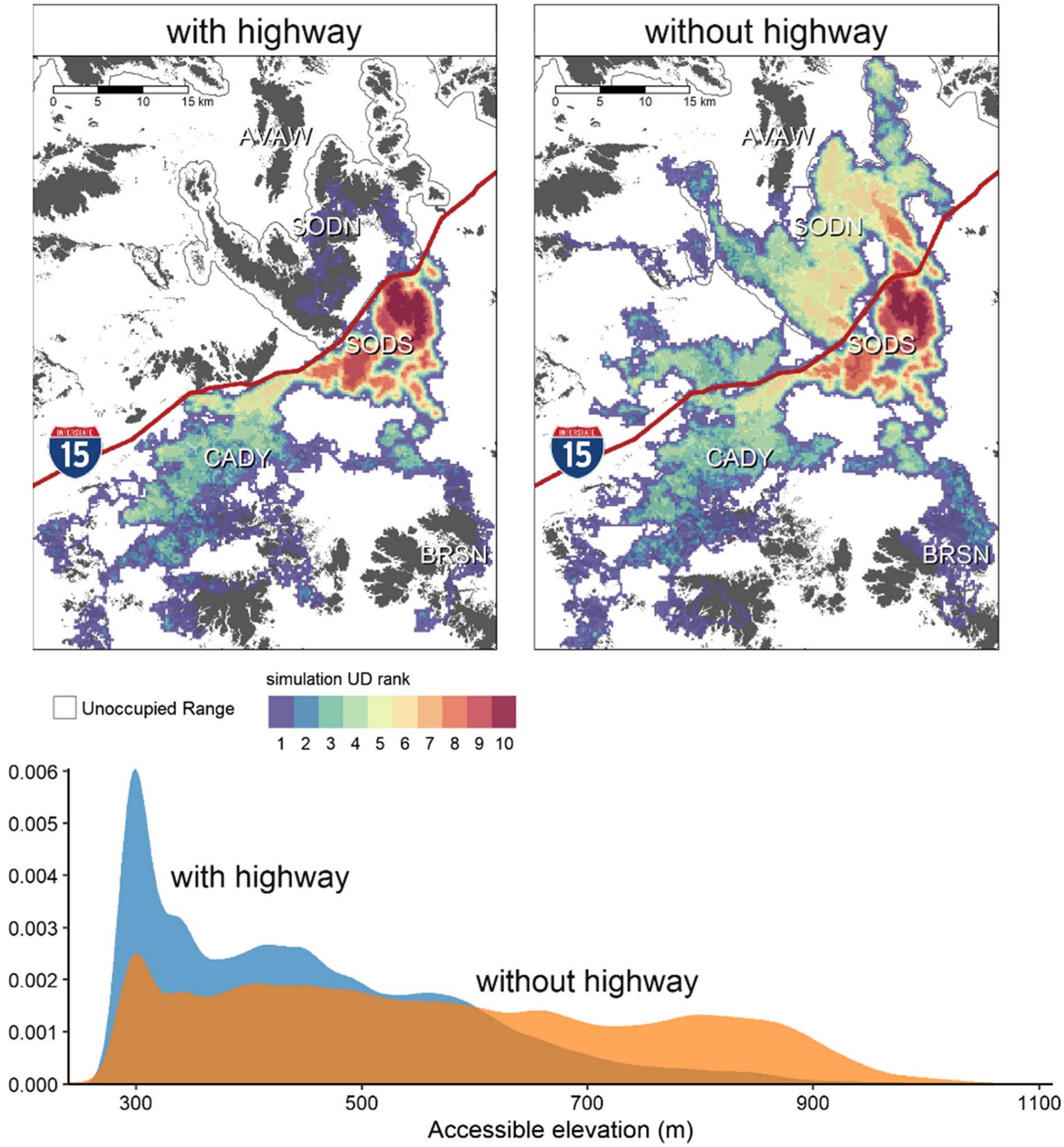

Fig. 6 Map showing differences in habitat (above) and elevation (below) accessibility at SODS under barrier-present (left) and barrier-free (right) conditions as represented by range-averaged simulation UDs. We excluded cells ranked 1–3 when estimating elevation profiles

for a subset of individuals, and often greatly reduced AIC values compared to the terrain model (Online Resources 3). While the data may support selection for these resources in some cases, we found that they did not necessarily improve the accuracy of our simulations at broader scales. When research goals focus on spatial prediction instead of inference, our results suggest iSSF-comparisons should be based in the predictive process (simulation) as opposed to other metrics like information criterion.

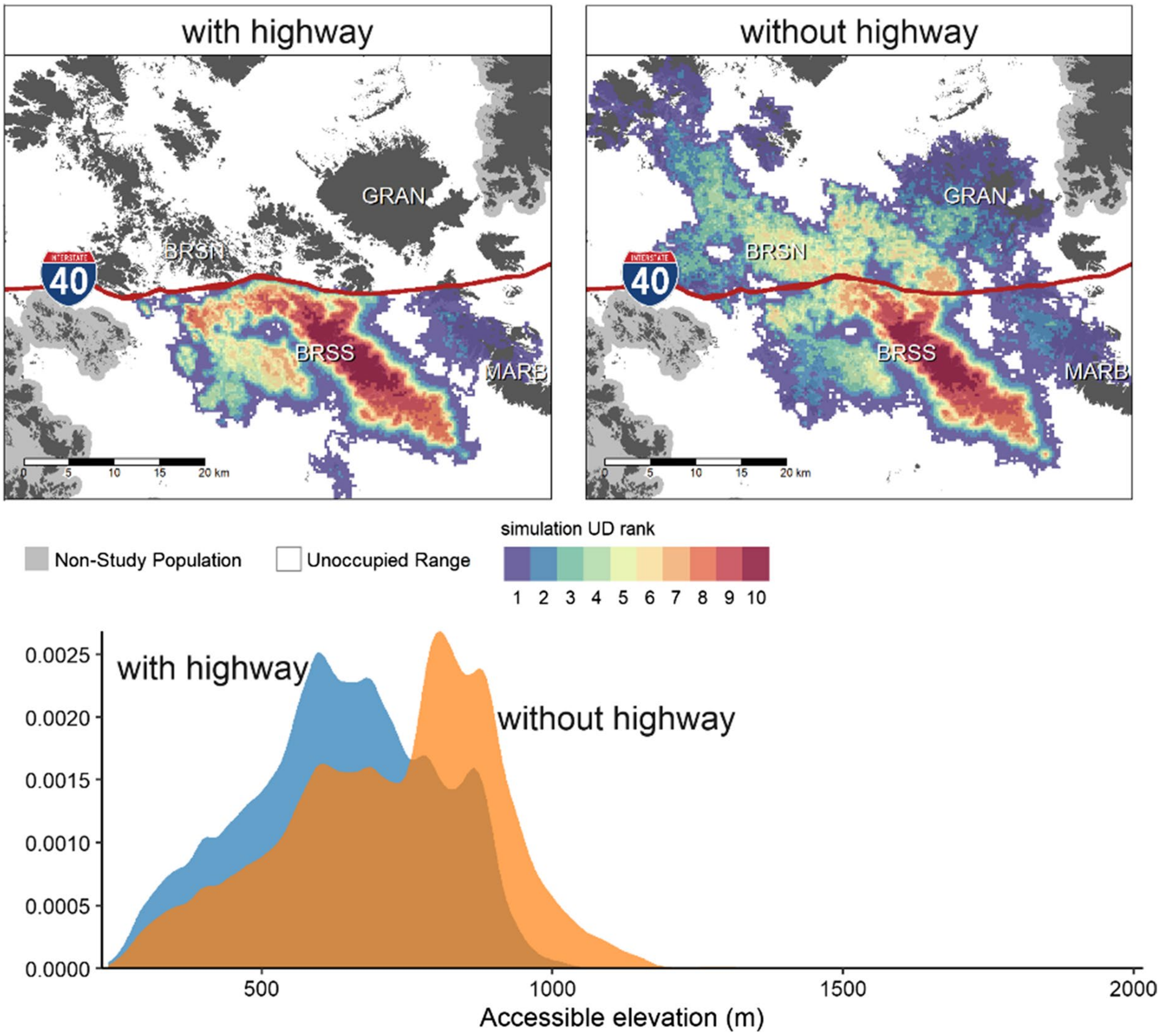

Fig. 7 Map showing differences in habitat (above) and elevation (below) accessibility at BRSS under barrier-present (left) and barrier-free (right) conditions as represented by range-averaged simulation UDs. We excluded cells ranked 1–3 when estimating elevation profiles

In our study, precipitation and forage conditions varied annually and their effect on movement may have differed between the model-fitting and withheld-data periods. Given the additional range-to-range variation in resource needs, and the potential influence of individual preference and memory, it may be necessary to build more individualized models or collect more years of data to better capture fine-scale variation in forage and water use. While further adjusting the forage and water models may have led to improved predictions, we did not deem it necessary to reach our goals given the performance of the terrain model.

Simulation-based predictions help quantify impacts and prioritize mitigation efforts

We found that without barriers, the potential increase in used bighorn habitat could be substantial, and would include high-elevation resources for populations in low-elevation ranges at risk of climate-related extinction. Without the highway, simulations suggest that South Soda Mountains and South Bristol Mountains bighorn could access 138% and 59% more habitat than currently accessible with the highway. Both populations would also be able to access higher elevations. Epps et al. (2004) indicated that habitat elevation influences the probability of local population extinction, and more stable, high-elevation populations tend to harbor greater genetic diversity as a result (Epps et al. 2006). The South Soda Mountains were only recently re-colonized by desert bighorn (Epps et al. 2018) and is at high risk based on the parameters of the Epps et al. (2004) extinction model. The South Bristol Mountains also were identified as a population of high risk to future extinction (Epps et al. 2004) and climate change impacts (Creech et al. 2020). By mitigating the highway barrier near these two populations, managers could increase access to higher elevation habitats and potentially increase the long-term persistence of these populations.

We built iSSFs from a small subset of bighorn over a 2-year period; it is important to recognize that our models unlikely cover the full range of movement behavior in this region. This dataset notably lacked many long-distance forays observed in other GPS-recorded bighorn movements (Prentice et al. 2018). Our results may therefore underestimate desert bighorn movement potential and indeed, past data include (rare) observed movements between habitat patches not predicted by our simulations. We expect that additional long-distance movements in the dataset would primarily affect predicted infrequent movements (UD ranks 1–3), and not alter identified highway crossing sites or estimated habitat availability changes; we intentionally excluded areas of predicted rare movement to focus conclusions on regular habitat use at local scales. When inferences about large-scale connectivity are of interest, we recommend building models from data with dispersal and foray behavior or running a larger set of simulations to capture rare movements.

Still, the local habitat gains predicted here present long-term benefits to connectivity and metapopulation dynamics. With barrier mitigation, bighorn populations along both highways would likely see more opportunities for inter-population interactions, especially along I-40 where numerous occupied habitats occur near both sides of the highway. Along I-15, vacant habitat creates gaps between populations, but barrier mitigation could greatly reduce this gap. The transient use of newly reachable habitat could increase the potential for overlap with the nearest populations. To make large-scale improvements to bighorn metapopulation connectivity, Creech et al. (2014) identified a multi-step approach based on network analysis. This approach included restoring the North Soda Mountains as an occupied patch, and then restoring movement between the North and South Sodas and between the Granite and Marble Mountains across I-40. Our results suggest that increasing access to the North Soda Mountains alone may allow functional connectivity between the metapopulation units separated by I-15. Along I-40, the restoration of the North-South Bristol connection might be prioritized: the South Bristol and Marble bighorn populations are well connected, and so restoring the Bristols connection would both increase high-elevation habitat access for the BRSS population and regional genetic connectivity.

Conclusion

Combined with the widely available GPS data gathered on wildlife worldwide, movement models allow researchers to predict how animals move through landscapes—both real and hypothetical. This approach avoids many assumptions that over-simplify animal behavior and through simulation allows researchers to explore predicted patterns of habitat use and connectivity that result from certain model or landscape characteristics. Despite the processing power required, movement simulation can address diverse questions in connectivity and conservation research and will likely play an increasing role in the effort to restore wildlife connectivity.

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Author contributions CMA designed and performed data analysis and wrote the manuscript, CWE and NLG designed initial project, acquired funding, contributed to logistics, design, and major writing revisions, PRP contributed to design, field logistics and data collection, NWD and DH assisted with

field logistics, and all authors contributed to revisions and gave final approval for submission and publication.

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Data availability The final simulation products generated by this study can be accessed from a figshare repository at: https://doi.org/10.6084/m9.figshare.21720533. The datasets analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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