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Extreme droughts shrink suitable habitats and reduce fitness for large mammals in the American West

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Droughts are intensifying across the biosphere, yet the consequences of this phenomenon for wildlife habitat suitability and fitness are poorly studied. We analyzed 12 years of GPS telemetry data for three large mammal species—herbivorous mule deer ($N = 2854$), omnivorous black bears ($N = 103$), and carnivorous cougars ($N = 105$)—to evaluate the effects of drought on each species' habitat selection across a 500,000-km^2 aridity gradient in the interior West, USA. Additionally, we evaluated interannual variation in mule deer reproduction as a function of drought intensity. Severe drought reduced the area of highly selected habitat by 10.0% for mule deer, 14.3% for black bears, and 18.2% for cougars, suggesting stronger negative effects of drought at upper trophic levels. We also found that mule deer fawn recruitment decreased by >34% under extreme drought conditions. Our findings highlight the critical influence of drought on habitat selection of large mammals and common indices of mule deer fitness. Furthermore, we underscore the need for integrating predictions of climate-driven environmental changes into wildlife conservation planning.

Droughts are increasing in frequency, severity, and duration across biomes globally, and are among the most pressing climate-induced threats to wildlife habitats and populations[1–4]. Prolonged water shortages and shifting precipitation patterns reduce primary production and biomass[5–8] while contributing to both short- and long-term restructuring of plant community composition[9–12]. The bottom-up effects of reduced resources as well as changes in plant composition likely propagate through trophic levels via direct and indirect pathways, but there is little evidence regarding which trophic levels are most vulnerable to drought impacts[13]. Understanding how drought influences wildlife habitat selection across trophic levels—as well as how those effects translate to fitness outcomes for animal populations—is crucial, particularly as population declines[14] and range shifts[15] become more pronounced under climate change.

The demographic effects of drought vary across trophic levels, though prevailing hypotheses produce disparate predictions. The theory of ecological efficiency predicts widely negative effects of reduced ecosystem productivity on wildlife habitats because drought-induced limitations in primary production constrain the energy available to sustain upper trophic levels[16,17]. Across biomes, the biomass of predators scales with that of their prey, a relationship that is directly linked to the availability of energy in the ecosystem in the form of primary productivity[18,19]. Where ungulate populations are predicted to decline under intensifying drought conditions[20], it follows that carnivores with high metabolic needs will face similar outcomes.

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Indeed, Prugh et al.[13] found that declines in species abundance caused by drought were strongest at the bottom (plants) and top (carnivore) of the food web.

Yet from animal behavioral perspectives such as those considered under optimal foraging theory[21], droughts could lead to advantages in some scenarios. For example, carnivores might benefit during droughts by exploiting reductions in prey body condition that confer increased hunting success[22], allowing them to maximize their energy efficiency and enabling more adaptive population responses to extreme conditions. The environmental constraints imposed by droughts can also lead to dramatic changes in habitat selection as animals experience tradeoffs in resource acquisition and safety, sometimes leading to increased herbivore vulnerability to predation[23]. However, benefits to predator foraging are likely to be temporary, as prey population declines will reduce carnivore success, and ultimately fitness. Unfortunately, difficulty predicting demographic responses to drought conditions is compounded by limited data on wildlife population changes across broad geographic domains.

In light of these data scarcities and competing theories (ecological efficiency vs optimal foraging theory), disentangling the impacts of drought on mammal habitat selection and fitness remains challenging. Habitat selection modeling—a common tool for identifying priority habitats for wildlife conservation—can provide a framework that bridges the gap between environmental conditions and wildlife fitness by capitalizing on more readily available habitat use data. Predicted 'suitable' habitats can be conceptualized as representing a species' fundamental niche, the environmental space that hypothetically supports the persistence or growth of populations, and should thus be generally representative of animals' fitness outcomes[24–28]. Yet, very few wildlife studies have directly linked environmental changes and predicted habitat selection to measures of population growth or reproductive success[29,30], and certainly not at geographic scales relevant for conserving large, far-ranging mammals in the face of expansive drought impacts.

Here, we assessed the impacts of drought on wildlife habitat selection in the American West, an arid region experiencing—and forecasted to continue—changes in drought frequency and severity[4,31–33]. We analyzed 12 years of high-resolution GPS telemetry measurements for three large mammal species with distinct dietary niches—herbivorous mule deer (*Odocoileus hemionus*), omnivorous black bears (*Ursus americanus*), and carnivorous cougars (*Puma concolor*)—at 56 study sites in Utah and Nevada, USA (Fig. 1). We first assessed habitat selection responses to coincident, satellite-based measurements of vegetation productivity, biomass, and terrain using individual-level resource selection functions (RSFs), from which we produced high-resolution models of species-level annual habitat selection patterns from 2010-2021. We then quantified reductions in the annual area of highly selected habitat caused by drought and predict (P1) that drought intensity will decrease the area of highly selected habitat for mule deer, black bears, and cougars. If we expect those highly selected habitats to represent species' fundamental niche, then the theory of ecological efficiency predicts (P1a) that upper trophic levels will be more strongly impacted by drought intensity, leading to larger decreases in highly selected habitat for cougars and bears relative to mule deer. Alternatively, based on optimal foraging theory, we predict (P1b) that, because of the direct relationship with vegetation, drought intensity will decrease the area of highly selected habitat more strongly for mule deer than for black bears and cougars. We also assessed the contribution of both habitat selection and drought conditions to annual mule deer fawn recruitment, represented by the number of fawns per 100 does across a subset of 23 study sites in Utah from 2012 to 2021, using generalized additive mixed effects models (GAMMs). We hypothesize that mule deer fawn recruitment is influenced by environmental conditions experienced by a female during the last stage of gestation, as well as the early-life environmental conditions experienced by a fawn. Therefore, we predict that (P2) drought intensity will decrease mule deer fawn recruitment, while areas of highly selected habitat will increase fawn recruitment. We only have a proxy of fitness for mule deer, preventing us from testing the effect of habitat selection on fitness proxies for black bears and cougars. Importantly, annual mule deer fawn production plays a dominant role in supporting reproduction of large-bodied carnivores and some omnivores in these systems[24,34]. Thus, drought-induced changes to mule deer reproduction across the macroscale of our study system would likely reverberate up through higher trophic levels. Further, integrating habitat selection outputs with mule deer recruitment data allowed us to test the efficacy of extrapolating population fitness outcomes from broad-scale habitat selection model predictions.

Results

Drought-induced changes in habitat selection

The area of highly selected habitat per year tracked closely with the average annual drought intensity (Fig. 2A), ranging from 46,864 km^2 to 53,720 km^2 for mule deer, from 46,405 km^2 to 54,829 km^2 for black bears, and from 45,221 km^2 to 56,399 km^2 for cougars. Highly selected habitats were designated as pixels with annual RSF scores greater than the 90th percentile of mean suitability surfaces, or 0.81, 0.44, and 0.82 for mule deer, black bears, and cougars, respectively. Bears in this arid region are found in lower densities due to the generally lower productive habitat, and omnivore selection in general tends to be weaker than other consumer groups, which may explain the lower RSF scores for black bear compared to mule deer and cougar. High levels of drought severity, which ranged from 0 (no drought) to 5 (most severe drought) as derived from U.S. Drought Monitor, significantly reduced the amount of highly selected habitat for all three species and trophic levels (Fig. 2B; mule deer: $\beta = -0.58$, se = 0.11, $p < 0.001$; black bears: $\beta = -0.85$, se = 0.15, $p < 0.001$; cougars: $\beta = -1.10$, se = 0.17, $p < 0.001$). Across the region, models predicted 10.0%, 14.3% and 18.2% declines in highly selected habitat for mule deer, black bears, and cougars, respectively, between the least (i.e., wettest) and most severe drought years of the study period.

Species-averaged habitat selection, derived from individual RSF models, was dependent on several environmental characteristics, resulting in broad scale spatial heterogeneity across Utah and Nevada (Fig. 3). Black bears ($\beta = 0.50$, se = 0.08) and cougars ($\beta = 0.21$, se = 0.07) selected areas with higher above ground biomass, whereas mule deer ($\beta = -0.42$, se = 0.021) avoided areas with higher above ground biomass (Fig. 4). Shrub habitat type was used in proportion to its availability by mule deer (Fig. 4), but it was avoided by cougars ($\beta = -0.46$, se = 0.02) and black bears ($\beta = -0.91$, se = 0.09). Mule deer shifted to preferring shrub habitats when they contained more biomass ($\beta = 0.18$, se = 0.02), but there was no evidence that cougars or bears adjusted their selection for shrub cover when biomass varied (Fig. 4). All three species selected for intermediate elevations and higher NDVI (Fig. 4). The annual habitat selection models had high predictive performance with overall accuracies of 0.93 ± 0.02 (mean ± sd), 0.90 ± 0.07, and 0.92 ± 0.06 for mule deer, black bears, and cougars, respectively, as measured by Spearman rank correlation with k-fold cross validation ($k = 5$).

Mule deer recruitment

Fawn recruitment of mule deer populations was greatly reduced by high-intensity drought conditions. Median fawn recruitment during the study was 58 fawns per 100 adult females, ranging from 39 (5th percentile) to 74 (95th percentile), while drought intensity varied markedly through time (Supplementary Fig. 1). Annual fawn recruitment was negatively correlated to drought intensity (EDF = 3.37, $F = 6.687$, $p < 0.001$), with the GAMM explaining 32.4% of the deviance in fawn recruitment. We observed an apparent threshold effect in which fawn recruitment rates dropped precipitously when drought intensity passed from moderate (drought intensity of 2) to more severe drought conditions (Fig. 5A). We also found a positive relationship between fawn recruitment and habitat selection at the study area scale (EDF = 2.37, F = 3.013, $p = 0.027$, 26.7% deviance explained), with a notable uptick in fawn recruitment rates at study sites with a higher habitat selection score (Fig. 5B). The habitat selection score at used locations had the lowest explanatory power for mule deer recruitment with 12.9% of deviance explained, and there was a positive, though non-significant, relationship with fawn recruitment (EDF = 1.34, $F = 3.090$, $p = 0.099$) (Fig. 5C).

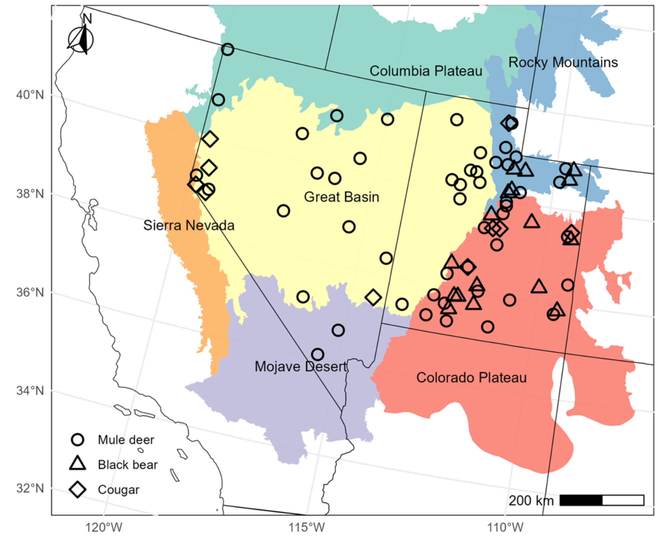

Fig. 1 | Map showing the location of the 56 study areas. Location of study areas of mule deer ($n = 2854$), black bear ($n = 103$), and cougar ($n = 105$) used to assess habitat selection patterns. The different background color represents the different ecoregions.

Discussion

Drought is a strong limitation on the amount of energy available for primary and secondary consumers[6,35–37]. Yet, we have a limited understanding of how droughts affect wildlife habitat selection, and moreover, whether the environmental impacts of drought explain and predict variation in species fitness. As predicted (P1), we found that the availability of highly selected habitats of three species with distinct dietary niches (herbivores: mule deer, omnivores: black bears, and strict carnivores: cougars) was substantially diminished by drought. We also found that, in accordance with P2, mule deer fawn recruitment declined sharply with increasing drought intensity and was positively correlated with highly selected habitat. In line with findings of carnivore population sensitivity to droughts in California by Prugh et al.[13], the negative effects of drought on habitat selection were strongest at higher trophic levels (in accordance with P1a and contrary to P1b), i.e., cougars and bears compared to mule deer. Similarly, Stoner et al.[19] found that primary productivity explained more of the variance in cougar abundance than it did for mule deer ($r^2 = 0.67$ vs 0.58, respectively), suggesting that declines in primary production ultimately had stronger impacts on top carnivores than on their herbivore prey. Our results, combined with the previous work of Stoner et al.[19] and Prugh et al.[13], suggest that the fitness consequences of drought on higher trophic levels may be more severe than at lower trophic levels because of the exponential decline in energy transfer across higher trophic levels, though we require additional data on the reproductive output of these species to establish those linkages. Overall, our results highlight the risks to animal reproduction and abundance posed by

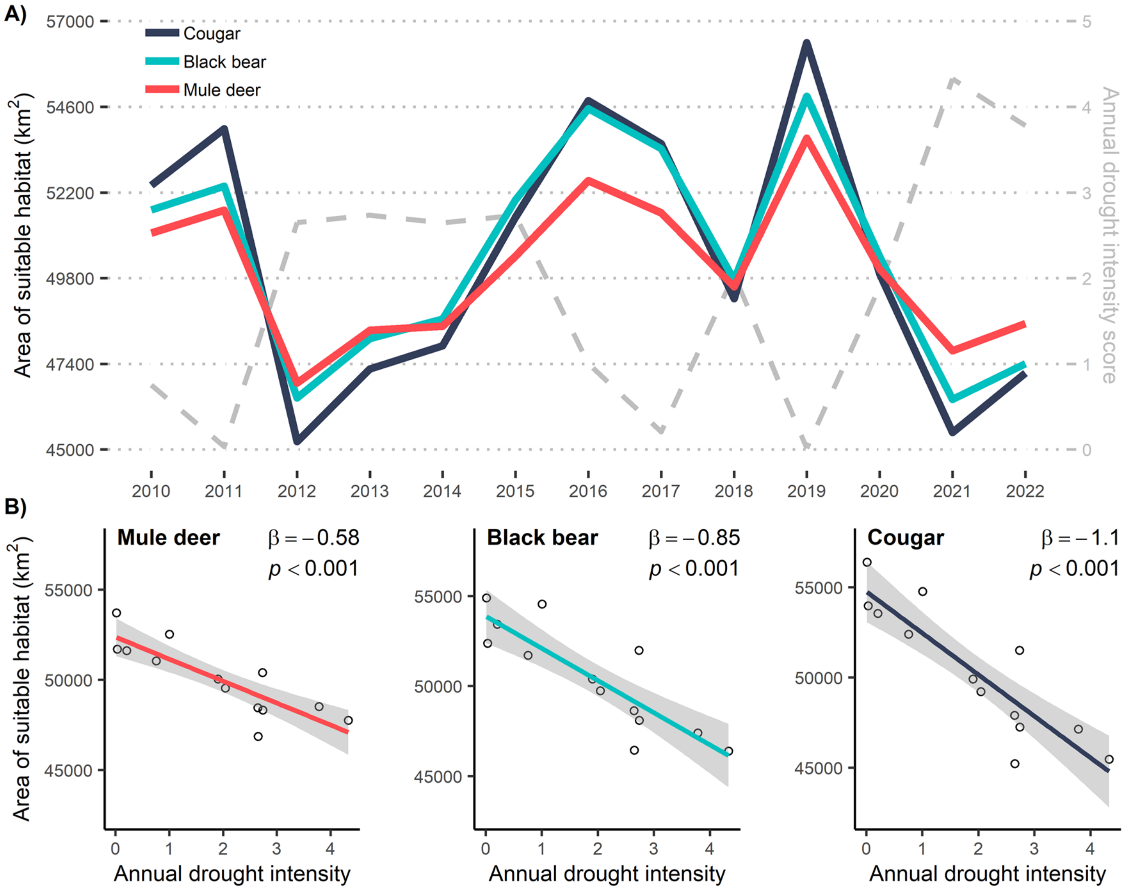

Fig. 2 | Relationship between drought intensity and highly selected habitats for mule deer, black bear, and cougar. These figures show **A** Trends in highly selected habitat area (predicted RSF habitat score > species 90th percentile RSF score, left-hand y-axis) and mean annual drought intensity score (right-hand y-axis, dashed line) through time. **B** Prediction (line) and confidence intervals for generalized linear model comparing annual drought severity across Utah and Nevada to the total area of highly selected habitat for each species. Each point represents values for 1 year (2010–2022). Axes values were back-transformed from scaled values used in GLMs for easier interpretation of fitted relationships. Mean annual drought intensity (**A**: right-hand y-axis, **B**: x-axis) was calculated as the average weekly drought monitor severity category (0–5), weighted by area, for Utah and Nevada per year.

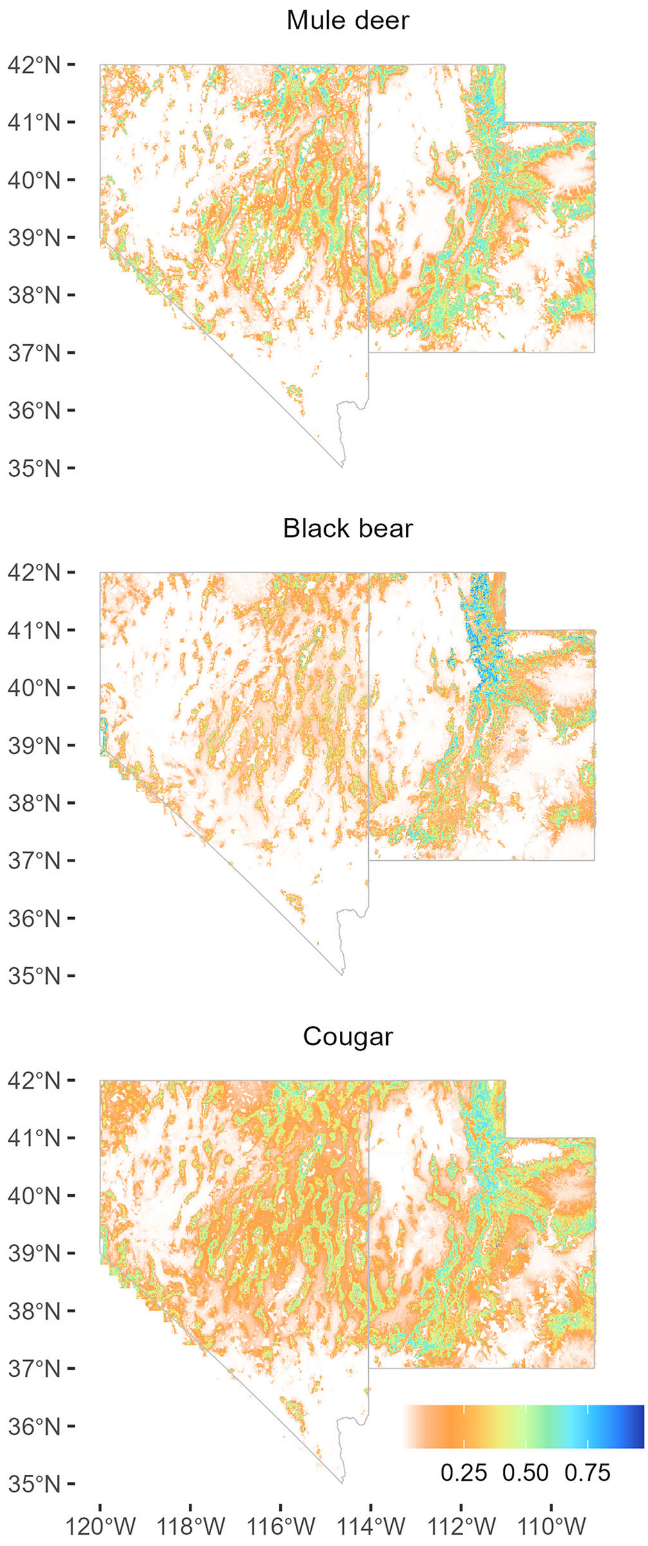

Fig. 3 | Average predictive surfaces of habitat selection models. This figure shows the spatial heterogeneity of the relative habitat selection strength of mule deer, black bear, and cougar in Utah and Nevada, USA. The relative habitat selection strength is not comparable across species and shows the relative probability a location would be selected if available by an animal given the variables included in the model. It does not represent the probability of using a location, nor do they directly reflect wildlife abundance. Therefore, these maps should be viewed as predictions of core and critical habitat and possible species range expansions.

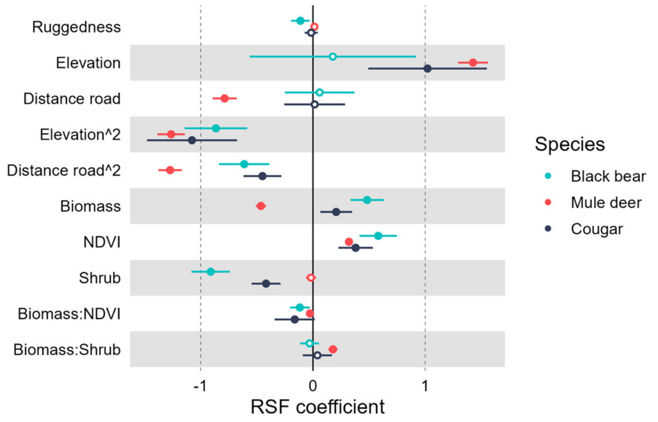

Fig. 4 | Forest plot of habitat selection model coefficients. Species level resource selection function coefficients of mule deer ($n = 2854$), black bear ($n = 103$), and cougar ($n = 105$) habitat selection from 2010 to 2021.

increasing drought occurrences and severity that are forecasted to impact the American West and other sub-tropical and temperate biomes around the world[1,2,31].

Mule deer adaptability to drought conditions may be conferred by their increased selection of shrub cover relative to the other species. Whereas black bears and cougars showed negative selection for shrub habitats, mule deer incorporated more shrub cover into their habitat selection during drought (Supplementary Fig. 2). Though shrub habitats were not shielded from drought-induced declines in NDVI (Supplementary Fig. 3), shrublands are generally more resistant to intense drought impacts compared to herbaceous cover[38]. Mule deer are a well-established edge species with a preference for ecotones and shrub habitats[39,40], and our findings suggest that deer use of shrub habitats could offset the effects of decreased vegetation quality during drought periods. Though the effects of drought on mule deer habitat selection appear to be reduced relative to higher trophic levels, droughts still led to less highly selected habitat for deer accompanied by negative effects on mule deer recruitment.

We found a substantial negative effect of drought intensity on mule deer fawn recruitment, leading to an over 34% decrease in fawn recruitment between no drought and the most severe drought conditions (Fig. 5A). Along with reductions in the overall amount of forage available, drought also diminishes the nutrition and palatability of remaining food resources that support growth and lactation for mule deer during summer months and subsequent overwinter survival[41,42]. Such impacts on mule deer body condition and the maternal ability to support juvenile survival are strongest during summer when fawns are still nursing. Unfortunately, these drought effects are not captured in the RSF analysis, which likely contributes to our observations of much stronger direct effects of drought on fawn recruitment relative to the mule deer habitat selection scores (Fig. 5C). Harsh environmental conditions leading to diminished food supply and worsened maternal body condition have been linked to reduced fawn recruitment, along with survival of other primary consumers, in a number of studies[43–46]. Droughts may have secondary effects, such as the reduction of vegetation structure that provides concealment from predators, or lead to animal aggregations around remaining water sources, increasing crowding, disease transmission, and vulnerability to predation for fawns[45,47]. Importantly, the high sensitivity of fawn recruitment to greater than moderate drought severities suggests that mule deer population growth in the region may be episodic, i.e., pulsed during relatively wet years with little recruitment during dry periods, with this effect being most pronounced in the driest and/or most climatically variable systems.

Though drought was the strongest predictor of mule deer recruitment rates, our results also aligned with predicted (P2) positive effects of highly

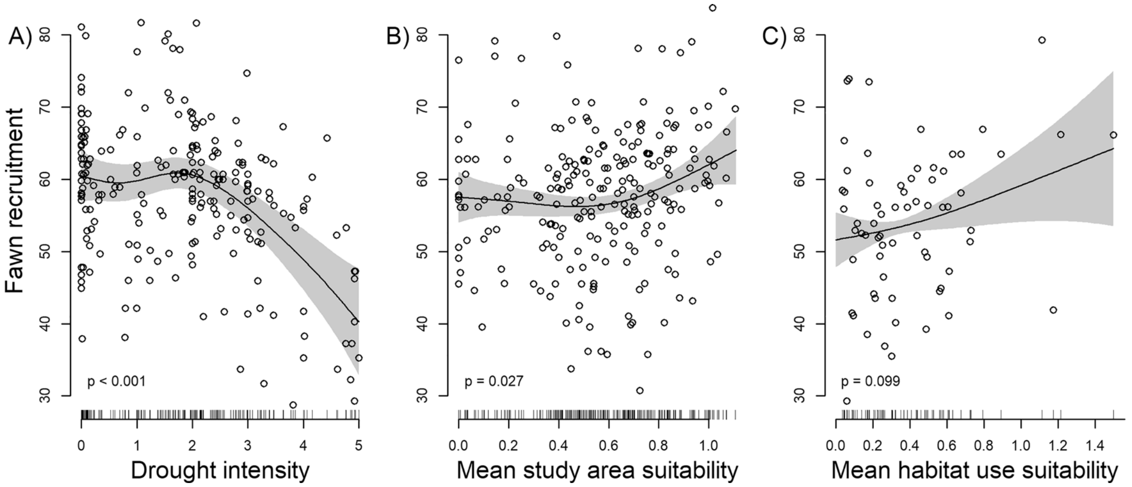

Fig. 5 | Effect of drought intensity and habitat suitability on mule deer fawn recruitment. Prediction (solid line), confidence intervals (shaded area), and partial residuals (dots) of the Generalized Additive Mixed Models used to determine the effect of **A** drought intensity, **B** study area habitat suitability, and **C** mule deer habitat use suitability on mule deer recruitment in Utah and Nevada. Drought intensity was calculated with data from the US drought monitor (https://droughtmonitor.unl.edu) where 0 = no drought conditions, 1 = abnormally dry conditions, 2 = moderate drought, 3 = severe drought, 4 = extreme drought, and 5 = exceptional drought conditions.

selected habitat on fawn recruitment (Fig. 5B, $p = 0.03$). Notably, fawn recruitment appeared to be highest in study areas with higher habitat selection scores, highlighting the link between selected habitat and fitness-related outcomes (Fig. 4). The observed positive relationship between habitat selection and mule deer recruitment suggests that highly selected habitat confers benefits to herbivores, supporting the use of habitat selection surfaces as representations of a species' fundamental niche. We thus effectively captured a link between a common proxy for fitness and frequently employed habitat selection models that measure animal behavior and inform habitat conservation efforts[48]. As such, maps providing robust predictions of habitat selection could be pivotal in the management of large mammal populations across broad spatiotemporal scales, particularly in the common cases of species or study areas where reliable measurements of fitness are hard to come by. In this case we have shown its utility for the management of mule deer, a species that is widespread throughout western North America and serves as both a driver of cougar abundance and distribution[19,24] as well as a major source of conservation revenue through hunting-related recreation[49].

We showed that mule deer fawn recruitment estimated during late autumn was influenced by environmental conditions experienced by a female and its fawn during summer. Although there is a temporal gap between measures of drought and fawn recruitment, drought intensity alone explained 32.4% of the deviance in mule deer fawn recruitment. Other factors not included in the analyses could have played an important role in fawn recruitment, including female pregnancy rate, fawn predation, and disease. How drought interacts with other sources of wildlife mortality is a question in need of additional research.

Given the observed sensitivity of habitat selection model predictions to drought for upper trophic level species (Fig. 4), as well as the magnified effect of droughts on carnivores observed by Prugh et al.[13], we speculate that the declining fawn recruitment of mule deer under drought conditions may also signal detrimental fitness consequences for predatory species that depend on annual ungulate production. Mule deer are the major food resource for cougars in western US ecosystems[50], and fawns are particularly important for post-parturient female cougars because of their low risk and high capture success[51]. Predation by black bears can also be a major source of fawn mortality, as fawns provide an important protein source as bears transition from early spring vegetation to summertime berry foraging[52,53]. In addition, kleptoparasitism by black bear can be important and was detected at 47.8% and 77.2% of cougar kill sites in Colorado and California, respectively[54], and kleptoparasitism intensity likely varies positively with drought severity. The limitation of productivity and therefore energy available to consumers appears to be a primary pathway through which drought effects propagate through upper trophic levels, likely offsetting any potential short-term foraging benefits that droughts could confer to carnivores[22]. However, given the long lifespans of these species and spatiotemporal heterogeneity of vertebrate population dynamics, we expect time-lags between herbivore reproductive failures and subsequent population declines at the next higher trophic level[24]. There is dire need for conservation action across broad scales to mitigate the deleterious effects of drought on habitats for far-ranging, large mammals, particularly at higher trophic levels most sensitive to demographic perturbations[55].

As wildlife face aridification at massive scales, habitat suitability assessments can offer insight into potential refugia—including agricultural and urban areas that offer relatively stable and productive environments during drought but elevated levels of human-wildlife risk, species range expansion opportunities, and critical habitats to prioritize for ecosystem management[56,57]. By producing habitat selection maps at a broad geographic extent for three wide-ranging mammals using RSFs, we provide a comprehensive view of the impacts of drought on wildlife habitats and link these effects to changes in mule deer recruitment that contribute to population viability. Our habitat selection models support many effects that have been previously identified for our three study species, such as avoidance of roads by mule deer[58], cougar preference for higher elevations[59], and black bear avoidance of non-forested habitats[60]. Similarly, Morano et al.[40], observed mule deer selection for high productivity habitats near the southwest edge of our study extent. However, some habitat effects can be context-dependent (Supplementary Note 1), revealed by observed effects inconsistent with available literature such as cougar avoidance of shrub habitat in our study areas that contrasts with previous works observing selection for shrub habitats in California[59]. We also show the unique contribution of aboveground biomass datasets in assessing wildlife habitat suitability, with distinct divergence in selection for biomass between herbivorous mule deer, omnivorous bears, and carnivorous cougars. We also observed selection patterns for mule deer that depended on habitat type, in which mule deer were more likely to select shrub habitats when the biomass was higher (Fig. 4). Context-dependency in habitat selection across space highlights the need for in-situ habitat use data to inform habitat suitability analyses for conservation targets.

Though intensifying droughts are only one facet of climate changes occurring globally, our findings present clear evidence of the threat to wildlife population viability stemming from reductions in primary production in natural habitats. Wildlife habitat quality is intrinsically dependent on the availability of primary resources that are the energy base of ecosystems, and declines in ecosystem productivity due to climate change are highly likely to reduce animal fitness and overall carrying capacities[13,19]. Collectively, these patterns suggest range contractions for wildlife in what are currently marginal habitats and commensurate expansion into, or greater use of, anthropogenically subsidized environments such as agricultural and urban areas[19,61]. Such changes can lead to economic consequences that compound the detrimental ecological effects of global change, as wildland habitats harbor fewer animals and those in anthropogenic environments become a source of conflict and an economic burden[62–64]. In the arid environments of the American Intermountain West studied here, wildlife populations and habitats are expected to be drought tolerant to some extent, and thus our results may represent a conservative estimate of the negative consequences of severe droughts for less drought-adapted ecosystems. In more mesic systems, higher baseline productivity and greater canopy cover could reduce proportional contraction of highly selected habitat, at least for shorter-term drought conditions, but species may also be less adapted to moisture deficits from droughts, such that rare, prolonged droughts could still produce strong behavioral and demographic impacts. Given these collective challenges, incorporating the inherently dynamic nature of both wildlife habitat use and environmental characteristics into broad-scale habitat suitability analyses is paramount for natural resource managers aiming to prioritize core habitats and predict future habitat selection and range expansions, particularly during events like drought.

Methods

Study area

We analyzed GPS location data from radio-collared mule deer ($n = 2854$ individuals for 9,738,332 locations), black bears ($n = 103$ individuals for 1,263,018 locations), and cougars ($n = 105$ individuals for 1,274,388 locations) across 56 study areas mostly in the Great Basin, Rocky Mountains, Colorado Plateau, and Mojave Desert ecoregions from 2010 to 2021 (Fig. 1). Mean summer temperatures varied between 10 to 35 °C and precipitation varied from 10 to 1100 mm/year across the large geographical extent of the study, and elevation ranged from 1200 to 3000 m above sea level. The prevailing plant communities correspond to temperature and precipitation gradients associated with elevation. These include succulents and evergreen shrubs in the lowest and driest areas (<1540 m; *Yucca* sp., *Larrea tridentata*, *Coleogyne ramosissima, Artemisia tridentata*) and shrublands grading into piñon-juniper woodlands (*Pinus sp*., *Juniperus* sp.) at 1540 to 2460 m. Above 2150 m, higher precipitation and shorter growing seasons support montane and subalpine communities dominated by aspen and mixed conifer forests (*Populus tremuloides, Pinus ponderosa, Pseudotsuga menziesii, Picea engelmannii, Abies lasiocarpa*). Alpine communities can be found in mountain ranges that exceed ~3300 m[19].

Data collection

Wildlife GPS data was collected across Utah and Nevada, USA, between 2010 and 2021 by state and federal agencies and for university studies. Animal captures and handling were approved by an ethical committee (Brigham Young University IACUC protocol: #150110; USDA-NWRC IACUC for QA-3040; the Institutional Care and Use committee at the University of Nevada, Reno (protocol A06/07-28); Nevada Department of Wildlife ethical guidelines (Scientific Collection Permit #261454), see Van de Kerk et al.[65] and Kirkland[66] for more details. Original GPS positions were collected primarily at 2 h intervals, but for 1 h intervals we resampled the GPS positions tracks to 2 h. We visually inspected GPS tracks to remove outliers and unlikely movements. Individual annual home ranges were delineated using a 95% kernel density estimator[67] using the hr_kde function with the reference bandwidth (hr_kde_ref function) in the amt package[68]. We used kernel home range because we focus our analyses on where the animal was or tend to be found such as core areas and long-term space use. Within each individual's annual home range, we randomly generated available points at a density of 20 points per km^2 for a minimum of 365 random locations per individual, and removed locations identified as open water. Animal home ranges vary widely in size, and this approach ensured that we equally sampled the availability of resources spatially and temporally to assess third-order habitat selection[69]. Each random location drawn in the annual home range was assigned a time stamp randomly sampled from the corresponding animal's real GPS data to be able to extract the corresponding NDVI value during that day. We focused our analyses on locations with a timestamp during summer (May–July) which show contrasting drought intensity across year (Supplementary Fig. 1).

We used fawn recruitment data, determined as the ratio of fawns per 100 adult females, within Wildlife Management Units (WMUs) from the Utah Big Game Annual Report published by Utah Division of Wildlife Resources (UDWR). UDWR determined sex and age composition of mule deer population in December or January each year with ground and aerial classification counts (see refs. 70,71 for further details). WMUs were generally used to determine the study areas assigned to mule deer GPS collar data and thus align with those in the recruitment dataset.

Environmental determinants of recruitment for mule deer and habitat selection for all three species were derived from satellite imagery and other geospatial sources. We used an elevation layer with a 1 arc-second (ca. 30 m) resolution raster from the USGS published in 2020 (https://data.usgs.gov) to calculate Terrain Ruggedness Index (TRI) with the "terrain" function in the "terra" R package[72]. For each used and available location, we extracted both the elevation and TRI. We also extracted land cover types from the National Land Cover Dataset[73] and Normalized Difference Vegetation Index (NDVI) values at daily, 500 m resolution from MODIS (MCD43A4 Version 6.1). We extracted aboveground biomass, in units of Mg/pixel, at 30 m, annual resolution from 2010 to 2021. Aboveground biomass was estimated with a gradient-boosted regression tree[74] trained on GEDI L4A footprint estimates of aboveground biomass density (Mg/ha)[75] with Landsat-based metrics of tree cover (Sexton et al.[76]), phenology, disturbance history, and DEM-derived terrain variables as predictors[76]. Dynamic measures of NDVI and biomass were extracted for the time period (day for NDVI, year for biomass) matching each data point's timestamp. We computed Euclidean distance to the nearest road based on the USGS National Transportation Dataset[77].

To evaluate the effects of drought intensity on mule deer recruitment, we calculated the mean drought intensity in the summer months per study area per year using data from the U.S. Drought Monitor (https://droughtmonitor.unl.edu; Supplementary Fig. 1). The Drought Monitor calculates drought severity using a convergent data approach that integrates several biophysical metrics, including precipitation and temperature, as well as expert input and field observations. We converted the 6 categorical indicators of drought severity provided by the Drought Monitor ("None" = Normal or wet conditions, "D0" = Abnormally dry, "D1" = Moderate drought, "D2" = Severe drought, "D3" = Extreme drought, "D4" = Exceptional drought) to a continuous measure of drought by assigning each incremental category of increasing drought a value from 0 (values of "None") to 5 (values of "D4").

Statistical analyses

We used resource selection functions (RSFs) (i.e., general linear models with a logit link) to compare resources used at real GPS locations (coded 1) and habitat availability at random locations (coded 0) to investigate mule deer, black bear, and cougar habitat selection[78,79]. We ran one model for each individual per year that included TRI, elevation and elevation^2, distance to road and distance to road^2, NDVI, above ground biomass, and a categorical variable representing whether or not the location was in shrub habitat type (the only habitat type available in all study areas). To further explore the effect of above ground biomass on habitat selection, we included an interaction between biomass and NDVI, as well as an interaction between biomass and shrub cover. Multicollinearity was low with all Variance Inflation Factors (VIF) < 5[80]. Lastly, we scaled all numerical variables for easier convergence and comparison of effect sizes (mean = 0, sd = 1). We used non-parametric bootstrapping (np.boot function from the np.test package[81] with 9999 replicates) on individual coefficients to obtain median and standard-deviation species-level habitat selection coefficients for the entire 12-year study period. By running the same model for every individual, we were able to obtain comparable habitat selection estimates across species. We evaluated the predictive performance of RSF models using Spearman rank correlation with k-fold cross validation ($k = 5$) as a measure of overall accuracy, as shown by Johnson et al.[82], and spatial autocorrelation was not explicitly incorporated in defining the folds[79] (See Supplementary Note 2 for leave-one-out cross-validation results). We used the species-level RSF coefficients to produce annual (2010–2022) and average predictive surfaces that represent the relative habitat selection strength across all of Utah and Nevada for mule deer, black bear, and cougar, in which the RSF score values were the exponentiated output of the RSF model equations [e.g., RSF score $= \exp(\beta_1 X_1 + \beta_2 X_2 + \ldots\ \beta_n X_n)$][79]. Annual predictive surfaces were used to quantify highly selected habitat of mule deer, averaged per year across study areas and across mule deer GPS locations, in subsequent fawn recruitment analyses. The 12-year predictive surfaces were visualized by transforming each species' RSF scores using the logistic function ($P =$ RSF score/1 + RSF score), thus bounding selection strength values from 0 to 1. These values do not indicate true probabilities but are used solely for visualization of relative selection strength.

We calculated annual areas of highly selected habitat across the states of Utah and Nevada for each species using the predictive RSF surfaces. We defined "highly selected" habitat as RSF scores falling within the 90th percentile of the species' 12-year RSF scores and then calculated the area of the annual RSF surfaces where the RSF scores were classified as highly selected. We also calculated annual state-wide drought conditions by first finding the weekly average of drought scores (0–5, https://droughtmonitor.unl.edu), weighted by the total surface area per drought value, and then averaging weekly drought scores for May–July for each year across Utah and Nevada. We used a generalized linear model to compare the scaled annual area of highly selected habitat for each species to scaled drought intensity.

To evaluate the effect of drought intensity on mule deer recruitment, we used general additive mixed models (GAMMs) with fall fawn count (i.e., no. fawns/100 does) as the dependent variable and year as a random intercept. We independently assessed the effects of drought and highly selected habitat on calf recruitment by compiling three separate GAMM models for which three independent variables were assessed on an annual basis: (1) drought intensity, (2) mean mule deer habitat selection scores per study area extent representing habitat suitability at the population level in a given year, and (3) the mean habitat selection scores at used locations representing the habitat suitability used by GPS-collared individual. Study area extents were defined as the bounding box of 95% of all years of mule deer GPS locations per study area. In model 3, only data for years and sites for which GPS collar data was available were used in the model ($n = 68$), compared to all sites and years of recruitment data in models 1 and 2 ($n = 229$), which prevented us from using an AIC-based approach. All the independent variables were used with splines to detect non-linear trends in their effect on deer recruitment. All assumptions were successfully verified. All data processing and analyses were conducted using R 4.3.1[83].

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

Data[84] are available in Borealis at https://doi.org/10.5683/SP3/FSYE1M.

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Competing interests

The authors declare no competing interests

Additional information

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