



## ARTICLE

# Acute drought desiccates highly used habitat and drives herbivores into irrigated croplands

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## Abstract

In arid and semiarid regions, extreme, extended droughts are becoming more frequent due to climate change. Drought is driving wildlife to seek out food or water resources where they are not as limited, such as in irrigated croplands. We collected GPS locations from 41 mule deer, a generalist herbivore reliant on primary productivity, within three study areas in Utah, USA, during a summer without drought conditions and a summer with extreme drought. This natural experiment provided an opportunity to assess how mule deer shifted their habitat selection, specifically whether drought increased mule deer's use of anthropogenic resources. We integrated remotely sensed estimates from ECOSTRESS, an instrument mounted on the International Space Station that measures evapotranspiration, to characterize a shift in resource use. Mule deer resource use was strongly influenced by the amount of evapotranspiration. In the drought year, shrub habitats lost succulence and mule deer avoided them (57.0% shrub habitat use in baseline vs. 44.6% during drought) and sought out agricultural croplands (increase from 6.2% to 11.8% from baseline to drought). Critically, this behavioral switch from shrub to crop was mediated by the rate of evapotranspiration and we identify the shift when evapotranspiration was >1.03 mm/day. We estimated that the proportion of shrub habitat in the study area with evapotranspiration >1.03 mm/day dropped from 68.8% to 27.2% between the baseline and the acute drought year. Evapotranspiration measured by ECOSTRESS provides complementary information to normalized

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difference vegetation index (NDVI), a commonly used metric of vegetative greenness, and offers a mechanistic understanding of ungulate resource use that increases the performance of habitat selection models for herbivores. As the impacts of climate change become more acute, wildlife will be drawn from natural areas to locations with anthropogenic resources, elevating the risk of human–wildlife conflict and mortality. Our study points to the need for the use of new data streams, like data derived from ECOSTRESS, into adaptive wildlife management and climate change adaptation planning to minimize human–wildlife risk and damages to humans.

#### KEYWORDS

alfalfa field, ECOSTRESS, evapotranspiration, mule deer, *Odocoileus hemionus*, remote sensing, shrub, Utah

## INTRODUCTION

Drought is a defining characteristic of arid and semiarid ecosystems worldwide. Recent climate projections indicate increasing volatility in the timing and amount of precipitation, including longer droughts of higher magnitude and frequency (Diffenbaugh et al., 2015; Overpeck & Udall, 2020; Williams et al., 2020). Extended dry spells can reduce vegetation productivity (Chen et al., 2013; Lei et al., 2020; Peñuelas et al., 2007) and decrease the nutritive value of herbaceous perennial plants (Liu et al., 2018; Staniak, 2019). In turn, herbivores use different behavioral tactics to cope with acute drought conditions and associated reductions in food availability, including increased movement and home range expansions, which can reduce reproductive output and lower juvenile survival rates (Bender et al., 2011; Heffelfinger et al., 2018; McKee et al., 2015). However, changes in land use by humans and anthropogenic subsidies may alter these patterns for wildlife. An underexplored question is whether behavioral coping strategies may cause herbivores to forage in anthropogenic landscapes more frequently, where nutrient-rich plants and water can be concentrated, potentially exacerbating human–wildlife conflict.

Expansion and proliferation of irrigated landscapes, including croplands and urban horticulture, offer an evolutionarily novel option to mitigate the otherwise synoptic impacts of drought. Wildlife can seek climatic refugia by using subsidized environments where human land modifications buffer wildlife against acute climate events. Humans create environments in which water resources are continuously available, such as in cities, gardens, and irrigated crops, which can provide stable resources that are less influenced by environmental conditions (Buyantuyev & Wu, 2012; Ditmer et al., 2016; Hansen

et al., 2020; Sochat et al., 2006). However, these stable yet artificial environments also come with an increased risk of human encounters, which may result in conflict (Beckmann & Berger, 2003) and mortality (Olson et al., 2015). Indeed, Abrahms (2021) linked the increasing variability of the climate to altered food sources and the associated spikes in human–wildlife conflict globally. Water scarcity within natural habitats was at the root of many of these conflicts.

Arid environments are especially vulnerable to human–wildlife conflict because the environmental condition gradient between the natural and artificial landscape is steep. This is particularly true in the American Southwest. More than 92% of the region's cropland is irrigated, with agricultural uses accounting for 79% of all water withdrawals from river systems and aquifers (Kenny et al., 2009; Richter et al., 2024). Since 2000, the region has experienced increased aridity while the human population has increased by 28% (Williams et al., 2020, 2022). As such, forecasts indicate significant shortfalls between projected water supplies and demands by people in the coming decades (Department of Interior, 2012). Drought is a major cause of large-scale reproductive failure and population declines in wildlife (Duncan et al., 2012). Dwindling water sources—with those remaining increasingly linked with humans—are thus a crucial resource for the region's wildlife. For example, in the southwestern deserts of North America, Longshore et al. (2009) showed that without artificial water sources, about half of bighorn sheep (*Ovis canadensis*) habitat would be lost in Joshua Tree National Park, California. Conversely, in a subsequent study, Longshore et al. (2016) found that bighorn sheep with access to an irrigated city park showed consistent lamb production, in stark contrast to adjacent populations without anthropogenic subsidies, for which lamb

production closely paralleled autumn precipitation. It stands to reason that an acute drought could fundamentally alter how the region's wildlife interact with both natural and anthropogenic landscapes, creating pronounced spatial variation in population dynamics.

Here, we use an acute drought in the American Southwest that occurred during summer 2021 (Osman et al., 2022) as a natural experiment to understand how mule deer (*Odocoileus hemionus*) adjust their behavior in response to drought. Mule deer are generalist herbivores with a cosmopolitan distribution, whose numbers strongly track temporal and spatial fluctuations in primary productivity (Pierce et al., 2012; Stoner et al., 2018). However, when the abundance and quality of forage are poor in natural environments, mule deer may adjust their food-risk trade-off by selecting irrigated crops, which may increase human–wildlife conflict, such as deer eating crops and deer–vehicle collisions (Carrollo et al., 2017; Johnson et al., 2014; Nielsen et al., 2003). Previous studies that measure forage availability for mule deer across macroecological scales typically use the normalized difference vegetation index (NDVI) derived from satellite imagery. However, the NDVI does not directly measure succulence in plants, which is a key measure of water flux and stress in vegetation in arid environments, and therefore nutritional quality. Thus, we utilized newly available, high-resolution (70 × 70 m) data on evapotranspiration from NASA's Ecosystem Spaceborne Thermal Radiometer Experiment on Space Station (ECOSTRESS) mission (Fisher et al., 2020). ECOSTRESS-derived measures of evapotranspiration (sum of water evaporation from the ground and plant transpiration) hold great promise in wildlife ecology by quantifying evapotranspiration at large spatial scales that allow us to explore more mechanistic linkages between water scarcity, vegetation productivity, and the behavioral coping strategies herbivores employ in water-limited environments, or in times of water stress.

We hypothesized that, once preferred natural forage became desiccated, mule deer would seek out areas of irrigated croplands, which maintained relatively high rates of evapotranspiration despite drought conditions. To test this hypothesis, we compared the selection of croplands among other habitats by mule deer during an acute drought (2021) versus baseline conditions (2019) in Utah—one of the driest states in the United States. We tested (1) if and how mule deer habitat selection changed during acute drought conditions, (2) whether irrigated crops were selected over natural forage options; and (3) how evapotranspiration estimated by ECOSTRESS could be leveraged to identify when crops are preferred to natural forage. We further evaluated if ECOSTRESS improves our understanding of mule deer resource use.

Given the economic impacts stemming from wildlife use of anthropogenic landscapes, combined with human population growth in the arid western United States (Hansen et al., 2002), and expected climatic variability during the coming century, understanding how wildlife adjust their behavior in response to drought is critical for developing proactive management strategies to conserve biodiversity and minimize human–wildlife conflict.

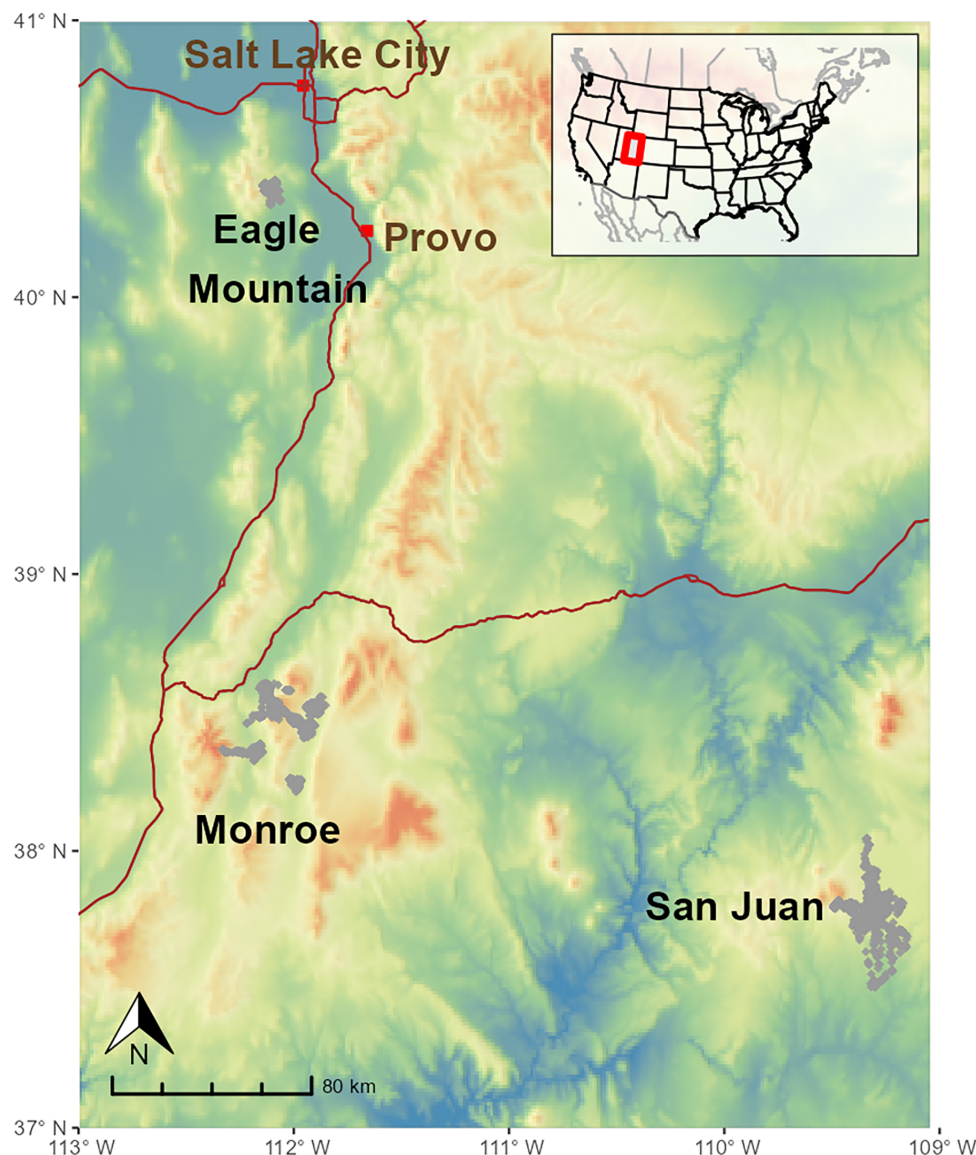
## MATERIALS AND METHODS

### Study area

We evaluated these hypotheses on three sites in Utah, which included Eagle Mountain in the north (Lat: 40.28, Long: −111.94), Monroe Mountain in the central part of the state (Lat: 38.55, Long: −112.03), and the San Juan Mountains in the southeast (Lat: 37.75, Long: −109.75; Figure 1). The Eagle Mountain population is in the Great Basin ecoregion, the Monroe population straddles the Great Basin and the Colorado Plateau ecoregions, and the San Juan population is within the Colorado Plateau ecoregion. Cropland covered approximately 20%, 3%, and 17% of Eagle Mountain, Monroe, and San Juan study areas, respectively. We contrasted mule deer habitat selection patterns during summer 2019, which represented a typical year in which 99% of the state was not in drought conditions (hereafter, “baseline”), to summer 2021, when >90% of Utah (including the three study areas) was in extreme or exceptional drought conditions (<https://droughtmonitor.unl.edu/>; USDA, 2021). All study areas were under exceptional (1 in 50–100 year event) or extreme (1 in 20 year event) drought conditions in June 2021, while no drought conditions were detected in 2019. We also observed decreases in the rate of evapotranspiration between 2019 and 2021, particularly in shrublands, the landcover type most commonly associated with mule deer habitat (Mackie et al., 2003; Figure 2).

### Mule deer capture and data handling

Mule deer were captured between late November and early March each winter using standard aerial techniques in both 2019 and 2021 (Van De Kerk et al., 2020). This involved pursuit and net-gunning from a helicopter. Animals were then hobbled and moved to a central processing site where they were measured and fitted with GPS collars (model type G2110E2H, G5-2DH, or W300; Advanced Telemetry Systems, Isanti, MN, USA). See Van de Kerk et al. (2020) for further details about animal

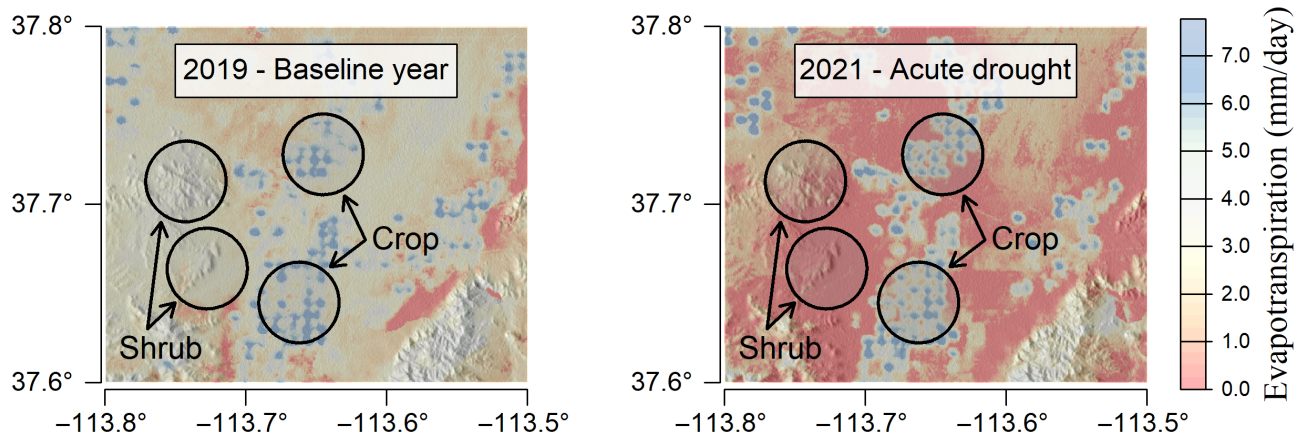


**FIGURE 1** GPS location (gray dots) of mule deer from the San Juan ( $n = 15,768$  from 16 IDs), Monroe ( $n = 13,609$  from 13 IDs), and Eagle Mountain ( $n = 14,553$  from 12 IDs) populations in Utah, USA, used to assess the effect of croplands and evapotranspiration on habitat selection during summer (2019 and 2021). Elevation is presented as the background map.

capture and handling (Brigham Young University IACUC protocol number 150110). Mule deer GPS tracks were resampled to 2-h intervals and visually inspected to remove outliers and unlikely movements. The annual home range of each mule deer was delineated using a 95% kernel density estimator (Keating & Cherry, 2009). Within each individual's annual home range, we created random points with a density of 20 points per  $\text{km}^2$  within the home range and a minimum of 365 random locations per individual. We masked open water so random points were not allowed to be in open water. Mule deer home ranges vary widely in size, and this approach ensured that we equally sampled the availability of resources spatially and temporally. Each random

location was assigned a time stamp randomly sampled from the corresponding animal's real GPS data. We focused our analyses during summer (May–June–July) when deer are giving birth and lactating to support neonates (Pekins et al., 1998; Sadler, 1982). This is when deer are most sensitive to variation in the nutritional value of forage plants. We quantified mule deer behavior in temporally stable non-drought (2019) versus acute drought (2021) conditions (Figure 2). We obtained a final dataset of 55,333 random locations and 43,930 real GPS locations belonging to 19 mule deer in 2019 (Eagle Mountain = 9, Monroe = 7, San Juan = 3) and 26 mule deer in 2021 (Eagle Mountain = 5, Monroe = 7, San Juan = 14). We monitored 41 unique mule deer, and





**FIGURE 2** Spatial variation in the mean daily rate of evapotranspiration (in millimeters per day) in June derived from ECOSTRESS between the baseline year (2019) and an acute drought year (2021). Crop and most of the shrub habitat showed evaporation rates above 2 mm/day during the baseline year. The rate of evapotranspiration in shrub decreased during the acute drought year, while the evapotranspiration rate in crop was stable between both years.

4 of those were monitored in both 2019 and 2021 (Eagle Mountain = 2, Monroe = 1, San Juan = 1). Given the capture technique was standardized, we assume we captured a random sample from the population in both 2019 and 2021.

For all real and random locations, we extracted elevation from a 1 arc-second (ca. 30 m) resolution raster from the USGS published in 2020 (<https://data.usgs.gov>). We also extracted information on habitat type from the annual Cropland Data Layer (CDL), which uses the National Land Cover Dataset for non-agricultural land cover classes (Boryan et al., 2011). In our analyses, we considered three habitat types: Shrub (“Shrubland” from CDL), Forest (“Evergreen Forest,” “Deciduous Forest,” and “Mixed Forest” from CDL), and crops (all crop types except tree crops, “Fallow/Idle Cropland,” and winter wheat which is harvested in early summer). All mule deer, except one from San Juan in 2019, used crop. We extracted daily NDVI values at a 500-m resolution from MODIS (MCD43A4 Version 6.1). We chose daily NDVI at a 500-m resolution as opposed to finer spatial, but coarser temporal resolution products because we prioritized capturing shifts in behavior at the finest temporal scale (e.g., switching to crop use), and it provided continuity across the years of mule deer GPS sampling. We quantified evapotranspiration from the NASA Jet Propulsion Laboratory ECOSTRESS Level-3 DisALEXI-JPL Evapotranspiration (ECO3ETALEXI) data product (<https://lpdaac.usgs.gov/products/eco3etalexiv001/>) derived from level-2 ECOSTRESS land surface temperature and emissivity data products based on spatial disaggregation of regional-scale fluxes from the Atmosphere Land Exchange Inverse (ALEXI) SEB model (Cawse-Nicholson & Anderson, 2021). To mitigate data quality and

consistency issues, a threshold of 20° was applied to the viewing zenith angle to filter out observations with suboptimal viewing geometry (Anderson et al., 2021). We extracted all filtered ECO3ETALEXI data and created composites of monthly mean of these data (70 × 70 m resolution). Finally, in addition to the extraction of evapotranspiration at random and real GPS locations, we further extracted evapotranspiration values in 2019 and 2021 in shrub habitat across the three study areas to quantify the effect of an acute drought on the most available and used habitat type by mule deer.

## Statistical analyses

To investigate mule deer habitat selection, we contrasted environmental conditions at real GPS locations and environmental conditions at random locations (Northrup et al., 2021). We used general additive mixed models (GAMMs) with a logit link to compare used (coded 1) and available resources (coded 0). GAMMs allowed us to model nonlinear relationships of independent variables on selection. We included the animal ID and the study area as random intercepts and carried out model selection (Table 1) to determine the most parsimonious fixed effect structure using Akaike information criterion (AIC) (Burnham & Anderson, 2002). Our base model included *Elevation*, *NDVI*, and binary values (0–1 dummy coded) for *Forest*, *Shrub*, and *Crop* variables as fixed effects. We created a second model using the base model and adding an interaction between all variables and *Year* (2019/2021). The interaction allowed us to determine if mule deer habitat selection differed between the baseline (2019) and acute drought (2021) conditions. We created

**TABLE 1** Candidate models tested to assess habitat selection of mule deer (*Odocoileus hemionus*) during summer in Utah, USA.

Model	Fixed effect	LL	AIC	$\Delta$ AIC	$w_i$
1	(Elevation + NDVI + Shrub + Forest + Crop)	−57,259	114,534	6617	0
2	(Elevation + NDVI + Shrub + Forest + Crop) × Year	−54,666	109,361	1444	0
3	(Elevation + NDVI + Shrub + Forest + Crop + Evapo)	−56,966	113,950	6033	0
4	(Elevation + NDVI + Shrub + Forest + Crop + Evapo) × Year	−54,428	108,887	970	0
5	Model 3 + spline (Evapo in Shrub) + spline (Evapo in Forest) + spline (Evapo in Crop)	−56,345	112,730	4813	0
6	Model 4 + spline (Evapo in Shrub) + spline (Evapo in Forest) + spline (Evapo in Crop)	−53,932	107,917	0	1

Note: We built a set of candidate models using general additive mixed models (GAMMs) that allowed us to verify (1) if habitat selection differ between an acute drought (2021) and a baseline (2019) summer and to verify (2) if selection for forest, shrub, and crops was influenced by the amount of evapotranspiration (Evapo). We used GAMMs to explore nonlinear relationships (spline) of evapotranspiration on habitat selection coefficient. Models are listed with their fixed effects (covariates), log likelihood (LL), differences in Akaike information criterion (AIC) in relation to the best supported model ( $\Delta$ AIC), and model weight ( $w_i$ ). All models were tested with mule deer identity and study area as random intercepts.

Abbreviation: NDVI, normalized difference vegetation index.

two additional candidate models where we added *Evapotranspiration* and the interaction between *Evapotranspiration* and *Year* to the previous models (Table 1). Those two models were used to investigate if the inclusion of evapotranspiration can further enhance understanding of mule deer behavior in addition to NDVI. We completed our candidate model set by adding nonlinear relationships of evapotranspiration by each habitat type (Table 1). The two last models allowed us to investigate if selection of forest, shrub, and crop was modulated by evapotranspiration. Multicollinearity was low with all variance inflation factor < 3 (Graham, 2003), and we scaled (mean = 0, SD = 1) all numerical variables for easier convergence and to facilitate the comparison of coefficients. We validated the best supported model using k-fold cross-validation following Johnson et al. (2006). Using our top model, we predicted the relative probability of selection of forest, shrub, and crops across a gradient of evapotranspiration for both the baseline and acute drought year. Predictions were made using the mean elevation and mean NDVI values in the dataset. The model predictions, in conjunction with the extraction of evapotranspiration values across shrub habitat type in 2019 and 2021, allowed us to quantify how acute drought impacts natural shrub habitat and to characterize the extent of mule deer behavioral response to drought. All data processing and analyses were conducted using R 4.3.1 (R Core Team, 2023).

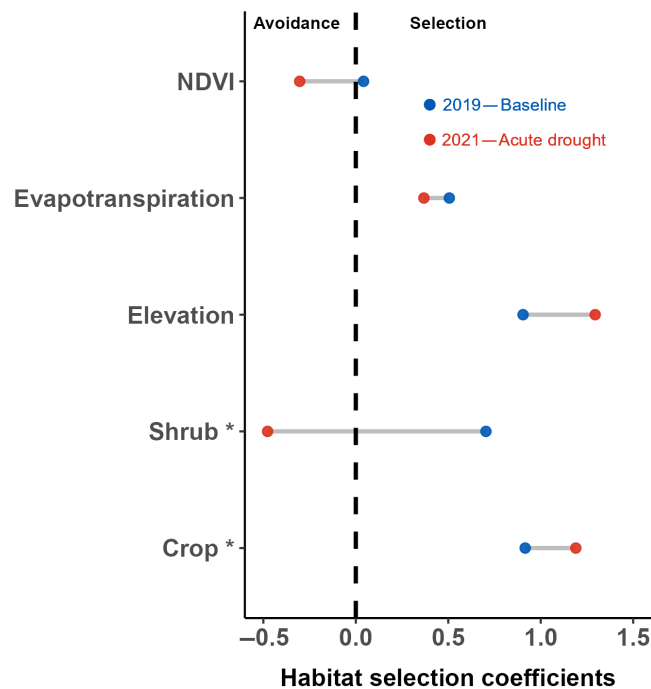
## RESULTS

Evapotranspiration played an important role in determining mule deer habitat selection. The candidate models

describing habitat selection patterns that included *Evapotranspiration* had far more support ( $\Delta$ AIC > 474) than those excluding it (Table 1). The top overall model also included interactions between *Evapotranspiration* and *Year* (Table 1), suggesting mule deer habitat selection was different between the years experiencing acute drought conditions compared to the baseline year. The complete model had good predictive performance with K-fold cross-validation correlation of  $0.916 \pm 0.052$  (mean  $\pm$  SD).

During drought conditions, mule deer selected for higher elevation relative to the baseline year and avoided areas with higher values of NDVI (Figure 3, Table 2). Mule deer exhibited stronger selection for *Shrub* and *Crop* relative to *Forest* (reference category) during the baseline year, but mule deer avoided *Shrub* habitat and increased their selection for *Crop* during the acute drought year (Figure 3). On average, mule deer decreased their use (based on real GPS locations only) of *Shrub* from 57.0% in the baseline year to 44.6% in the acute drought year. Conversely, mule deer increased their use of *Crops* from 6.2% in the baseline year to 11.8% in the acute drought year (Appendix S1: Table S1).

The behavioral switch from *Shrub* to *Crop* was mediated by the rate of *Evapotranspiration* during each year (Figure 4). Natural *Shrub* habitat was selected more strongly than *Crop* and *Forest* at lower rates of *Evapotranspiration* during normal baseline conditions, but mule deer switched their behavior and started to leave natural forage and selected *Crop* more strongly when *Evapotranspiration* was >1.03 mm/day (Figure 4A). In the acute drought year, however, mule deer selected *Forest* more strongly than *Shrub* habitat at lower *Evapotranspiration*, and they selected *Crop* more strongly than any



**FIGURE 3** Adjusted coefficient (dot) of the variable included in the most parsimonious model to assess change in habitat selection pattern of mule deer (*Odocoileus hemionus*) during an acute drought in summer in Utah, USA. The evapotranspiration variable was quantified using ECOSTRESS data. The *Shrub* and *Crop* variables (\*) must be interpreted relative to the selection of *Forest*, the habitat of reference.

**TABLE 2** Coefficients and SEs of the parameters in the most parsimonious model tested to assess change in habitat selection pattern of mule deer (*Odocoileus hemionus*) during an acute drought in summer in Utah, USA.

Variable	Estimated degree of freedom	Coefficient	SE	p-value
Elevation		0.904	0.015	<0.001
NDVI		0.042	0.013	0.002
Shrub		0.052	0.033	0.119
Forest		−0.652	0.045	<0.001
Crop		0.265	0.051	<0.001
Evapotranspiration		0.506	0.142	<0.001
Year_2021		1.115	0.043	<0.001
Elevation × Year_2021		0.390	0.025	<0.001
NDVI × Year_2021		−0.345	0.021	<0.001
Shrub × Year_2021		0.056	0.044	0.205
Forest × Year_2021		0.533	0.055	<0.001
Crop × Year_2021		0.807	0.069	<0.001
Evapotranspiration × Year_2021		−0.137	0.019	<0.001
Nonlinear effect				
Evapotranspiration in shrub	1.912			<0.001
Evapotranspiration in crop	0.040			0.872
Evapotranspiration in forest	2.653			<0.001

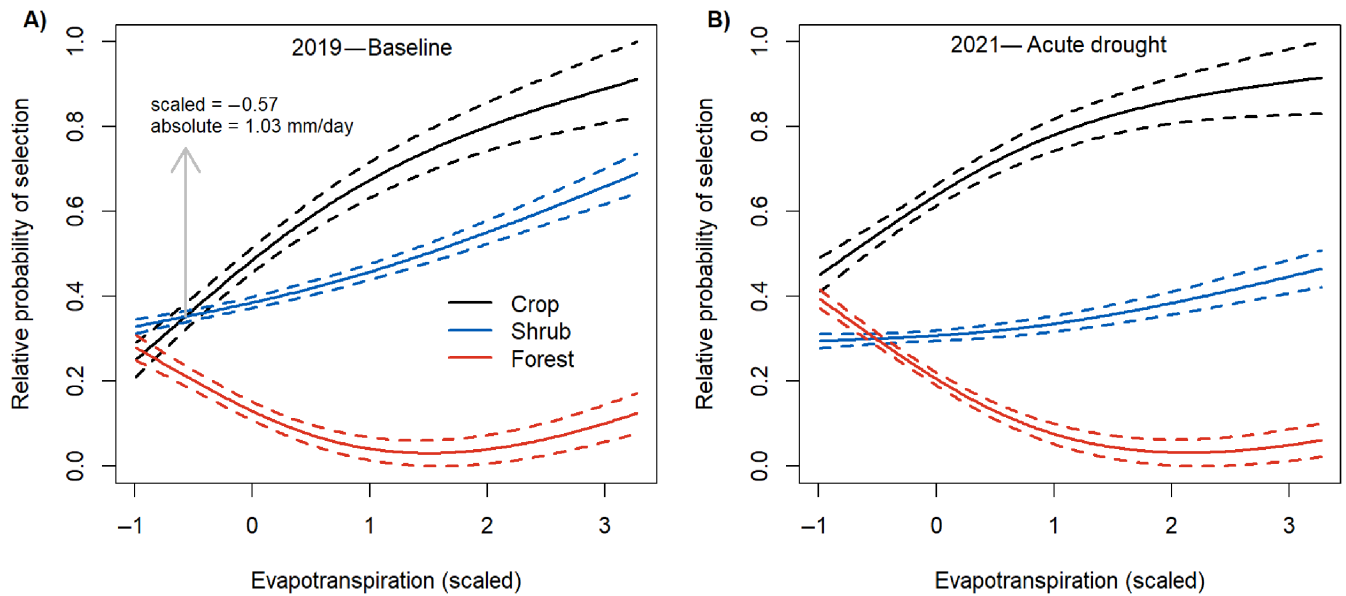
Note: All numeric variables were scaled, and the model included animal ID and study area as random intercepts. Abbreviation: NDVI, normalized difference vegetation index.

other habitat types at any level of *Evapotranspiration* (Figure 4B).

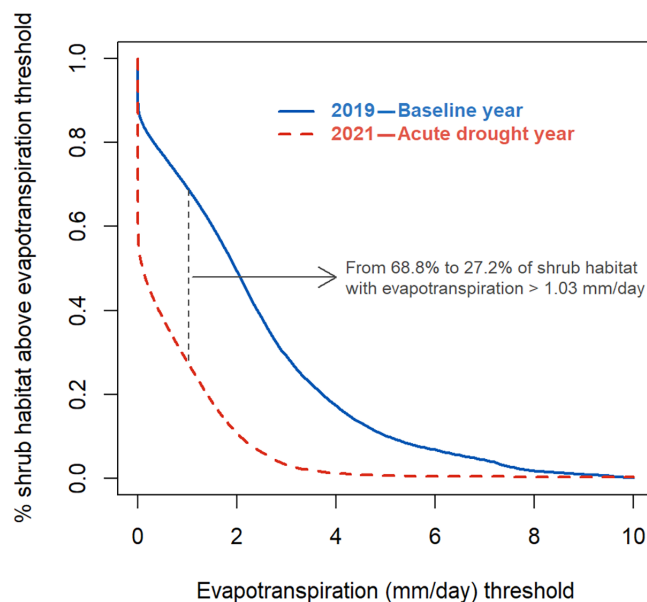
*Shrub* was the most frequently used and most available habitat (52.3%) in our study areas. However, *shrub* habitat desiccated, as measured by *Evapotranspiration*, during the drought year compared to the baseline year (Figure 5). For instance, the proportion of *shrub* available within our study areas with >1.03 mm/day of evapotranspiration (when mule deer leave *Shrub* and select more strongly for *Crop*, Figure 4A) decreased from 68.8% to 27.2% between the baseline and the acute drought year (Figure 5). This suggests that acute drought decreased the amount of prime shrub habitat by at least 41.6%, which represents about 21.8% of the study area.

## DISCUSSION

Climate changes during the coming century are expected to increase the variability in the amount of precipitation and cause longer droughts of higher magnitude and frequency (Diffenbaugh et al., 2015; Overpeck & Udall, 2020; Williams et al., 2020). Understanding how wildlife adjust their behavior in acute drought conditions, particularly their use of anthropogenic landscapes where water availability is more predictable, is critical for



**FIGURE 4** Predictions for 2019 (baseline, panel A) and 2021 (acute drought, panel B) using the most parsimonious model describing the relative probability of selection of *Forest*, *Crop*, and *Shrub* as a function of evapotranspiration during summer for mule deer (*Odocoileus hemionus*) in Utah, USA. Mule deer select more strongly *Crops* and less strongly *Shrub* during the acute drought (2021) compared to the baseline year (2019), and mule deer select more strongly areas with higher evapotranspiration for shrub and crop in both years. Predictions were made using the mean elevation and mean normalized difference vegetation index (NDVI) values in the dataset.



**FIGURE 5** Proportion of shrub habitat in three mule deer study areas in relation to the amount of evapotranspiration (in millimeters per day) quantified from ECOSTRESS. The proportion of shrub habitat having evapotranspiration above 1.03 mm/day (when crop is preferred to shrub in the baseline year, Figure 4A) decreased from 68.8% to 27.2% between the baseline (2019) and the acute drought year (2021) in Utah, USA.

developing proactive management strategies and reducing human–wildlife conflict. In this study, we showed that, in accordance with our predictions, mule deer

selected for areas exhibiting higher evapotranspiration rates and that during the acute drought year mule deer increasingly sought out crops and avoided natural shrub habitat (Figures 3 and 4). We also showed that shrub habitat was more desiccated during the acute drought year (Figure 5). Finally, we showed that evapotranspiration measured by ECOSTRESS refined our understanding of mule deer behavior and conveys complementary information to NDVI. All of these indices suggest succulence of available forage is a major determinant of mule deer habitat use during the late gestation and lactation phases of reproduction.

During the baseline year, when the region did not experience drought conditions, mule deer strongly selected shrub and crop compared to forest, and their selection was mediated by the rate of evapotranspiration (Figure 4a). When the rate of evapotranspiration was low in both shrub and crop, mule deer selected for natural shrub habitat that offered both food and low risk of human encounters, and the use of shrub is consistent with other studies on mule deer in similar ecosystems (Bender et al., 2022; Morano et al., 2019). As evapotranspiration rates increased, the selection for shrub increased (Figure 4a,b), suggesting food palatability was positively correlated with evapotranspiration rate (Nakano et al., 2020; Schuyler et al., 2021), that is, plants could transpire because they had access to ground water, which maintained succulence. Additionally, during times of elevated evapotranspiration rates, we observed stronger



selection for croplands. During the baseline year, evapotranspiration rates exceeding 1.03 mm/day represented a point in a continuum beyond which croplands were selected more strongly than shrub dominated habitats (Figure 4a). We argue that mule deer tolerate the risks associated with greater human presence when evapotranspiration rates exceed 1.03 mm/day as forage quality is superior in crops. Unsurprisingly, we also found that evapotranspiration rates are lower in natural shrub habitat during drought conditions (Figure 5). By combining both results, we showed that the proportion of shrub habitat with evapotranspiration values  $>1.03$  mm/day, that is, when mule deer increase their risk-taking behavior to access better food quality, decreases from 68.8% during the baseline year to 27.2% during drought conditions (Figure 5). During the acute drought year, we observed a similar habitat selection pattern, but mule deer selected crops more strongly and selected shrub less strongly than the baseline year (Figure 5). Previous work has shown that during drought conditions, the growing season ends earlier, and forage abundance, succulence, and overall quality are expected to be lower in natural shrub habitat (Chen et al., 2013; Lei et al., 2020; Peñuelas et al., 2007; Schuyler et al., 2021). Indeed, on many lower elevation shrublands in the southwestern ecosystems, the growing season can end as early as July due to desiccation (Stoner et al., 2020). Greater water limitation during drought is likely modifying the food-risk trade-off employed by mule deer, as they adjust their foraging behavior by seeking those limiting resources in nearby crops close to the human-wildland interface (Figure 4b). Our results suggest that drought conditions decrease the quality of shrubland habitats, and that cropland food resources are maintained due to irrigation, which in turn attracts mule deer during drought.

The North American monsoon is strongest in central Mexico and exhibits greater variation in frequency and magnitude at higher latitudes (Adams & Comrie, 1997). Monsoonal moisture provides growing season precipitation, and therefore the frequency of this climatic phenomenon may alter the patterns described herein. However, as yet, climate forecasts regarding the North American monsoon are fraught with uncertainty (IPCC, 2021). Globally, climate change is expected to increase human-wildlife conflict (Abrahms, 2021; Abrahms et al., 2023; Newsom et al., 2023), and here, we showed that mule deer increased their use of crop during an acute drought year, mediated by water fluxes in vegetation as measured by evapotranspiration. This response is not specific to mule deer, and when resources are limited in the environment, many species seek resources in the wildland-human interface. Indeed, black bear (*Ursus americanus*) in the United States (Baruch-Mordo

et al., 2014), elephant (*Loxodonta africana*) in Tanzania (Mariki et al., 2015), and Baird's tapirs (*Tapirus bairdii*) in Mexico (Pérez-Flores et al., 2021) increased their use of anthropogenic landscapes during drought or when natural forage production was low. Mule deer increased their use of crops (from 6.6% to 11.2%) during drought conditions, and we speculate that this behavior may potentially limit the negative effect of drought on mule deer. Indeed, agricultural crop consumption by sika deer (*Cervus nippon*) improved their physical characteristics and reproductive performance (Hata et al., 2021), but Heffelfinger et al. (2023) showed that mule deer that did not use cropland exhibited morphological and nutritional indices similar to those that did. Considering the physiological and fitness consequences of droughts for populations with and without access to croplands or other anthropogenic resources is another critical question in need of additional research. The increased use of anthropogenic landscapes does not only provide benefits but also increases the chances of potentially harmful interactions between wildlife and people, including damages to crops and property and risks to human safety (Newsom et al., 2023). With increasing drought intensity and frequency, in addition to other climate stressors, such as extreme snow years, many large-bodied, vagile wildlife species may more routinely use the wildland-human interface, creating new challenges for human-wildlife coexistence. These changes also offer new opportunities to study and design communities that minimize risks to both human and wildlife (Killion et al., 2021; Zellmer & Goto, 2022). For example, establishing movement corridors and road crossing structures (e.g., under or overpasses) that enhance wildlife access to limited water and forage while directing them away from high-risk areas (e.g., croplands; O'Farrill et al., 2014), or removing artificial watering holes near human settlements as they can attract large, and sometimes dangerous, wildlife to them during drought (Janecke, 2021). Research that integrates climate change and wildlife physiology into existing habitat selection and connectivity models may elucidate other ways the human-wildlife interface may shift in the future.

In this study, we used a novel data source, ECOSTRESS, to quantify the rate of evapotranspiration across a climatic gradient in an arid state, which provided an important predictor of mule deer behavior. Indeed, models including the evapotranspiration variable performed better than those without it (Table 1). Numerous studies have shown the importance of NDVI on herbivore foraging and habitat selection (Hamel et al., 2009; Pettorelli et al., 2011), and here, we show that evapotranspiration is a complementary metric that can be incorporated into models to further our understanding of

animal movement. Ground measurements of fine-scale forage quality and evapotranspiration, combined with herbivore physiology, could improve our ability to decipher when and how water availability mediates foraging decisions in many herbivorous species.

Wildlife will face important variation in environmental conditions caused by climate change in the next decades and centuries. To limit the effect of climate change on wildlife populations and reduce human–wildlife conflict, we suggest adaptive wildlife management planning together with climate change adaptation planning. Indeed, human and wildlife are tracking similar resources, particularly in arid environments. For instance, irrigated agriculture is responsible for 74% of direct human uses and 52% of overall water consumption of the Colorado River (Richter et al., 2024), and the human population is expected to continue increasing in the coming decades. Knowing that water is a limiting resource for wildlife, we expect that the steeper the productivity gradient between natural environment and croplands (or anthropogenic landscape), the more attractive irrigated crops will be for wildlife. New tools, such as ECOSTRESS, can thus benefit wildlife managers by providing high-resolution and near-real-time information on evapotranspiration, enabling better predictions of wildlife response and interactions with humans under conditions of greater water limitation.

## AUTHOR CONTRIBUTIONS

**Funding and supervision:** Neil H. Carter, David C. Stoner, Joseph O. Sexton, Mark A. Ditmer. **Data handling and curation:** Martin Leclerc, Mark A. Ditmer, Panshi Wang, David C. Stoner, Joseph O. Sexton. **Data analyses:** Martin Leclerc, Mark A. Ditmer, Panshi Wang. All authors contributed to the conceptualization of the study, to drafts, and gave final approval for publication.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Data (Leclerc et al., 2025) are available in Borealis at <https://doi.org/10.5683/SP3/YKNWEQ>.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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