Tule elk selection of surface water and forage is mediated by season and drought

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FULL RESEARCH ARTICLE

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Abstract

Climate change is expected to affect arid-system ungulate populations by altering the distribution and availability of critical resources such as water and forage, particularly through more frequent and extreme droughts. Tule elk (*Cervus canadensis nannodes*), a subspecies of North American elk endemic to the Mediterranean climate regions of California, USA, can provide insight into the habitat selection behaviors arid-system ungulate populations use in response to changing resource availability. We used location data collected between 2005–2017 from GPS-collared tule elk to model elk response to surface water sources, forage dynamics (i.e., spatio-temporal changes in forage quality and abundance), and drought in the wet and dry seasons. These data spanned the extreme drought that occurred from 2012–2017, a time when survival was apparently stable in the population. We found that, in the dry season, tule elk localized around water sources but selected areas farther from water with greater forage abundance. In the wet season, high quality forage and road avoidance were the primary factors influencing selection. These patterns were intensified by the extreme drought, with elk selecting areas closer to water in the dry season and farther from water sources in the wet season. Tule elk appeared to modify their behavior to minimize the impacts of drought on their survival. These findings suggest that water source availability and the relationship between water sources and other landscape features, including forage and roads, are a critical component of ungulate management in drought-prone regions.

Key words: arid system ungulates, artificial water sources, climate change, forage dynamics, human disturbance, NDVI, resource selection functions, RSF

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Introduction

As a result of climate change, historical temperature and precipitation regimes are being disrupted (Parmesan and Yohe 2003; Trenberth 2011; Trenberth et al. 2014), and ungulate populations face altered and increasingly variable patterns of resource availability (Duncan et al. 2012; Beever et al. 2017). These challenges are especially critical in arid and semi-arid regions, where increased frequency and greater severity of drought can cause ungulate population reductions and mass mortality events (Young 1994; Epps et al. 2004). For ungulates in these systems, future population size, stability, or even viability may depend on behavioral adaptations to changing resource conditions (Duncan et al. 2012). In the same manner, ungulate conservation and management practices will need to adapt to these new paradigms (Beschta et al. 2013). Effective management therefore necessitates greater understanding of how ungulate populations in arid systems use water and forage resources and respond to seasonal and drought-induced shifts in resource availability (Denryter and Fischer 2022).

Forage selection is fundamental to understanding how herbivore populations acquire energy and protein reserves for reproduction and maintenance. Changes in the quality and abundance of available forage during the growing season drive ungulate habitat selection at local and landscape scales (White et al. 1975; Bischof et al. 2012; Merkle et al. 2016). Forage selection patterns vary between populations and reflect adaptations based on physiology and life-history (Hebblewhite et al. 2008). During periods when forage is scarce, ungulates may respond in a variety of ways including altering their diet selection, reducing energy expenditure, or increasing movement rate to locate remaining food sources (Zweifel-Schielly et al. 2012; Miranda et al. 2012; Owen-Smith 2013). In arid systems, ungulate foraging decisions are also influenced, in terms of forage selection and spatial distribution, by the availability of water sources (Beale and Smith 1970; Polansky et al. 2015; Nandintsetseg et al. 2016).

In arid systems, dependence on surface water sources has a variety of implications for community and population dynamics. Water dependence concentrates populations around water sources, especially during the dry season when water demands are high, forage moisture content is low, and fewer natural water sources are available (Western 1975; Ogutu et al. 2014; Cain et al. 2006). Localization around these discrete landscape features impacts population growth and stability in a variety of ways including forage distribution, increased competition and greater predation risk (Coppolillo 2001; Rozen-Rechels et al. 2015; Hall et al. 2018). Understanding ungulates' use of water in arid systems is therefore important for land managers to make decisions about the distribution of artificial water sources, public access, land-use, and development.

One species that can provide insight into the behavioral adaptations of arid-system ungulates is the tule elk (*Cervus canadensis nannodes*). Tule elk are endemic to the Mediterranean climate regions of California, which are characterized by large seasonal fluctuations in water and forage availability, forage quality, as well as frequent drought (McCullough 1969). Tule elk range has become warmer and drier during the 20th century, and this trend is predicted to continue under current climate change scenarios (Cayan et al. 2008; Diffenbaugh et al. 2015; Monteverde and De Sales 2020). Despite the harshening conditions, tule elk populations grew steadily 1970–2017 and survival in the La Panza Elk Management Unit did not differ between the historically extreme drought of 2012–2017 and a period of mild drought 2005–2009 (Griffin and Anchukaitis 2015; Brazeal 2017; CDFW 2018). For these reasons, tule elk offer unique insight into wildlife management that accounts for the effects of climate change. Accordingly, we investigated tule elk habitat selection patterns within their dynamic resource landscapes in relation to season and drought. We hypothesized that surface water sources and forage quality would be the main drivers of selection in the dry and wet seasons, respectively, and that drought would amplify dependence on water sources. Specifically, we predicted that elk would select areas closer to water sources during the dry season, and they would select high quality forage sources during the wet season. We predicted these patterns to be even stronger during the drought – that is, elk would be more likely to use areas farther from water sources during the wet season to seek out high quality forage and select areas closer to water sources during the dry season.

Methods

Study Area

The study took place in the La Panza Elk Management Unit, in and around the Carrizo Plain in eastern San Luis Obispo County, California (35.152° N, 120.011° W; **Fig. 1**). We defined the study area as a 100% minimum convex polygon (MCP) calculated using all elk locations collected during this study, with a 2.3 km buffer. This buffer reflected a mean 13-hour movement distance estimated from studies of Rocky Mountain elk (*C.c. nelsoni*) in a variety of habitat types (Strohmeyer and Peek 1996). The area was comprised of a mixture of state, federal, and private land ownership, including two large industrial solar arrays. The climate was semi-arid with mean annual precipitation ~20 cm, most of which fell in the form of winter and spring rains. During the period 2006–2019, mean daily maximum temperature in summer was 36° C, while mean daily winter temperature was 18° C (NOAA 2019). Elevations ranged between 450–1550 m. Vegetation classes consisted primarily of California prairie, Piñon-juniper, oak woodland, and chaparral (Buck-Diaz and Evens 2011). Cattle grazing occurred in parts of state and federal lands and throughout adjacent private ranchlands, but usage of specific grazing allotments varied among years. Potential elk predators in the area included mountain lions (*Puma concolor*), black bears (*Ursus americanus*), bobcats (*Lynx rufus*), and coyotes (*Canis latrans*). Elk hunting permits are allocated each year by the California Department of Fish and Wildlife (CDFW) and various hunting seasons with different regulations (e.g., general draw, Private Lands Management tags) occur between late August and early December each year. The amount of hunting pressure varied across the study area due to differences in access restrictions.

Figure 1. Map of the study area overlaid with agency ownership. Study area was defined by a 100% Minimum Convex Polygon (MCP) with a 2.3 km buffer of all tule elk locations collected via GPS collar between 2005–2017, CA, USA.

Data Collection

Between 2005 and 2017, we collected location data using GPS collars deployed on 36 tule elk (23 females, 13 males) via helicopter net-capture and free-range darting. This time contained a mixture of wet and dry years, but the majority of collars (n = 24) were deployed in 2015, which coincided with the most severe period of the 2012–2017 drought. Collars were distributed among four sub-groups designated by CDFW (“California Valley”, “American”, “Chimineas”, “Cedar Canyon”), referring to geographic areas of the management unit. The areas used by the sub-groups differed in relation to land cover composition, proximity to human development, and property ownership (**Fig. 2**). Collars were programmed to record a location every 13 hours and monitored for the duration of the battery life or until the animal died. All captures were conducted by CDFW and their contractor following internal animal use protocols. This study was conducted under Humboldt State University IACUC #16/17.W.94-E.

Figure 2. Map of study area showing the distribution of GPS-collared tule elk home ranges overlaid on habitat layer in San Luis Obispo County, California, USA, 2005–2017. Study animals were distributed in four distinct sub-herds. Home ranges were created using time-based local convex hulls (T-LoCoH).

We evaluated elk habitat selection using a resource selection framework (Manly et al. 2002). Available locations were randomly generated within elk home ranges, corresponding to third order habitat selection (Johnson 1980). We calculated home ranges with the tlocoh package (Lyons et al. 2013) in program R version 3.6.0 (R Core Team 2019) using the 95% isopleth from a time-local convex hullset (T-LoCoH), with V_{max} set to the greatest distance between two consecutive points and hulls constructed from the nearest 15 locations. We sampled a number of available locations equal to the number of used locations for that elk; for time-dependent predictors, we used the same date as the corresponding used location was collected. Locations missing one or more environmental predictors were censored from the analysis (n = 873). Most censored locations were caused by missing forage abundance data. We examined the effect of seasonality on selection by splitting the data into wet season and dry season locations and ran separate model selection analyses for each season. Wet season was defined as 16 Nov–15 May, and dry season from 16 May–15 Nov. We chose these periods to align with typical annual changes in water and forage availability.

We selected 13 spatially-explicit predictor variables related to resource availability, risk, and energy expenditure which were known drivers of elk habitat selection in other populations or potential influences on habitat selection within this system (Skovlin et al. 2002). We used a land cover layer (*life_form*) with 10 land cover types (MLRC 2011). We estimated slope (*slope*), topographic position (*TPI*), and aspect (*northness*, *eastness*; sin and cosine of aspect * π/180, respectively) from a digital elevation model to account for energy expenditure (NASA 2000). We estimated quantity of available forage using the normalized difference vegetation index (*NDVI*) measured from MODIS satellite imagery with a 250m spatial resolution and 8-day interval between images (NASA 2018). Between successive images, NDVI values were interpolated to derive a daily estimate of NDVI at each used and available location, using the Phenology function in the greenbrown package (Forkel and Wutzler 2015). We used the daily change in NDVI (*Δ NDVI*) to estimate forage quality (Hamel et al. 2009). More background about how forage metrics were calculated is provided in Supplementary Information A. We conducted an extensive effort to locate natural and artificial water sources and estimate availability using satellite imagery (Supplementary Information B), from which we calculated distance to nearest water source (*water_dist*). Frequently elk habitat selection studies have relied on datasets that only account for perennial, natural water sources to estimate water availability (e.g., Beck et al. 2013; Roberts et al. 2017; Lamont et al. 2019); however, this data does not account for seasonal changes in availability, nor does it account for artificial water sources such as stock troughs. Our approach for estimating water availability was therefore an attempt to better capture the dynamic and ephemeral nature of water availability in the study area. We used the Palmer Drought Severity Index (PDSI), for quantifying the effects of long-term drought, measured monthly at the geographic center of the study area (Palmer 1965; Abatzoglou et al. 2017). We incorporated PDSI in order to capture the broader context within which elk were making fine-scale resource selection decisions. On the PDSI scale, a value < –4 represents extreme drought conditions while a value of > 4 represents extremely wet conditions, with 0 representing average conditions. We calculated distance to nearest road (*road_dist*) to account for the effects of human disturbance (USCB2018; McCorquodale 2013). We also included distance to nearest solar production site (*solar_dist*) as an additional potential disturbance source due to the construction of two large solar farms that occurred during the study period. All distance metrics were calculated using the spDistsN1 function in the sp package (Pebesma 2018). Variables were standardized using the rescale function in the arm package (Gelman et al. 2013).

We developed Resource Selection Functions (RSFs) using mixed effects generalized linear models with a logit link (Johnson et al. 2006, Lele et al. 2013). Due to our relatively small sample size, we did not fit separate models based on sex. In a preliminary analysis we compared models with individual elk ID included as a random effect with models where sub-herd was included as either a fixed or random effect and found that individual ID performed similarly or slightly better than models that included sub-herd. To identify possible interactions between water and drought on foraging dynamics while limiting the complexity and total number of candidate models, we used a two-step approach for building and selecting a top model for each season (Nichols et al. 1997; Burnham and Anderson 2002; Rowland et al. 2018). For both seasons, we constructed two sets of candidate models with differing sets of interactions. One set included interactions between distance to water source and each potential combination of drought severity, forage abundance (NDVI), and forage quality (Δ NDVI). The second set of models was identical except distance to water was swapped with drought severity in all the interactions. We then identified the best-performing models from each set by comparing AIC scores and selected the least complex model within 2 AIC of the lowest scoring model as the top model for each set. We then merged these two models into a single combined model and performed another round of model selection, comparing the combined model with the full set of models, and again selected the least complex model within 2 AIC of the lowest scoring model as the top model for each season (Arnold 2010). We tested for collinearity among predictor variables, and variables that had a Pearson's correlation coefficient of $r > 0.60$ were excluded from the same model. To assess model accuracy, we used 5-fold partitioning to calculate the Continuous Boyce Index (Boyce et al. 2002; Hirzel et al. 2006) using the ecospat.boyce function in package *ecospat* (Broennimann et al. 2022).

Results

Collar Data

A total of 30,667 elk locations were used in the analysis, with a range of 115–1406 locations per individual elk. Locations were relatively evenly distributed between the dry and wet season, with 17,415 and 13,525 locations, respectively. In terms of drought, the data were skewed towards drought conditions, with 25,561 locations collected with PDSI < 0, and only 5,379 locations with PDSI > 0.

Dry Season

In the dry season, the top model contained all the distance to water interactions and no additional drought interactions (**Table 1**). Distance to water source and the interactions between distance to water & NDVI and distance to water & Δ NDVI were the most influential variables (**Fig. 3**). Elk selected areas closer to water sources regardless of NDVI but were more likely to select areas farther from water when those areas had higher NDVI (**Fig. 4**). Similarly, elk selected areas closer to water regardless of drought conditions, but selected areas closer to water during extreme drought compared to less severe drought or average conditions (**Fig. 5**). Elk did not have a strong response to either NDVI or ΔNDVI in the dry season (**Fig. 8**). The mean Continuous Boyce Index for the dry season was 0.97 (SE = 0.01).

Table 1. Dry season model selection results table. Models describe 3rd order habitat selection in a population of GPS-collared tule elk in CA, USA, 2005–2017. Bold text indicates top models in their respective section (i.e., water or PDSI interactions only), italicized text indicates combined model. Note the combined model did not substantially improve model performance compared to the top model from the water interaction section. Each model contained the same set of fixed predictor variables with elk ID included as a random effect. Model abbreviations were as follows: NDVI = normalized difference vegetation index; PDSI = Palmer drought severity index, water = distance to nearest water source.

Interaction Terms	**K**	**logLik**	**AIC_c**	**ΔAIC_c**	**ω_i**
*Water * NDVI, Water * Δ NDVI, Water * PDSI, PDSI * Δ NDVI*	25	–21633.5	43317.02	0	0.64
Water * NDVI, Water * Δ NDVI, Water * PDSI	24	–21635.1	43318.16	1.14	0.36
Water * NDVI, Water * Δ NDVI	23	–21640.8	43327.58	10.56	0
Water * NDVI, Water * PDSI	23	–21714.1	43474.25	157.22	0
Water * PDSI	22	–21727.8	43499.61	182.59	0
Water * Δ NDVI, Water * PDSI	23	–21749.2	43544.53	227.51	0
PDSI * Water, PDSI * NDVI, PDSI * Δ NDVI	24	–21749.1	43546.30	229.28	0
PDSI * Water, PDSI * Δ NDVI	23	–21751.1	43548.27	231.25	0
Water * NDVI	22	–21752.9	43549.87	232.85	0
PDSI * Water, PDSI * NDVI	23	–21752.8	43551.67	234.64	0

Interaction Terms	**K**	**logLik**	**AIC_c**	**ΔAIC_c**	**ω_i**
PDSI * NDVI, PDSI * Δ NDVI	23	–21784.4	43614.82	297.79	0
PDSI * Δ NDVI	22	–21786.3	43616.65	299.63	0
Water * Δ NDVI	22	–21788.2	43620.43	303.41	0
Null model	21	–21789.4	43620.80	303.78	0
PDSI * NDVI	22	–21789.4	43622.80	305.77	0

Figure 3. Standardized beta values of the top model explaining seasonal 3rd order habitat selection patterns in a population of GPS-collared tule elk in California, USA, 2005–2017. Values above 1 and below 1 represent selection for greater and lesser values, respectively. Model abbreviations were as follows: NDVI = normalized difference vegetation index; PDSI = Palmer drought severity index, TPI = Topographic position index, Water = distance to nearest water source.

Figure 4. Interaction plots showing seasonal 3rd order habitat selection for water sources changes in response to forage availability, measured via Normalized Difference Vegetation Index (NDVI) values, for a population of GPS-collared tule elk in California, USA, 2005–2017. Higher NDVI values correspond with greater amounts of green vegetation. Shaded areas represent 95% confidence intervals. For each season, NDVI response lines represent mean NDVI +/– 1 standard deviation.

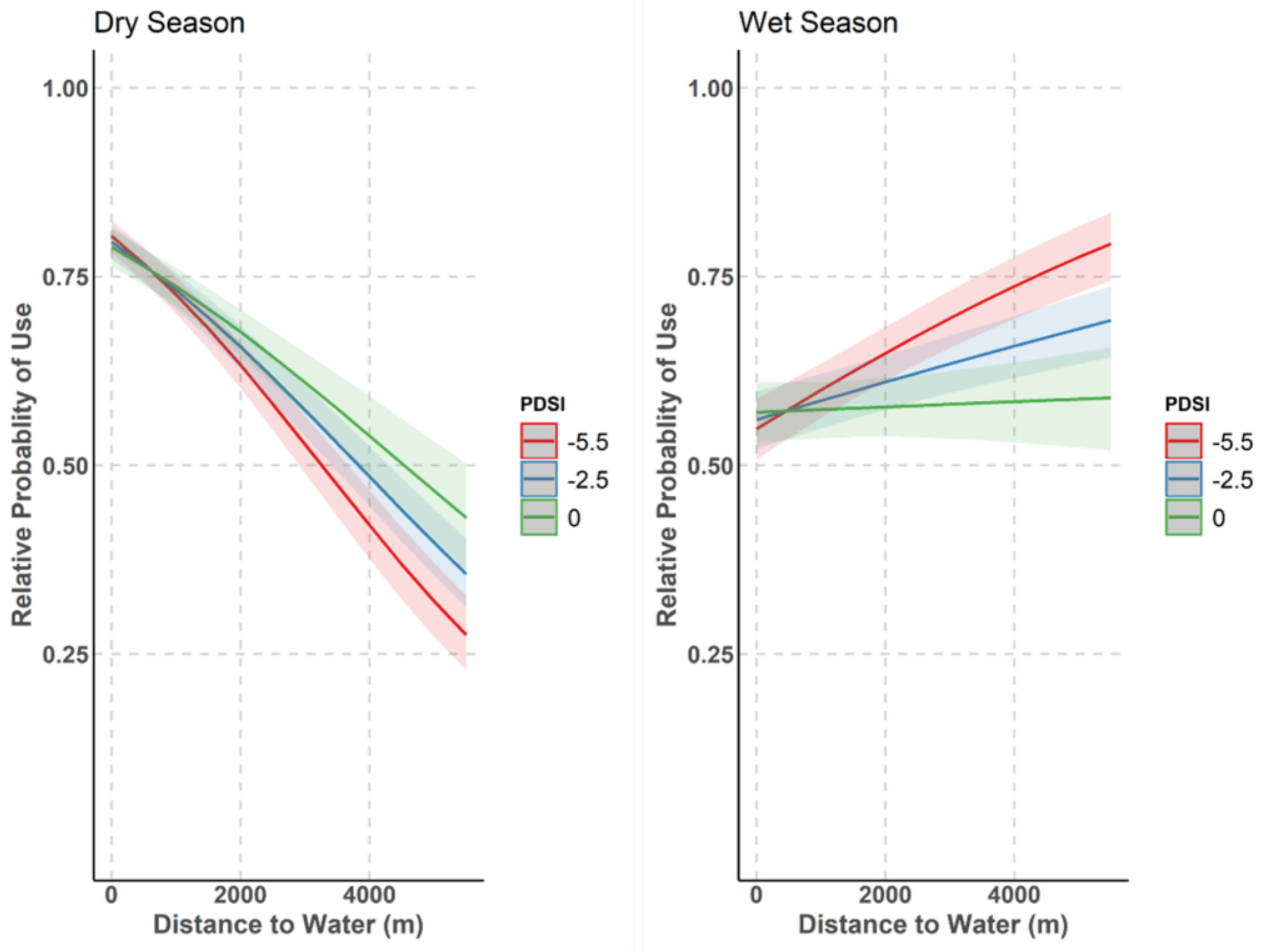

Figure 5. Interaction plots showing seasonal 3rd order habitat selection for water sources changes in response to drought, measured via the Palmer Drought Severity Index (PDSI), for a population of GPS-collared tule elk in CA, USA, 2005–2017. PDSI values < –4.0 correspond to extreme drought, with 0 representing average conditions. Shaded areas represent 95% confidence intervals.

Wet Season

In the wet season, the top model was the combined model, which included all the distance to water interactions and the interaction between drought and forage quality (Table 2). Distance to nearest road was the most influential variable in the model, with elk selecting areas farther from roads (Figs. 3, 7). As in the dry season, elk were more likely to use areas farther from water sources with greater NDVI (Fig. 4). In contrast to the dry season, during times of extreme drought elk were more likely to select areas farther from water, compared to periods with less severe drought or average conditions (Figs. 5, 6). Elk selected for greater ΔNDVI, which was the second most influential variable after distance to road (Figs. 3, 8). The mean Continuous Boyce Index for the wet season was 0.93 (SE = 0.04).

Table 2. Wet season model selection results table. Models describe 3rd order habitat selection in a population of GPS-collared tule elk in California, USA, 2005–2017. Bold text indicates top models in their respective section (i.e., water or PDSI interactions only), italicized text indicates combined model. Each

model contained the same set of fixed predictor variables, with elk ID included as a random effect. Model abbreviations were as follows: NDVI = normalized difference vegetation index; PDSI = Palmer drought severity index, Water = distance to nearest water source.

Interaction Terms	**K**	**logLik**	**AIC_c**	**ΔAIC_c**	**ω_i**
*Water * NDVI, Water * Δ NDVI, Water * PDSI, PDSI * Δ NDVI*	25	–19850.6	39751.23	0	0.84
Water * NDVI, Water * Δ NDVI, Water * PDSI	24	–19853.3	39754.63	3.4	0.15
Water * NDVI, Water * PDSI	23	–19857.6	39761.26	10.03	0.01
Water * NDVI, Water * Δ NDVII	23	–19866.0	39777.96	26.73	0
Water * PDSI	22	–19867.0	39778.07	26.84	0
Water * Δ NDVI, Water * PDSI	23	–21749.2	43544.53	227.51	0
PDSI * Water, PDSI * NDVI	23	–19875.6	39797.15	45.91	0
PDSI * Water, PDSI * NDVI, PDSI * Δ NDVI	24	–19875.2	39798.36	47.13	0
Water * Δ NDVI, Water * PDSI	23	–19876.2	39798.48	47.24	0
Water * NDVI	22	–19878.5	39801.11	49.87	0
PDSI * Water, PDSI * NDVI	23	–19878.3	39802.60	51.37	0
PDSI * Δ NDVI	22	–19882.5	39809.03	57.79	0
PDSI * NDVI, PDSI * Δ NDVI	23	–19882.1	39810.27	59.03	0
Null model	21	–19885.3	39812.71	61.48	0
Water * Δ NDVI	22	–19884.9	39813.79	62.55	0
PDSI * NDVI	22	–19885.1	39814.22	62.99	0

Figure 6. Response plot showing seasonal differences in 3rd order habitat selection for water sources for a population of GPS-collared tule elk in CA, USA, 2005–2017. Shaded areas represent 95% confidence intervals.

Figure 7. Response plot showing seasonal differences in 3rd order habitat selection in relation to roads for a population of GPS-collared tule elk in CA, USA, 2005–2017. Shaded areas represent 95% confidence intervals.

Figure 8. Response plot showing seasonal differences in 3rd order habitat selection in relation to forage abundance, estimated via the Normalized Difference Vegetation Index (NDVI) and forage quality, estimated via daily change in NDVI (Δ NDVI) for a population of GPS-collared tule elk population in CA, USA, 2005–2017. Shaded areas represent 95% confidence intervals.

Discussion

We found that water sources and forage quality played an important role in tule elk habitat selection, and selection was mediated by both season and drought. Elk selected areas near water sources in the dry season, particularly during extreme drought. The opposite was true during the wet season, as elk were more likely to select areas farther from water sources, and this effect was strongest during extreme drought conditions. In both seasons, elk were more likely to select areas farther from water if those areas had higher NDVI values. To summarize, elk selected areas near water sources and with areas high-quality forage during the dry season, selecting areas near water sources and with high-quality forage. In the wet season, elk selected areas farther from roads water sources and areas with high-quality forage.

Selection patterns were consistent with our expectation that tule elk localize around water sources and make recursive movements between forage and water in the dry season. In the dry season, the interaction between distance to water and forage abundance was the most important variable in the model. The pattern we observed of elk selecting areas with greater forage availability farther from water sources may have been due to forage depletion near water sources. For large herbivores, localization can create spatial gradients in forage availability around water sources due to concentrated foraging activity (Andrew 1988). The extreme drought which occurred in the study area between 2012–2016 likely caused elk to select areas farther from water sources as forage was depleted, as evidenced by selection for areas with greater NDVI farther from water during extreme wet season drought. Similar seasonal patterns of habitat selection have also been observed in African herbivore communities, characterized by concentration around water sources in the dry season and dispersal away from water in the wet season (Western 1975; Ogutu et al. 2014).

Forage moisture content was likely a major influence on wet season habitat selection patterns. In the wet season, we observed that elk selected areas farther from water sources and selected forage sources which would have contained higher forage moisture content, specifically areas with high quality forage and areas of greater forage abundance further from surface water sources. Taken together, these results suggests that elk were largely able to meet their water requirements from forage moisture in the wet season. Forage moisture is a main factor in ungulate water budgets (Cain et al. 2006) and the higher moisture content of photosynthetically active plants (i.e., areas with greater NDVI and ΔNDVI), as well as the milder temperatures of the wet season, would have reduced the need for elk to drink. Similar relationships showing reduced dependence on surface water sources when forage moisture content was high have been found in African ungulates (Jarman 1973), pronghorn (*Antilocapra americana*; Beale and Smith 1970), and Rocky Mountain elk in New Mexico (Harris et al. 2015). The greater availability of forage moisture in the wet season and, conversely, greater dependence on surface water sources in the dry season, would also explain why road avoidance was much stronger in the wet season than in the dry season since water sources in the study area are typically associated with roads.

Forage quality, in addition to road avoidance, was the most significant factor in the wet season habitat selection. Many migratory ungulates track changes in forage quality across the landscape during the growing season (Bischof et al. 2012; Merkel et al. 2016; Aikens et al. 2017; Hebblewhite et al. 2008), although non-migratory populations can track forage quality as well (Hebblewhite et al. 2008). Extended access to peak green-up has been linked to higher fitness in ungulates (Pettorelli et al. 2007; Monteith et al. 2015; Middleton et al. 2018). While the elk in this study were non-migratory, their relatively large home ranges likely allowed them to exploit fine-scale changes in forage quality caused by differences in elevation, aspect, and forage species phenology. For ungulates, body reserves accumulated during periods with high quality forage are critical for survival and reproduction during periods when forage is less abundant and nutritious (Parker et al. 1999; Cook et al. 2004, 2013; Barboza and Parker 2008; Denryter et al. 2022). The strong seasonal selection for forage quality we observed in the wet season, as well as the relative unimportance of the forage variables in the dry season, suggests that the wet season is a vital period in which tule elk build the energy and protein reserves necessary to sustain themselves through the dry season and during drought, periods when forage is less nutritious and abundant in the study area (Larsen et al. 2012).

The provision of artificial water sources has become a subject of keen interest and debate in arid system management (Broyles 1996; Rosenstock et al. 1999; Krausman et al. 2006). Evidence suggests that additional water sources can increase available habitat for some arid system ungulates populations (Rich et al. 2019); however, other studies have shown possible side-effects, such as increasing population volatility during drought (Walker et al. 1987; Illius and O’Connor 2000; Owen-Smith 2004). While we observed the interaction between water sources and forage abundance was an important factor in the dry season, the coarseness of our GPS-collar’s relocation intervals (~13 hours) and water availability data make it impossible for us to answer more specific questions about how elk in this study related to water sources, such as how often they visited or identify optimal water source densities. High quality water availability data paired with annual population counts would be invaluable for examining the relationship between water source densities and population dynamics (Bleich 2006; Larsen et al. 2012). Much like water in the desert, water availability data is a limiting factor for managers. Addressing this challenge will be immensely beneficial for answering management questions surrounding artificial water source allocation and setting population objectives.

Anthropogenic activities which reduce the availability of water sources and high-quality forage are likely more detrimental to tule elk when populations are concentrated around water sources and forage is less abundant and nutritious, such as in the dry season and during drought. Human disturbance, in addition to causing greater stress and energy expenditure (Seip et al. 2007; Zbyryt et al. 2018), can reduce ungulate fitness by interfering with foraging and calf-rearing behaviors (Phillips and Alldredge 2000; Shively et al. 2005; Dwinnell et al. 2019). Tule elk face growing levels of human disturbance as California’s rangeland ecosystems, traditional tule elk habitat, are projected to experience continued urban and agricultural development (Sleeter et al. 2017). In addition to increasing landscape connectivity that would enable tule elk to seek suitable habitats as climate conditions change (Denryter and Fischer 2022), our results indicate that management actions which reduce disturbance, such as road closure, seasonal access restriction, and locating artificial water sources away from roads would increase tule elk habitat availability and suitability.

Tule elk habitat selection patterns corresponded to seasonal and drought-induced changes in water and forage availability. In the dry season, elk selected areas near water sources, but used areas farther from water that had greater forage abundance. In the wet season, elk tracked spatio-temporal changes in forage quality across their home ranges, selecting areas with higher quality forage while avoiding human disturbance. Drought impacted these patterns, as elk selected areas closer to water sources during dry season drought, but farther from water sources during wet season drought. Management efforts should be taken to reduce anthropogenic disturbance near water sources, particularly during the dry season and during drought when elk are more dependent on drinking water. As droughts becomes increasingly frequent and severe across western North America, future research elucidating how population dynamics correspond to the spatial distribution water sources and forage will be vital to identifying optimal densities of artificial water sources and sustainable population levels.

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