



## Extreme drought and adaptive resource selection by a desert mammal

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**Abstract.** When animals select areas to occupy, decisions involve trade-offs between the fitness benefits of obtaining critical resources and minimizing costs of biotic and abiotic factors that constrain their use. These processes can be more dynamic and complex for species inhabiting desert environments, where highly variable spatial and temporal distribution of precipitation can create high intra- and inter-annual variability in forage conditions and water availability, and thermal constraints can differ significantly among seasons and diel periods. We examined resource selection in desert bighorn sheep (*Ovis canadensis mexicana*) in Cabeza Prieta National Wildlife Refuge, Arizona, USA, at multiple spatial and temporal scales to gain insight into how a desert mammal responds to variations in climatic conditions. We used resource selection functions to test topographic, forage, and environmental features among seasons and diel periods, and between non-drought and drought conditions at the population and home-range scale. When precipitation was average, sheep selected for topographic features that were beneficial for predator avoidance (i.e., escape terrain—steep, rugged areas with high visibility) and locations near perennial water. When drought occurred, they ranged further from preferred escape terrain and perennial water, perhaps seeking forage conditions suitable to meet their nutritional requirements. On early (April–June) and late (July–September) summer days, sheep selected for more northerly aspects and locations with lower solar radiation, and in some periods, selection for these cooler areas coincided with periods when forage covariates, proximity to perennial water, and several topographic features were uninformative in resource selection models. These choices may be necessary trade-offs, foregoing good escape terrain and foraging areas, and access to water, for improved thermoregulation. This study highlights the importance of identifying resource selection at variable spatial and temporal scales when investigating the interrelationship between species and their environment. It provides insight into the dynamics of resource selection in desert mammals, and how they respond to constraints imposed on them by their environment. This work can serve to inform strategies for managing and conserving species living in arid environments when faced with climate change.

**Key words:** climate change; desert bighorn sheep; diel period; environment; forage; habitat use; scale; topography.

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## INTRODUCTION

Foraging ecology, dispersal, ecophysiology, predator–prey and plant–animal interactions, and population dynamics can be linked through habitat selection (Morris 2003). Although acting at different spatial and temporal scales, these processes all influence how animals select areas to occupy when seeking forage and water, avoiding adverse interspecific interactions, or mitigating environmental challenges for thermoregulation and water balance. Behavioral decisions made by animals to acquire resources and to avoid predators are manifested in their movement patterns, and animal movements connect these behavioral decisions to broadscale patterns of species range, population distribution, and home-range use (Turchin 1998, Owen-Smith and Cain 2007, Fuller et al. 2016). Thus, knowledge of the factors that influence the behaviors integrated in the habitat selection process is important for more detailed understanding of species ecology and has implications for species management and conservation (Berger-Tal et al. 2011).

Natural selection should favor individuals that select and occupy home ranges that contain an optimal combination of elements necessary for survival and reproduction (Powell and Mitchell 2012). Selection of these areas involve trade-offs between the benefits of obtaining critical resources (e.g., food, water, cover, and birthing sites) and minimizing costs of the biotic and abiotic factors that constrain their use (e.g., predation risk, competition, and exposure to disease, adverse weather, or anthropogenic disturbance; e.g., Festa-Bianchet 1988, Mysterud et al. 2007, Hoglander et al. 2015), and this can have important fitness consequences (e.g., Lowrey and Longshore 2017, Abernathy et al. 2019). Furthermore, species inhabiting highly variable environments must frequently cope with changes in environmental conditions by adjusting activity budgets, movement patterns, foraging behaviors, diet, or habitat selection (Seddon and Ismail 2002, Owen-Smith and Cain 2007, Cain et al. 2017). Natural and human-induced environmental changes challenge the adaptive capacity of animals to respond to these changes, and those species or populations with higher levels of behavioral plasticity may be better able to do so.

Indeed, biotic and abiotic factors that constrain habitat selection may be as important as or more important than resource availability in determining habitat selection patterns, yet the effects of these constraints are often not incorporated into habitat selection studies (Morrison 2001).

Resource selection studies often focus on only a single component of a species' environment, such as topography (Sawyer et al. 2006), vegetation type (Devore et al. 2016), or climatic factors (Fitzgerald and Nelson 2011). It is, however, the suite of habitat components that together constitute the overall requirements of a species. Moreover, often these separate elements interact to create conditions that either augment or diminish benefit to an individual. Habitat conditions are also dynamic across the short and long term. In response to short-term changes in habitat, species may vary their areas of use across seasons (Zweifel-Shielly et al. 2009), climatic conditions (Pauley et al. 1993), or diel periods (Roberts et al. 2017). Therefore, resource selection can be more complex for species inhabiting arid regions where highly variable spatial and temporal distribution of precipitation can create high annual and seasonal variability in forage conditions and water availability, and thermal constraints can differ significantly among seasons and diel periods. Over the long term, significant modifications of habitat or the distribution of resources can occur in response to climate change, and species may alter their range or populations may shift their distribution to occupy areas within their physiological tolerance (Lou et al. 2015). Consequently, species habitat selection can vary across multiple spatio-temporal scales (e.g., decadal, annual, seasonal, or daily; Boyce 2006, Blix et al. 2014), and when predicting species resource use, temporally appropriate sampling is necessary to detect scale-specific resource selection. Therefore, the ecological processes associated with resources selected by a species must be carefully considered and integrated into analyses to elucidate their critical resource requirements.

We investigated resource selection in desert bighorn sheep (*Ovis canadensis mexicana*), a species that is morphologically, physiologically, and behaviorally adapted to an arid environment (Cain et al. 2006). Thus, they are an ideal species for examining the influence of variable climatic conditions on resource selection in desert species.

Previous studies of resource selection in desert bighorn sheep have primarily focused on components of the landscape and vegetation associations (e.g., Krausman and Leopold 1986, Hoglander et al. 2015); however, abiotic factors in a desert climate likely exert a significant influence on resource selection and should also be considered. Also, species often utilize essential resources for short time periods only, and if an inappropriate sampling period is selected, important habitat components may not be detected (White and Garrott 1990). In particular, the high intra-season variation in timing and distribution of precipitation and significant diel temperature variability are inherent in desert environments and could result in some critical resources for desert-dwelling species not being identified. Thus, it is important to employ a sampling protocol that allows reliable detection of differences in resource selection among seasons and diel periods. Furthermore, desert bighorn sheep range in arid regions of the southwestern United States and northern Mexico (Hansen 1990), where global climate models predict significant temperature increases, changing precipitation patterns, and declining water balances during this century (Garfin et al. 2013). Therefore, identifying desert bighorn sheep resource selection in response to variable climatic conditions is essential for understanding the resources necessary for desert mammals to persist in a changing climate.

We examined desert bighorn sheep selection for topographic, forage, and environmental features at multiple spatial and temporal scales to gain insight into how a desert mammal responds to variations in climatic conditions across seasons and diel periods. We predicted that when precipitation significantly decreases, sheep would prioritize alternate important habitat features. Under normal precipitation, we predicted that sheep would select for topographic features that minimize risk of predation (i.e., escape terrain—steep, rugged areas with high visibility), and diminished forage conditions in the dry early summer (April–June) and during drought in other seasons, would cause sheep to shift to topography that was less suitable as escape terrain but provided better forage. We also predicted that high temperatures in early and late (July–September) summer and dry conditions

during drought would result in sheep selecting locations beneficial for thermoregulation, and this would vary by diel period. Findings advance our understanding of how resource selection in desert mammals occurs at different spatial and temporal scales, and highlight the importance of considering future changes in climate when determining critical resource requirements of species inhabiting arid regions.

## MATERIALS AND METHODS

### *Study area*

This study was conducted in the Cabeza Prieta National Wildlife Refuge (CPNWR); 3,480 km<sup>2</sup> in the Sonoran Desert in southwestern Arizona, USA (Appendix S1: Fig. S1). The area consists of a series of rugged mountain ranges (elevation 200–900 m) separated by wide alluvial valleys. The study sites were the Cabeza Prieta (CP) and Sierra Pinta (SP) mountains in western CPNWR. Ephemeral water sources occur on these ranges following precipitation, in natural rock depressions and desert washes. The only known sources of perennial water occur in modified catchments: four on CP and three on SP (Appendix S1: Fig. S1). A detailed description of the study area is found in Cain et al. (2008a).

Based on temperature and precipitation data (1969–2005) from the weather station nearest to CPNWR (Tacna, Arizona, ~64 km north; Western Regional Climate Data Center 2005), we defined seasons as winter (January–March), early summer (April–June), late summer (July–September), and autumn (October–December). Mean annual precipitation in CPNWR is 101 mm with peaks in late summer and winter, which together account for 69% of total annual rainfall, and precipitation in this area has high inter-annual variability (CV = 56%). In summer, mean daily low temperature is 22°C and mean daily high temperature is 41°C, with temperatures commonly exceeding 45°C. In winter, mean daily low and high temperatures are 3° and 21°C, respectively.

### *Captures and monitoring*

We captured 37 adult female desert bighorn sheep from 2002 to 2004 with a net gun fired from a helicopter (Krausman et al. 1985) and fitted them with global positioning system (GPS) telemetry collars (900 g; models 440 and 3580,

Telonic, Mesa, Arizona) programmed with a 13-h fix interval. Additional sheep were collared to replace collars with expired batteries and study animals lost to mortality, such that each mountain range had 6–10 radio-collared sheep throughout the study. All capture and handling procedures followed acceptable methods (Sikes et al. 2011) and were approved by the University of Arizona Animal Care and Use Committee (Protocols 01-191 and 04-180).

#### Data compilation

We classified climatic conditions as drought and non-drought based on three-month Standardized Precipitation Index (SPI; McKee et al. 1993; see Appendix S1: Fig. S2 for how climatic conditions were defined). We classified diel periods as day, crepuscular (3 h following civil twilight in the morning and prior to civil twilight in the evening), and night (US Naval Observatory 2015).

We used ArcGIS 10.3 with Spatial Analyst extension (Esri, Redlands, California, USA) to develop spatial models of the area used by desert bighorn sheep. We used Geospatial Modelling Environment program (Beyer 2015) to generate 95% kernel density estimates of seasonal home ranges around locations for each female and 100% minimum convex polygons of home range around all sheep locations for each population. Based on mean displacement distances between 13-h GPS locations, we added a 300-m buffer around each individual home range and a 500-m buffer around each population home range (Roerick et al. 2019). We considered all habitat within buffered 95% home range or population polygons as available for use by sheep at the within home range, and population levels, respectively. We then generated an equal number of random points for locations within each home range or population polygon.

For each sheep and random location, we extracted habitat variables that were previously shown to be important in desert bighorn sheep habitat selection (e.g., Krausman and Leopold 1986, Etchberger et al. 1989, Alvarez-Cárdenas et al. 2001, Bangs et al. 2005a, Bleich et al. 2010, Hoglander et al. 2015), and added other variables that we thought could also be influential. We derived elevation (m) and other topographic features at each location from a 10-m resolution digital elevation model (U.S. Geological Survey

2015). We determined distance (km) from each location to the nearest perennial water source (i.e., water catchment) using the ArcGIS Near tool (Esri, Redlands, California, USA). As part of a separate study, water catchments on SP were maintained empty commencing March 2004, and thus, sheep locations from the SP population during this period were excluded from analyses. We used the Land Facet Corridor 1.2.9 extension (Jenness et al. 2013) for ArcGIS to classify topographic position index (TPI) as valley, slope (reference), and ridgeline, using a  $3 \times 3$  cell neighborhood. We used the Benthic Terrain Modeler 3.0 extension (Wright et al. 2012) for ArcGIS to derive slope ( $^{\circ}$ ), aspect, and terrain ruggedness. Aspect was trigonometrically transformed to represent relation to north (northness; Zar 1999; range  $-1$  [south] to  $1$  [north]; Eq. 1).

$$\text{Northness} = \cos((\text{aspect} \times \pi)/180) \quad (1)$$

We included aspect with slope as an interaction term, because aspect-influencing solar exposure decreases as slope increases. Terrain ruggedness is a vector ruggedness measure ranging from 0 (flat) to 1 (most rugged; Sappington et al. 2007) and was calculated using a  $3 \times 3$  cell neighborhood. The rugged topography of desert bighorn sheep habitat suggests there would be high spatio-temporal variation in surface heat load. Therefore, for each location, we derived date- and time-specific solar radiation ( $\text{W}/\text{m}^2$ ) using *r.sun.mp* (Hofierka and Suri 2002) in GRASS-GIS (GRASS Development Team 2017), which accounts for atmospheric effects, daily and seasonal sun angle, latitude, elevation, slope, aspect, and topographic shading.

The Normalized Difference Vegetation Index (NDVI) uses remote sensing data to predict primary production and can be used to assess timing of forage emergence and senescence (Pettorelli et al. 2005). We compiled  $250 \times 250$  m Moderate-Resolution Imaging Spectroradiometer raw reflectance images for each 8-d period during the study (Didan et al. 2015), extracted location and time-specific raw reflectance values to each random and used location for each spatial scale, and then calculated NDVI (Eq. 2). We used NDVI values and NDVI rates (i.e., percent changes over the previous 8, 16, and 32 d) as proxies for available forage biomass and quality, respectively.

$$\text{NDVI}_i = \frac{(\text{NIR}_i - \text{Red}_i)}{\text{NIR}_i + \text{Red}_i} \quad (2)$$

here,  $\text{NIR}_i$  ( $\lambda = 841\text{--}876$  nm) and  $\text{Red}_i$  ( $\lambda = 620\text{--}670$  nm) are spectral reflectance measurements for location  $i$  acquired in the near-infrared and red regions, respectively.

We rescaled ruggedness and NDVI values in our study area to range from 0 to 1.

### Resource selection models

We divided habitat variables among three habitat feature classes; topographic (slope, elevation, ruggedness, TPI, and aspect), forage (NDVI and NDVI rate), and environmental (solar radiation and distance to perennial water). These habitat feature classes were combined in models to represent a priori hypotheses for testing desert bighorn sheep resource selection (Appendix S1: Table S1). Before constructing a priori models, we used Spearman rank correlations ( $|\rho| < 0.6$ ) to test for correlation between all predictor variables (Lehmann and D'Abbrera 1998); correlated predictor variables were not included in the same models. Prior to analyses, solar radiation was log-transformed and continuous data were scaled by subtracting the mean and dividing by two standard deviations (Gelman 2008). We ran generalized linear mixed-effects logistic regression models in R 3.5.1 (R Core Team 2018) using the lme4 package (Bates et al. 2015) to assess the relationship between seasonal and diel sheep resource selection and topographic, environmental, and forage habitat features (Manly et al. 2002). The binary response variable was observed or random locations (Keating and Cherry 2004). We tested the effect of drought on sheep resource selection by comparing models with and without the categorical covariate precipitation (i.e., non-drought/drought period classified based on the 3-month SPI). Every model included a fixed effect for range to account for variation among populations and random effects for female ID. We examined two spatial scales: home range (third-order selection analyzing sheep locations within their home range) and population (second-order selection analyzing sheep home ranges within the population range; Johnson 1980). We constructed 23 candidate models (Appendix S1: Table S1) and evaluated model performance using second-order Akaike's

information criterion ( $\text{AIC}_c$ ; Burnham and Anderson 2002). We ran separate model sets for day, crepuscular, and night within each season and at each spatial scale, and for the top model in each set, we further examined which habitat covariates most strongly influenced the model. We further tested for multicollinearity among covariates in the most supported models with variance inflation factors (all variables  $< 10.0$ ; Neter et al. 1996). We used five-fold cross-validation (bins = 20) to evaluate predictive performance of models (Boyce et al. 2002).

We expected relationships between forage components (i.e., abundance and quality) and sheep selection would be dynamic among scales, seasons, and diel periods. We wanted to include forage covariates that best-supported the data for each model set, and therefore, we conducted preliminary analyses to determine the best combination of NDVI (linear or quadratic term) and/or NDVI rate (previous 8, 16, or 32 d) for predicting sheep selection in each diel period within each season at both scales and included those covariates as the parameter "Forage" in models (Appendix S1: Tables S1 and S2).

## RESULTS

We used 15,085 locations from 28 female desert bighorn sheep (mean  $\pm$  SD [range]:  $539 \pm 469$  [69–1,602] locations/female) from February 2002 to September 2005 in our resource selection models. The mean number of GPS locations per study animal for each climate period (mean locations/climate period: non-drought, 5636; drought, 9412) and season (mean locations/female: autumn, 150; winter, 135; early summer, 185; late summer, 162) was sufficient to define seasonal home-range areas and to provide robust estimates of resource selection. January 2002–February 2003 and July–October 2004 were classified as drought (Appendix S1: Fig. S2). Based on 5-fold cross-validation, predictive success for the top models ranged from  $\rho = 0.91\text{--}0.99$  at the population scale and  $\rho = 0.94\text{--}0.99$  at the home-range scale.

Preliminary models to determine which form of topographic covariates best predicted sheep resource selection indicated curvilinear relationships for slope, elevation, and ruggedness, and thus, quadratic terms for these covariates were

used in the resource selection models. At the population scale, preliminary Forage models indicated there was a curvilinear relationship between forage biomass ( $\text{NDVI}^2$ ) and sheep selection in all top models, and forage quality (NDVI rate of change) was important in all, but one top model (Appendix S1: Table S2). At the home-range scale, forage biomass exhibited quadratic and linear relationships in 58% and 17% of the top Forage models, respectively, and forage quality was important in 75% of the top Forage models: Both forage biomass and quality were important in half of the top Forage models at the home-range scale (Appendix S1: Table S2).

Topographic covariates (i.e., slope, elevation, ruggedness, aspect, and TPI) featured in the most parsimonious resource selection models for all seasons and diel periods at both spatial scales (Appendix S1: Tables S3–S10). Solar radiation was only included in day and crepuscular models and appeared in one quarter of the best-supported models (Appendix S1: Tables S5, S6, S9, and S10). The only top models that did not include distance to perennial water were in early and late summer during crepuscular periods at the home-range scale (Appendix S1: Tables S9 and S10). Forage covariates were in all top resource selection models at the population scale (Appendix S1: Tables S3–S6), and at the home-range scale, appeared in all autumn and winter models, but in summer, only during day in early summer (Appendix S1: Tables S7–S9). There were important differences between non-drought and drought conditions during all seasons and diel periods, except for late summer day and night at the population scale, and at the home-range scale, autumn day and crepuscular, and late summer day (Appendix S1: Tables S3–S10).

#### Population-scale selection

*Autumn.*—Desert bighorn sheep selected for intermediate elevations in non-drought and as precipitation decreased, they shifted selection to lower and higher elevations ( $Z \geq 3.13$ ,  $P \leq 0.002$ ; Fig. 1; Appendix S1: Table S11). Intermediate slopes were selected by sheep under both precipitation conditions (non-significant during crepuscular period in drought), and during drought, lower slopes were selected (Appendix S1: Fig. S4 and Table S11). Sheep selected for locations with intermediate ruggedness in day (drought) and

night (non-drought and drought), and at night, ruggedness of selected locations decreased as a function of decreasing precipitation ( $Z = -2.07$ ,  $P = 0.039$ ; Fig. 2; Appendix S1: Fig. S5 and Table S11).

Sheep exhibited strong selection for areas closer to perennial water under both precipitation conditions (non-drought,  $Z \leq -4.69$ ,  $P < 0.001$ ; drought,  $Z \leq -2.58$ ,  $P \leq 0.010$ ; Appendix S1: Fig. S6 and Table S11). Sheep selected locations with lower quality forage during non-drought ( $Z \leq -2.61$ ,  $P \leq 0.009$ ), and at night, declines in precipitation were correlated with sheep selecting for areas with higher quality forage ( $Z = 2.05$ ,  $P = 0.040$ ; Fig. 3; Appendix S1: Fig. S7 and Table S11).

*Winter.*—Intermediate elevations were selected by sheep during non-drought (except during crepuscular period), and as precipitation decreased, selection shifted to lower and higher elevations during day and night ( $Z \geq 2.99$ ,  $P \leq 0.003$ ; Fig. 1; Appendix S1: Table S12). Sheep selected for intermediate slopes in day (drought) and intermediate ruggedness at night (non-drought and drought; Appendix S1: Figs. S4 and S5, and Table S12). Aspect influenced sheep resource selection during day, when selection for northness increased as a function of increasing slope in drought (Fig. 4; Appendix S1: Table S12).

Sheep exhibited strong selection for locations closer to perennial water under both precipitation conditions (non-drought,  $Z \leq -6.21$ ,  $P < 0.001$ ; drought,  $Z \leq -2.38$ ,  $P \leq 0.018$ ), and selection for areas further from water increased as a function of decreasing precipitation in day and crepuscular ( $Z \geq 1.92$ ,  $P \leq 0.055$ ; Fig. 5; Appendix S1: Table S12).

*Early and late summer.*—Sheep selected for intermediate elevations in early summer crepuscular and late summer (except in non-drought; Appendix S1: Fig. S3, and Tables S13 and S14). Intermediate slopes were also selected by sheep in early and late summer, and in early summer night, slope of sheep locations decreased as precipitation decreased ( $Z = -2.14$ ,  $P = 0.033$ ; Fig. 2; Appendix S1: Fig. S4, and Tables S13 and S14). Sheep selected locations with intermediate ruggedness in early summer night during drought and late summer day and night (Appendix S1: Fig. S5, and Tables S13 and S14). Under drought conditions in early summer, less-

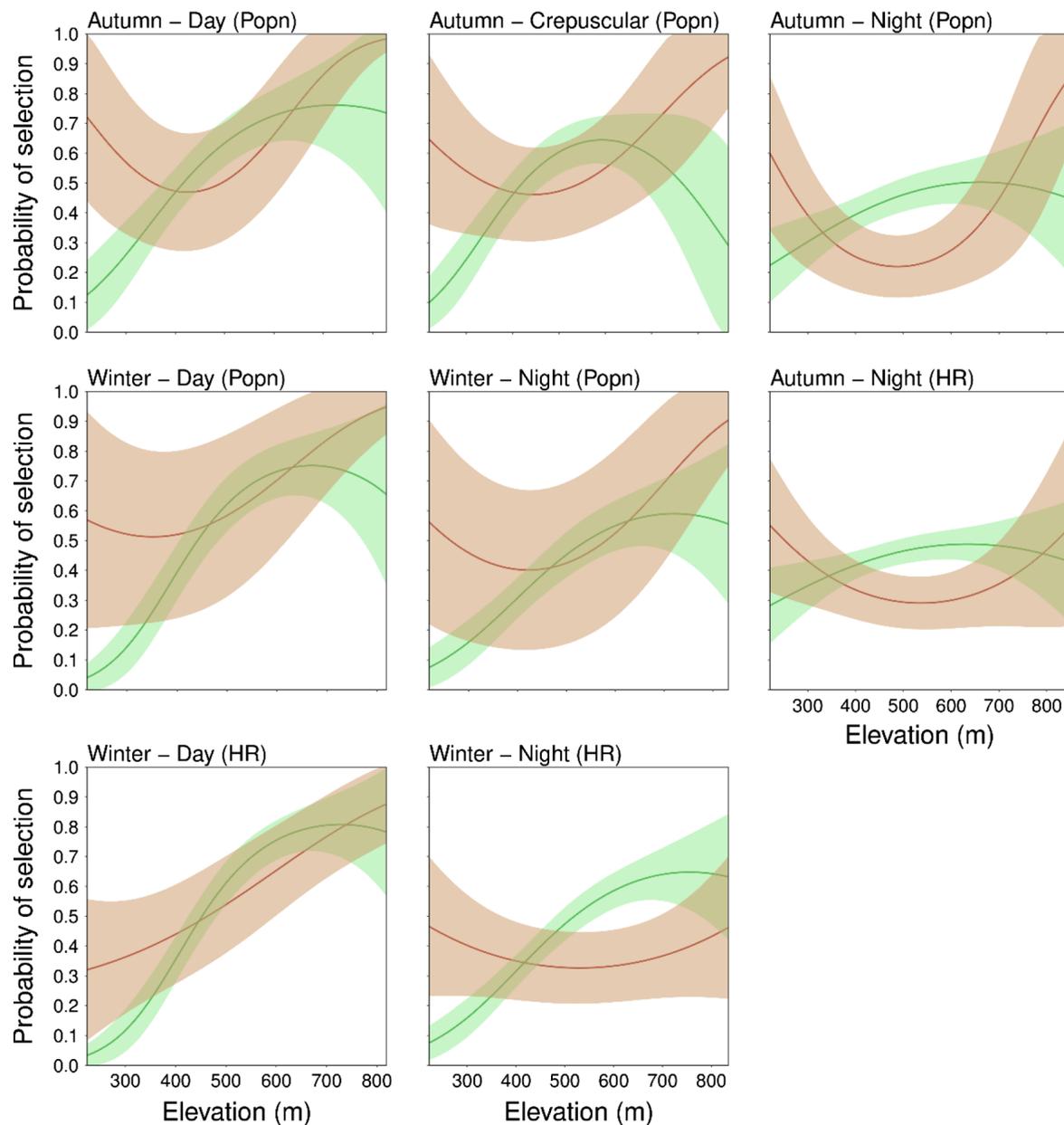


Fig. 1. Predicted probability of female desert bighorn sheep selection for elevation (m) in Cabeza Prieta National Wildlife Refuge, Arizona, USA (2002–2005), for seasons and diel periods (Popn, population scale; HR, home-range scale) where changes in selection from non-drought (green) to drought (brown) are significant ( $P < 0.05$ ). Shading represents 95% confidence intervals.

rugged areas (crepuscular) and less steep slopes were selected by sheep (Appendix S1: Figs. S4 and S5, and Table S13).

Sheep selected locations with lower solar radiation during day in early summer drought ( $Z = -2.08$ ,  $P = 0.038$ ) and late summer ( $Z = -1.87$ ,

$P = 0.061$ ; Fig. 6; Appendix S1: Tables S13 and S14). Aspect influenced sheep resource selection in early summer day, when selection for northness increased as a function of increasing slope (non-drought,  $Z = 2.23$ ,  $P = 0.026$ ; drought,  $Z = 2.68$ ,  $P = 0.007$ ; Fig. 4; Appendix S1: Table S13).

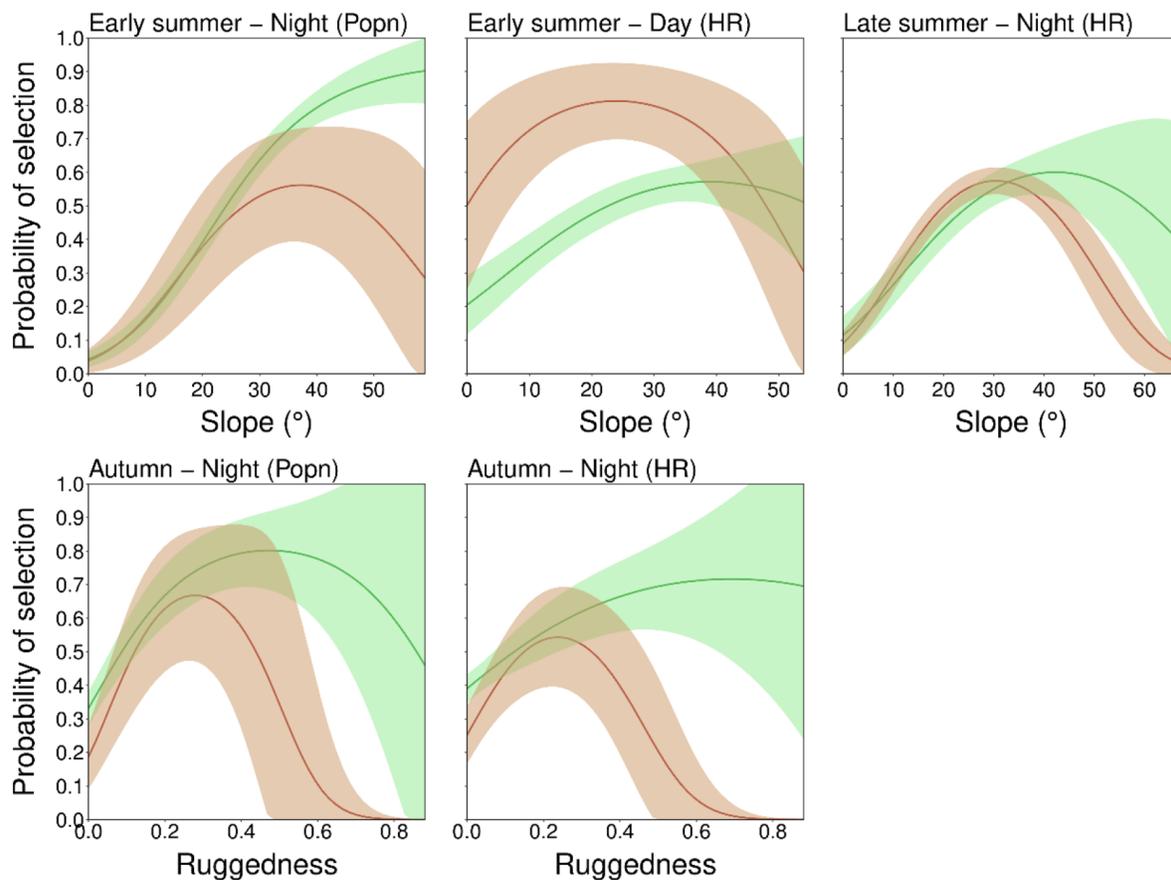


Fig. 2. Predicted probability of female desert bighorn sheep selection for slope ( $^{\circ}$ ) and ruggedness index in Cabeza Prieta National Wildlife Refuge, Arizona, USA (2002–2005), for seasons and diel periods (Popn, population scale; HR, home-range scale) where changes in selection from non-drought (green) to drought (brown) are significant ( $P < 0.05$ ; slope—early summer—day [HR],  $P = 0.062$ ). Shading represents 95% confidence intervals.

Sheep demonstrated strong selection for locations closer to perennial water in all diel periods (early summer,  $Z = -4.36$  to  $-9.09$ ,  $P < 0.001$ ; late summer,  $Z = -6.11$  to  $-11.54$ ,  $P < 0.001$ ), and distance from water increased as a function of decreasing precipitation in early summer day ( $Z = 2.77$ ,  $P = 0.006$ ; Fig. 5; Appendix S1: Fig. S6, and Tables S13 and S14). Sheep selected areas with intermediate forage biomass in early summer night and late summer (Fig. 6; Appendix S1: Fig. S7, and Tables S13 and S14). As precipitation decreased, selection for intermediate forage biomass became stronger in early summer night ( $Z = -2.81$ ,  $P = 0.005$ ), and they shifted to areas with higher and lower biomass in late summer crepuscular ( $Z = 3.90$ ,  $P < 0.001$ ;

Fig. 3; Appendix S1: Tables S13 and S14). Higher quality forage areas were selected by sheep in early summer day (non-drought) and night (drought), whereas in late summer night, sheep selected areas with lower quality forage (Fig. 3; Appendix S1: Fig. S7, and Tables S13 and S14). In early summer, declines in precipitation were correlated with sheep shifting to areas with higher quality forage at night ( $Z = 3.08$ ,  $P = 0.002$ ) and lower quality forage in day ( $Z = -2.80$ ,  $P = 0.005$ ; Fig. 3; Appendix S1: Table S13).

#### Home range-scale selection

*Autumn.*—As precipitation decreased, desert bighorn sheep shifted selection at night from intermediate to lower and higher elevations

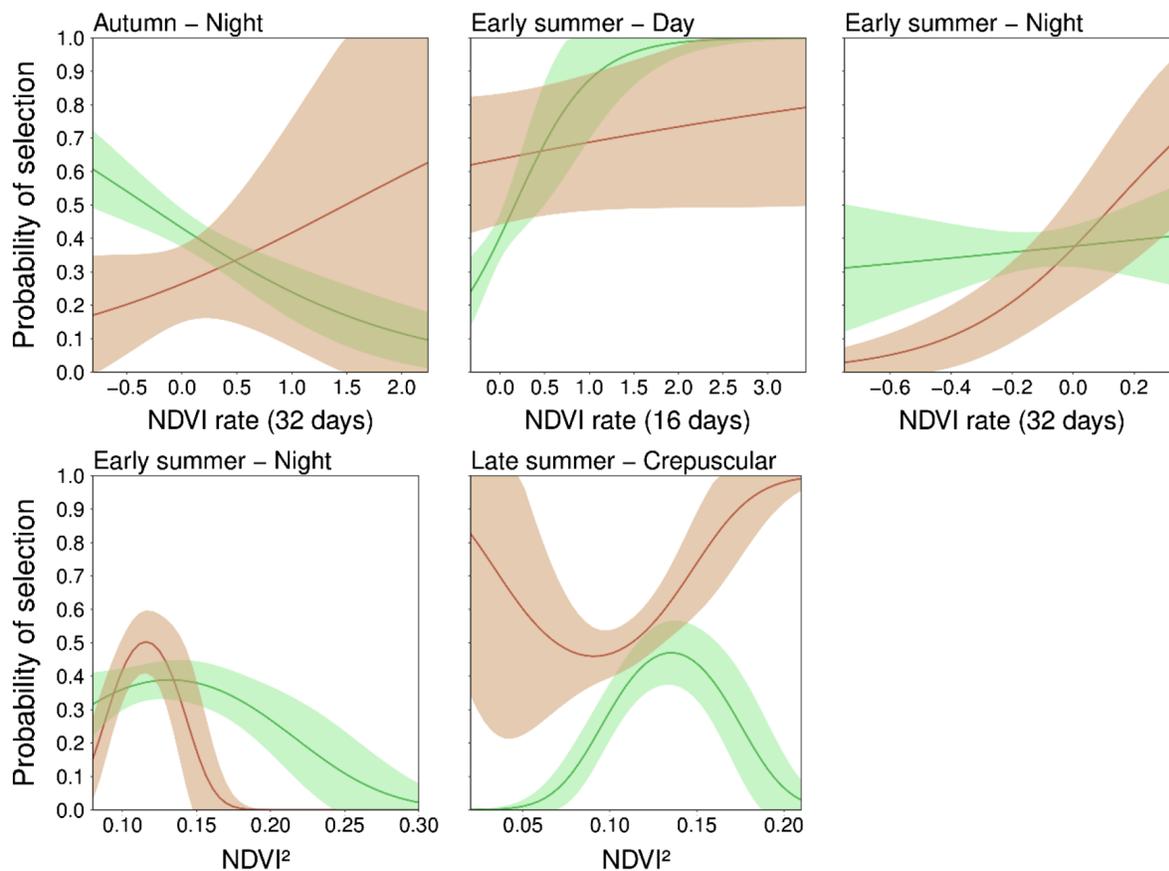


Fig. 3. Predicted probability of female desert bighorn sheep selection for forage features (biomass, Normalized Difference Vegetation Index [NDVI]; quality, NDVI rate of change over 16 or 32 d) in Cabeza Prieta National Wildlife Refuge, Arizona, USA (2002–2005), for seasons and diel periods at the population scale where changes in selection from non-drought (green) to drought (brown) are significant ( $P < 0.05$ ). Shading represents 95% confidence intervals.

( $Z = 2.77$ ,  $P = 0.006$ ; Fig. 1; Appendix S1: Table S15). Sheep selected for intermediate slopes during all diel periods and intermediate ruggedness at night (drought) and in day (Fig. 2; Appendix S1: Fig. S5 and S8, and Table S15). At night, sheep selection for intermediate ruggedness became stronger as precipitation decreased ( $Z = -2.91$ ,  $P = 0.004$ ), and less-rugged locations were selected by sheep during drought (Fig. 2; Appendix S1: Fig. S5 and Table S15). In non-drought conditions, more southerly aspects were selected by sheep at night as a function of increasing slope ( $Z = -2.10$ ,  $P = 0.036$ ; Fig. 4; Appendix S1: Table S15).

Contrary to population-scale selection, at the home-range scale, sheep selected locations

further from water (Appendix S1: Fig. S6 and Table S15). Sheep selected areas with lower and higher forage biomass at night during non-drought and lower quality forage in day (Appendix S1: Fig. S7 and Table S15).

*Winter.*—In day and night, sheep selected intermediate elevations during non-drought, and selection shifted more to lower and higher elevations as precipitation decreased (day,  $Z = 2.41$ ,  $P = 0.016$ ; night,  $Z = 2.27$ ,  $P = 0.023$ ; Fig. 1; Appendix S1: Table S16). Sheep selected for intermediate slopes in crepuscular during drought and areas with intermediate ruggedness in crepuscular (non-drought) and at night (drought; Appendix S1: Figs. S5 and S8, and Table S16). During drought day and night, more

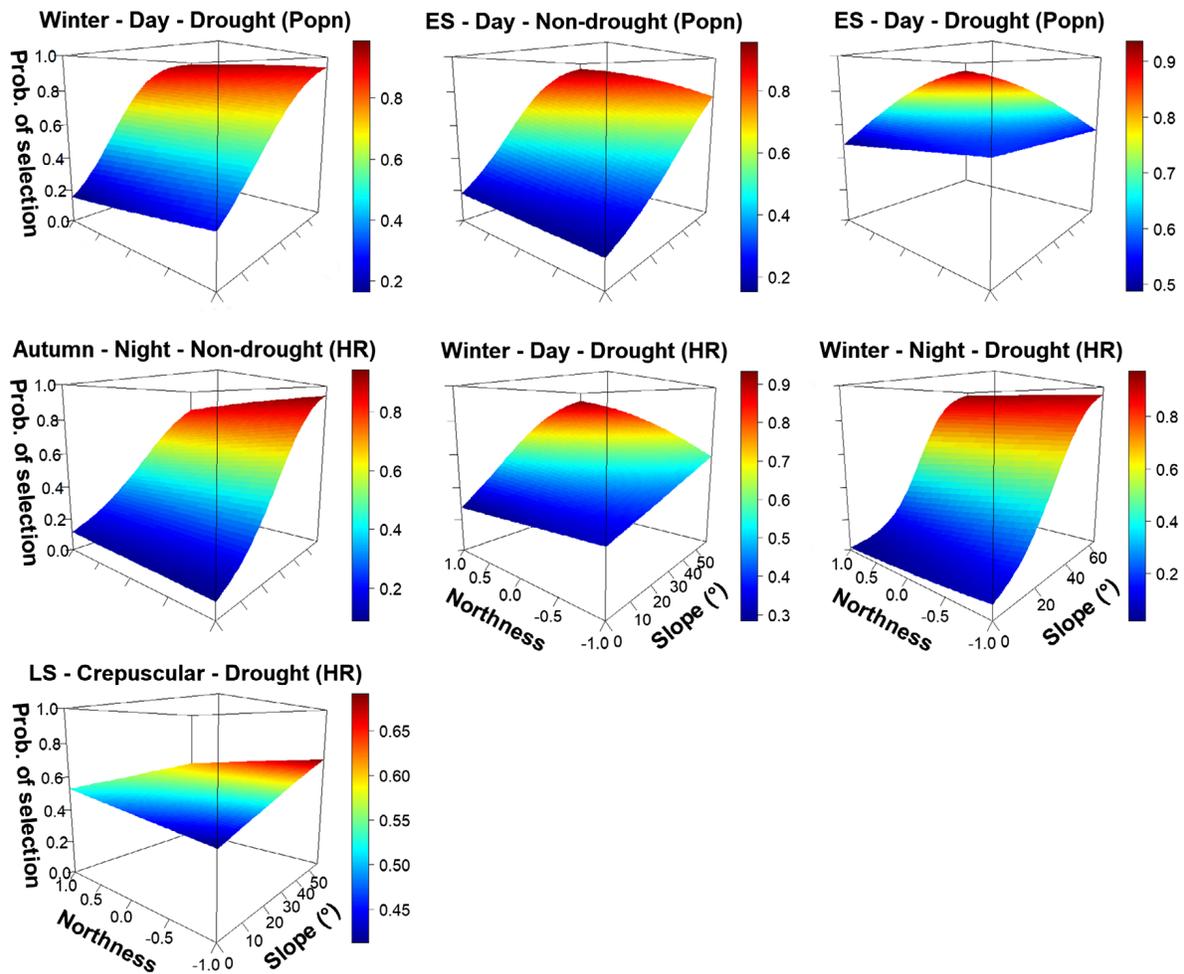


Fig. 4. Predicted probability of female desert bighorn sheep selection for northness (aspect) as a function of slope ( $^{\circ}$ ) in Cabeza Prieta National Wildlife Refuge, Arizona, USA (2002–2005), for seasons (ES, early summer; LS, late summer), diel periods, and precipitation conditions (Popn, population scale; HR, home-range scale) where selection is significant ( $P < 0.05$ ).

southerly aspects were selected by sheep as a function of increasing slope (Fig. 4; Appendix S1: Table S16).

Sheep selected for locations closer to perennial water in crepuscular (non-drought); however, distance from water increased as a function of decreasing precipitation in all diel periods ( $Z \geq 2.42$ ,  $P \leq 0.016$ ), and as such, during drought (all diel periods), sheep selected areas further from water (Fig. 5; Appendix S1: Table S16). Forage biomass and quality were not important predictors of sheep selection (Appendix S1: Table S16).

*Early and late summer.*—In early summer, sheep selected for lower and higher elevations in day (drought) and night (non-drought), whereas in late summer, they selected for intermediate elevations during crepuscular periods (drought) and at night (Appendix S1: Fig. S3, and Tables S17 and S18). Intermediate slopes were selected by sheep across all diel periods under both precipitation conditions (except early summer crepuscular during drought; Fig. 2; Appendix S1: Fig. S8, and Tables S17 and S18). Selection for intermediate slopes became stronger as precipitation decreased in late summer night ( $Z = -2.85$ ,

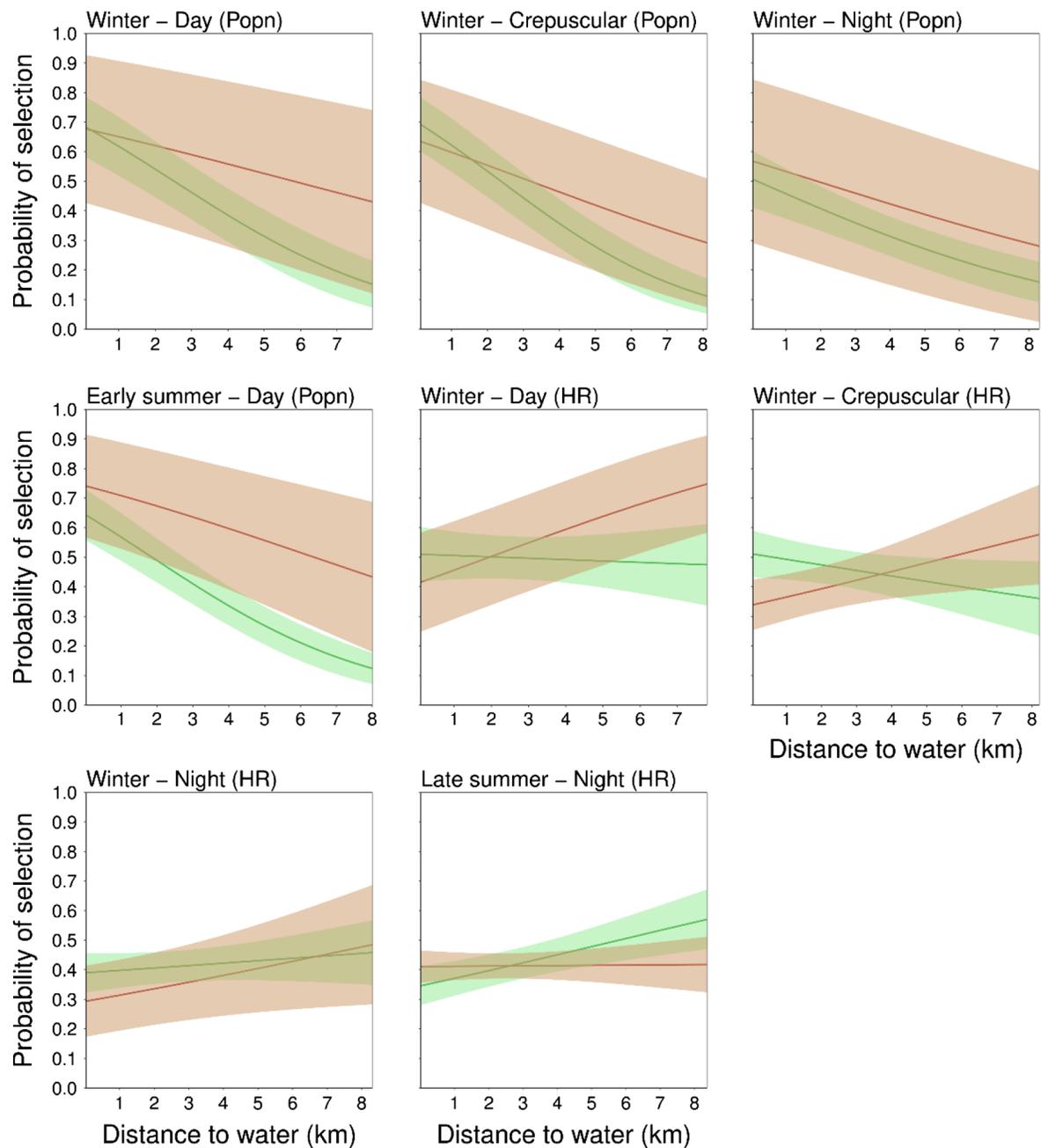


Fig. 5. Predicted probability of female desert bighorn sheep selection for distance to perennial water (km) in Cabeza Prieta National Wildlife Refuge, Arizona, USA (2002–2005), for seasons and diel periods (Popn, population scale; HR, home-range scale) where changes in selection from non-drought (green) to drought (brown) are significant ( $P < 0.05$ ; winter—night [Popn],  $P = 0.055$ ). Shading represents 95% confidence intervals.

$P = 0.004$ ) and early summer day ( $Z = -1.87$ ,  $P = 0.062$ ), and during drought, sheep selected for lower slopes in late summer night and early summer (Fig. 2; Appendix S1: Fig. S8, and Tables S17 and S18). Areas of intermediate ruggedness were selected by sheep in early summer day

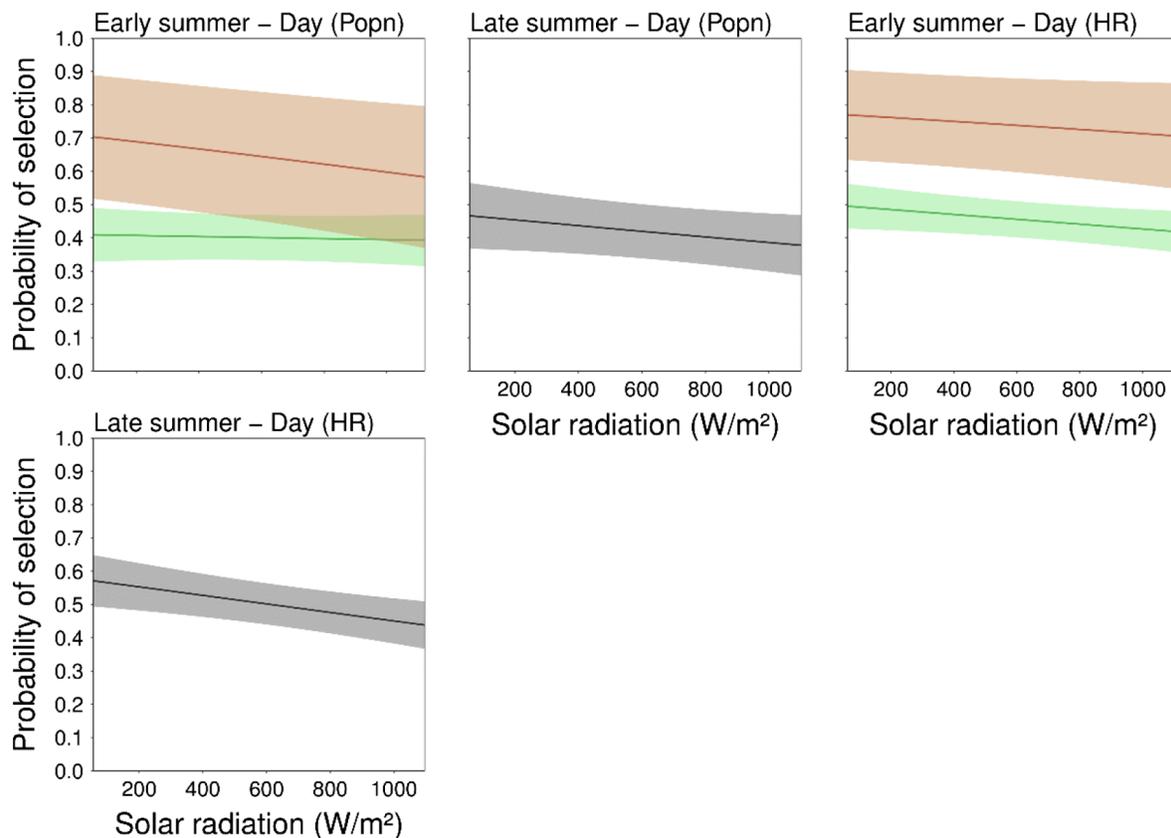


Fig. 6. Predicted probability of female desert bighorn sheep selection for solar radiation ( $\text{W/m}^2$ ) in Cabeza Prieta National Wildlife Refuge, Arizona, USA (2002–2005), for seasons and diel periods (Popn, population scale; HR, home-range scale) where relationships are significant ( $P < 0.05$ ; late summer—day [Popn],  $P = 0.061$ ) in non-drought (green) and/or drought (brown), or when the precipitation interaction was not in the top model (black). Shading represents 95% confidence intervals.

(non-drought) and during crepuscular periods, when they also selected locations with lower ruggedness (Appendix S1: Fig. S5 and Table S17).

Sheep selected locations with lower solar radiation in early summer during non-drought ( $Z = -2.10$ ,  $P = 0.036$ ) and in late summer ( $Z = -3.01$ ,  $P = 0.003$ ; Fig. 6; Appendix S1: Tables S17 and S18). In late summer crepuscular, as precipitation declined, sheep shifted their selection to more northerly aspects as a function of increasing slope ( $Z = 2.79$ ,  $P = 0.005$ ), and as such, selected for locations with higher northness in drought (Fig. 4; Appendix S1: Table S18).

In late summer night, sheep selected locations further from perennial water and increased their proximity to water as precipitation declined ( $Z = -2.25$ ,  $P = 0.025$ ; Fig. 5; Appendix S1:

Table S18). Sheep selected areas with lower and higher forage biomass in early summer day during drought (Fig. 3; Appendix S1: Table S17).

## DISCUSSION

Our investigation of desert bighorn sheep demonstrated how changes in climate can affect resource selection in a desert mammal, and how these influences can vary across seasons and diel periods. This study highlights the importance of considering temporal variation in resource selection when determining critical resource requirements, and the potential for future changes in climate to not only affect these requirements, but also how animals prioritize their selection.

Previous studies reported that topographic features (escape terrain) were dominant predictors of desert bighorn sheep habitat selection (Bangs et al. 2005a, Hoglander et al. 2015), and our results concur. We found, however, that sheep altered selection for topography in response to drought, potentially relegating them to poorer habitats, which could reduce fitness. Indeed, our population had lower survival and recruitment during drought (Cain et al. 2008a), and reduced recruitment has also been reported during drought in other desert bighorn sheep populations (Douglas 2001, McKinney et al. 2001). Sheep may be forced to range further from preferred escape terrain to meet their nutritional and water requirements in drought periods. For example, sheep typically selected ridgelines and avoided valleys during non-drought, whereas during drought, their selection for ridgelines declined and valleys increased, and in some periods, they selected areas with lower ruggedness and slope. As dry conditions persist, the valleys would likely retain soil moisture longest (via runoff from slopes), and this may be where sheep would find the last remaining palatable forage, and they must risk increased vulnerability to predation to meet their nutritional requirements. Similar trade-offs have been reported in other desert bighorn sheep populations and other desert ungulates. Sheep in the Sonoran Desert, Arizona, demonstrated seasonal trade-offs between escape terrain and limited forage and water resources (Hoglander et al. 2015). Under normal precipitation in the Chihuahuan Desert (Mexico), cover and visibility explained habitat use in mule deer (*Odocoileus hemionus*) and food resources were unimportant, whereas under drier conditions, habitat use was explained primarily by food resource variables and secondarily by variables associated with predation risk (Esparza-Carlos et al. 2011). In contrast, gemsbok (*Oryx g. gazella*) in Namibia during drought shifted their selection from low to high elevations, to greater use of hillsides, and from open-field habitats to riverbeds (Lehmann 2015). This highlights how the variable response of desert animals to decreasing precipitation can be species- and location-specific.

Herbivores must select areas with sufficient forage to meet their nutritional requirements, and NDVI can accurately predict primary

productivity across the landscape (Pettorelli et al. 2005). We would expect sheep to select locations with intermediate forage biomass, as higher biomass would not allow suitable visibility to detect predators, and lower biomass would not provide sufficient nutrition. Although we found this relationship in some periods at both scales, sheep did not select locations based on forage biomass in most periods. Cain et al. (2017) reported that forage selection by desert bighorn sheep is more strongly associated with nitrogen and water content than energy content. Therefore, it is not surprising that, although NDVI as a proxy for forage biomass appeared in many of the top models, confidence intervals of the parameter estimates frequently included zero, which limited its usefulness in predicting resource selection. Similarly, NDVI covariates were also in the top models in other Sonoran Desert ungulate populations, yet most forage parameter confidence intervals encompassed zero (e.g., mule deer, Marshal et al. 2006; desert bighorn sheep, Hoglander et al. 2015). Gemsbok habitat selection in arid regions of Namibia was also not associated with local NDVI values (Lehmann 2015). North-temperate ungulates are generally limited by the nitrogen and energy content of their forage (e.g., Rocky Mountain bighorn sheep, Festa-Bianchet 1988), whereas in desert ungulates, water and nitrogen content of forage may be more nutritionally limiting than digestible energy (Cain et al. 2017). Indeed, in our study area, many browse species are leguminous (i.e., nitrogen-fixing), thereby contributing more significantly to forage biomass than in temperate systems, and browse species comprise a high proportion of our desert bighorn sheep diet (Cain et al. 2008a, b, 2017). This likely renders NDVI a poor predictor for sheep resource selection.

Forage quality (as indexed by NDVI rate of change) was also generally not related to resource selection of desert bighorn sheep in our models, except in autumn during non-drought (population scale), when sheep selected areas with lower quality forage. Highly variable precipitation patterns in desert ecosystems lead to high spatial and temporal variability in plant phenology. In temperate systems, plant phenology follows a more predictable, longer-term seasonal trajectory (i.e., high quality during spring green-up, slowly diminishing quality as summer

progresses, then senescence and shedding of foliage in autumn), whereas in deserts, this process can occur over a very short term every time a substantial rain occurs followed by a dry period. Thus, NDVI rate of change over 8–32 d may not provide a precise measure of forage quality in more variable arid systems. In desert species, diet analyses may provide a better indicator of selection for forage quality than examining areas of use. Previous studies reported increased selection for higher quality forage in ungulate diets during drought (Lashley and Harper 2012, Cain et al. 2017). In our study, as precipitation decreased in early summer (population scale), sheep selection for higher quality forage became stronger at night (although during day they selected lower quality forage). This behavior follows the selective-quality hypothesis, which suggests that since selectivity is highest during periods of lowest available food resources, high-quality forages would be more important in the diet (Jarmin and Sinclair 1979, Weckerly and Kennedy 1992).

Access to water is critical for species living in arid environments, and thus, availability and distribution of water strongly influence species distributions (McKee et al. 2015). Sheep consistently exhibited strong selection for locations closer to perennial water at the population scale, and their proximity to water decreased as a function of decreasing precipitation. During drought, higher quality forages may become depleted near perennial water, forcing sheep to range further from reliable water sources to find suitable forage. In contrast, at the home-range scale, sheep selected locations further from water during drought in autumn and winter, and distance to water was unimportant in nearly all periods in summer. Sheep in this study area selected forages with higher water content during drought across all seasons and also during non-drought in summer (Cain et al. 2017), and so they may be acquiring a higher proportion of their water needs from forage, thereby relying less on surface water. Desert-dwelling mammals have evolved physiological adaptations to enable them to cope in their xeric environment (e.g., lowering respiratory and metabolic rates, producing low-moisture feces and highly concentrated urine, and varying body temperature; Cain et al. 2006). Gedir et al. (2016) proposed that based on the

water content of available forage in this study area, prudent foraging decisions could allow sheep to meet their daily water requirements solely from preformed water in their forage, even during drought. Alternatively, by using areas near perennial water at the population scale, sheep obviate the need to select for locations near water at the home-range scale, in that much of their home range will therefore lie within close proximity to water. This highlights the importance of examining resource selection at multiple spatial scales.

Very hot temperatures during summer days are characteristic of southern deserts, and desert-adapted species are able to cope with this extreme heat by selecting areas that allow them to reduce the cost of thermoregulation (Cain et al. 2006, 2008b). Indeed, sheep in our study selected locations with lower solar radiation and more northerly aspects during day in early and late summer. In early summer at the population scale during drought and at the home-range scale during non-drought, sheep selection for cooler locations coincided with forage covariates and several topographic features being unimportant in sheep selection. Similarly, in late summer at the home-range scale, it coincided with several topographic features and distance to water being unimportant. Perhaps these choices were necessary trade-offs, foregoing good escape terrain and foraging areas, and access to water, for improved thermoregulation. This agrees with a study which found elk (*Cervus elaphus*) in a desert environment selected areas that reduced thermoregulation costs over those that provided the highest-quality forage (Long et al. 2014). Another study in the hot, arid regions of Saudi Arabia reported that on warmer days, Arabian oryx (*Oryx leucoryx*) increased time resting in shade at the expense of feeding time, and when temperatures exceeded 40°C, some individuals more than halved their daily foraging time (Seddon and Ismail 2002). With predicted increases in temperature during this century throughout the southwest USA (Garfin et al. 2013), surface heat loads will increase significantly, and selecting locations in summer that reduce the cost of thermoregulation will become increasingly important for desert species.

Desert systems typically receive <250 mm of precipitation annually, and there can be considerable variation in the amount and distribution of

precipitation among deserts worldwide (Marshak 2019). We see this variation even among deserts within the relatively small area of the southwest United States (e.g., mean annual precipitation, peak season: Mojave, <50 mm, winter; Chihuahuan, 235 mm, summer; Sonoran [our study area], 101 mm, summer/winter; Western Regional Climate Data Center 2005). When drought ensues, we might not expect significant changes in resource selection for species living in the driest deserts (i.e., those with annual precipitation of ~100 mm or less), where precipitation is normally so low that drought-like conditions exist even in years with average precipitation. This situation exists in our study area during early summer when rain rarely occurs, resulting in drought-like conditions in this season nearly every year. Indeed, in early summer (home-range scale), for nearly all of the habitat covariates, sheep did not alter selection as precipitation decreased from non-drought to drought. Perhaps, in species that possess superior abilities for adapting to a desert environment (like the desert bighorn sheep), when conditions reach extremes of aridity, reduced opportunities for them to cope through behavioral modifications (e.g., habitat selection) force them to depend more on physiological adaptations (at least as a short-term measure). In areas such as this, effects of continued drought may instead manifest in reduced survival and reproduction (Douglas 2001, McKinney et al. 2001, Cain et al. 2008a), which could have detrimental effects on the persistence of a species or population, particularly in light of predicted changes in climate.

When determining critical resource requirements of a species or population, it is essential to consider the difference between their fundamental niche (i.e., the range they are capable of occupying) and their realized niche (i.e., the range of environmental conditions they actually occupy; Hutchinson 1957). Drought can affect a species' distribution or the range of a population in the same way as competition, in that they are confronted with restricted resources or constraints on resource use, they adjust their habitat utilization to compensate, and this determines their realized niche. Furthermore, desert bighorn sheep range in areas that are largely inaccessible to potential competitors for resources, and not only can drought force them to select locations

where they are more susceptible to predators, but these areas may also include other herbivore species that compete for dwindling resources.

Many elements in an animal's environment comprise the resource requirements of a species, and these elements interact and are dynamic across time and space. Desert-dwelling species are confronted with the added challenge of a highly variable and uncertain environment that is inherent to desert systems. In this study, we used resource selection functions that included multiple components of the desert bighorn sheep environment (i.e., topographic features, forage characteristics, and climatic conditions) to examine resource selection in a desert mammal. In the desert environment, there is high temporal and spatial variation in precipitation through the year, and temperatures can differ significantly by location and time of day; therefore, examining changes in sheep selection across diel periods and seasons allowed us to identify critical resource requirements that may otherwise have been overlooked. Furthermore, precipitation conditions over the study period ranged from severe drought to above average, and this enabled us to demonstrate how resource selection in a desert species can also be strongly influenced by climatic conditions. The suite of habitat components at any given location includes benefits and costs: Predation pressure may be greater in areas of preferred forage; superior thermoregulation sites may be further from water. Therefore, decision-making for resource selection involves trade-offs, whereby individuals must prioritize which beneficial features are of immediate concern, and balance that with minimizing costs imposed by other features. In addition, it should be noted that we investigated only female desert bighorn sheep and that seasonal resource requirements of females may differ from males (Bleich et al. 1997, Mooring et al. 2003, Hoglander et al. 2015). For example, lambing and lactation in desert bighorn sheep can potentially occur anytime from winter through late summer (Rubin et al. 2000, Bangs et al. 2005b, Karsch 2014). Fitness for females is directly related to offspring survival. During the time when mothers are with lambs, they will prioritize selection of habitat features (e.g., escape terrain) that would reduce lamb predation risk (Karsch et al. 2016). Conversely, fitness of males is determined

by successful breeding and because males provide no parental care, they frequently forage in areas away from escape terrain where they can acquire resources needed to increase body size. Thus, further research is recommended to examine how male desert bighorn sheep may alter their resource selection during drought to better understand critical resource requirements of a population of desert bighorn sheep in response to climate change.

Our results highlight the importance of identifying selection at multiple scales, both spatial and temporal, when examining the interrelationship between species and their environment. We have provided insight into the dynamics of resource selection in desert mammals, and how they respond to constraints imposed on them by their environment. This work can serve to inform strategies for managing and conserving species living in arid environments when faced with changes in climate.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3175/full>