A TALE OF TWO CERVIDS: HABITAT SELECTION AND SPATIAL ECOLOGY

OF ROOSEVELT AND TULE ELK IN CALIFORNIA

By

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PREFACE

California's Roosevelt (*Cervus canadensis rooseveltii*) and tule elk (*C. c. nannodes*) populations have experienced a remarkable recovery after over-hunting and habitat loss nearly extirpated them from the state (McCullough 1969, California Department of Fish and Wildlife 2018). The tule elk population has grown from fewer than 10 individuals in the late 1800s to nearly 6,000 in 2017 (McCullough 1969, California Department of Fish and Wildlife 2018). Roosevelt elk populations in California have experienced similarly dramatic population growth, and the state population now numbers approximately 6,000 (Barnes 1925a, 1925b, California Department of Fish and Wildlife 2018). Yet research on these two populations has not matched their rapid population growth, and knowledge gaps have formed regarding how these subspecies utilize and relate to their habitat. Greater clarity of Roosevelt and tule elk habitat selection patterns would help managers continue to effectively support the recovery of these two iconic subspecies. As the manner in which elk populations balance their competing resource needs is unique to each population (Skovlin et al. 2002), I have examined Roosevelt and tule elk habitat selection patterns in separate analyses and present these results in independent chapters. In both cases, I examine the role behavior can play in influencing habitat selection and fitness. Habitat selection models rely on a number of assumptions, which have proven difficult to test, particularly in regards to how behavior relates to perceived habitat suitability and resource availability. In this thesis, I address some of these assumptions by accounting for variation in elk behavior and changing resource conditions. My results

demonstrate the effect of behavioral variation on habitat suitability predictions and its

importance for consideration in population management decisions.

ACKNOWLEDGEMENTS

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

CHAPTER 1 : RISK PERCEPTION MODIFIES HABITAT SELECTION AND

POTENTIAL ABUNDANCE IN ROOSEVELT ELK

Abstract

Habitat selection models often assume individuals within a population behave identically, which is problematic as behavior can vary non-randomly due to differences in how individuals perceive and respond to predation risk. I used GPS location data and a measure of human-tolerance (on a scale of "bold" to "shy") to examine habitat selection patterns and make predictions about habitat suitability and potential abundance of Roosevelt elk in northwestern California, USA. Overall, elk selected for areas of open land cover types, in close proximity to forest edge, further from roads, and with gentle terrain. Shy elk remained closer to forest edge and further from roads compared to bold elk. Predicted elk habitat differed between bold and shy elk, but potential abundance estimates were relatively consistent at around 13,000-14,000 elk in the study area. Management decisions should be made at the level of individual elk groups when feasible, as decisions that affect an elk group's tolerance of human disturbance will impact the availability and composition of suitable habitat, and ultimately may affect potential abundance.

Introduction

Wildlife managers rely on models of habitat selection to inform land management decisions (e.g., habitat preservation, restoration, and modification). These models frequently assume that animals select habitat "optimally" – i.e., that individual animals select high quality resources to maximize their own fitness (Hildén 1965, Jaenike and Holt 1991, Orians and Wittenberger 1991, Martin 1998). However, resource selection is often mediated by other behavioral concerns, including limited access to high quality resources (Nilsen et al. 2004, Martin et al. 2008), intraspecific interactions (Kamler and Gipson 2000, Campomizzi et al. 2008, Farrell et al. 2012), and perceived predation risk (Creel et al. 2005, Heithaus and Dill 2006). In other words, animals may not use high quality resources because they cannot get to them, because they are prevented from doing so by their peers, or because they are afraid. These behavioral interactions can lead to poor inferences regarding habitat selection, as animals will appear to select resources that are in fact sub-optimal. Habitat modelers have developed a suite of approaches to cope with physical barriers in assessing habitat selection (Wilson et al. 1998, Getz et al. 2007, Horne et al. 2007), and a large theoretical framework has evolved to address how habitat selection is affected by intraspecific competition (Fretwell and Lucas 1970, Møller 1995, Calsbeek and Sinervo 2002). However, while many ecologists have explored the "landscape of fear," few have outlined the management consequences for ignoring fear in habitat models (Merrick and Koprowski 2017).

Fear is particularly problematic for habitat selection models as behavioral patterns can differ within a population due to genetic variation and differences in experience-based learning. A fear-based behavioral continuum describing individual response to potentially threating stimuli, ranging from shyness to boldness, has been observed in many species across a range of taxa (Wilson et al. 1994). These behavioral patterns correspond with ecologically significant activities such as migration, movement rate, and habitat use (Carrete and Tella 2009, Found and Clair 2016, Thurfjell et al. 2017). To add to the complexity, habitat selection can occur across multiple spatial and temporal scales simultaneously. In this manner, fear can affect the establishment of individuals' home ranges across the landscape (2nd order selection), as well as finer scale patterns of habitat use within home ranges (3rd order selection) (sensu Johnson 1980). The inconsistent role of fear in habitat selection is especially conspicuous in how individuals respond to human presence. Many animals perceive human disturbance as a type of predation risk and experience trade-offs between avoiding predation or obtaining resources (Frid and Dill 2002, Gavin and Komers 2006, Sawyer et al. 2009). Perceived risk elicits anti-predator behavioral responses including spatial and temporal avoidance of risky areas, increased vigilance, and lower feeding rates (Benhaiem et al. 2008, Proffitt et al. 2009, Sawyer et al. 2009).

How populations perceive and respond to human disturbance is especially important for game species, such as the North American elk (*Cervus canadensi*s spp.), a

group-living, generalist herbivore. Elk response to human disturbance can vary even within a population depending on a variety of factors, such as exposure level, type of disturbance, or the availability of refugia. (Thompson and Henderson 1998). Fear of predation can mediate elk space-use in relation to the use of refugia (e.g., forest cover) and risky habitats (e.g., areas near roads) (Wolff and Horn 2003, Creel et al. 2005, Frair et al. 2005, Hernández and Laundré 2005, Prokopenko et al. 2017). These risk mediation behaviors can result in reduced acquisition of resources and population declines (Dwinnel et al. 2019). On the other hand, some elk populations also benefit from human activity, which can serve as a "human shield" against natural predators and result in lower predation rates and increased calf survival (Hebblewhite 2005). Understanding how perception of human predation risk – which I'll refer to as human tolerance – affects elk habitat selection would provide insight into habitat suitability models and a habitat's capacity to support elk populations.

An ideal situation to study the effects of variable human tolerance in elk is present with the Roosevelt elk (*Cervus canadensis roosevelti*) population in northwestern California. While the population is recovering and expanding into new areas, patterns of habitat selection appear to be fairly idiosyncratic: some groups utilize areas with high human use, while others are reclusive and found deep in managed forests. Roosevelt elk are typically reliant on open areas with herbaceous growth (Rowland et al. 2018), yet despite the apparent availability of suitable habitat, the regional population remains below management objectives (CDFW 2018). I hypothesize that risk perception,

specifically risk perception due to fear or tolerance of humans, is a central driver of habitat selection in this population. If that is true, then resource selection functions (RSFs) should include a measure of elk response to human disturbance as an important contributor to selection models. Furthermore, fearful elk should remain closer to refugia, show greater avoidance of risky areas and consequently experience lower resource availability than less fearful elk. Ultimately, reduced access to high quality habitat for fearful elk should result in lower potential abundance estimates.

Materials and Methods

<u>Study area</u>

The study area was located in the North Coast Roosevelt Elk Management Unit ("North Coast") which is comprised of Humboldt and Del Norte counties (Figure 1.1). The study area was ~15,000 km^2 divided between state, federal, tribal and private ownership, with timber production and livestock-based agriculture comprising a large part of private land use. Elevation ranged between 0-2,000 m. The climate was generally mild and coastal-influenced, with high annual precipitation (annual average ~1,700 mm) typically in the form of winter rain (National Climate Data Center 2017). Lower elevations and coastal areas were dominated by forests with coastal redwood (*Sequoia sempervirens*), coast Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*), red alder (*Alnus rubra*.) and big-leaf maple (*Acer macrophyllum*) comprising the most abundant tree species. Interior and higher elevation areas were drier and characterized by montane forests with Ponderosa pine (*Pinus ponderosa*), white fir (*Abies concolor*), madrone (*Arbutus menziesii*), tanoak (*Lithocarpus densiflorus*) and oak *(Quercus* spp.*)*. Potential predators included mountain lions (*Puma concolor*), black bears (*Ursus americanus*), bobcats (*Lynx rufus*), and coyotes (*Canis latrans*). Hunting permits for Roosevelt elk were allocated as a combination of public draw tags and private landowner tags. Over the course of the study, 80-100 elk tags were issued each year, with high hunter success rates (i.e., >80% average success rate in the Northwestern and North Coast hunts 2007-2017,

CDFW 2018). An additional but unknown number of elk were killed each year due to poaching and vehicle collisions (C. Hilson, pers. comm., 2019). A portion of the region's elk lived in Redwood State and National Park, where no legal hunting occurs.
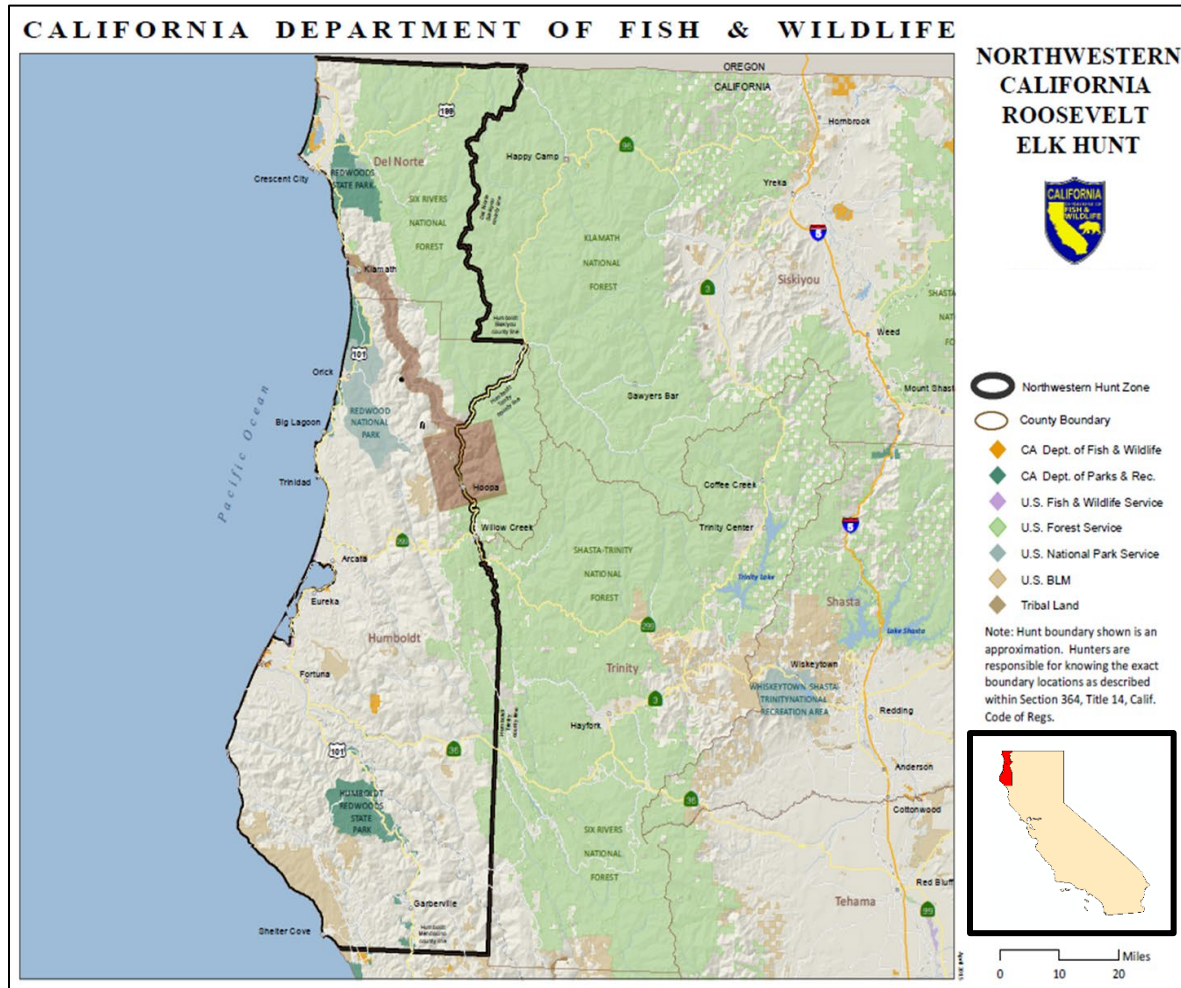
Figure 1.1: Map of the study area, the North Coast Elk Management Unit, California,

USA.

Data

In the fall and winter of 2017, 17 Roosevelt elk cows were chemically immobilized using dart projectors from the ground or a helicopter and fitted with GPS collars in Humboldt and Del Norte counties. An additional 20 cows were collared in the fall and winter of 2018. The distribution of collars was based on group size and capture opportunity, but effort was made to have representative samples of the entire population in terms of habitat type and land-use. All captures were conducted by California Department of Fish and Wildlife with approval from Humboldt State University (IACUC protocol #15/16.W.96-A). Collars were programmed to record a location every 4 hours, and every hour during calving season to assist with locating neonatal calves. To avoid seasonal bias in the collar data due to unequal relocation rate, I thinned the data to one location every 4 hours for all cows across seasons. Data were censored if the animal or collar died prematurely (<3 months from capture). The final dataset included 95,022 elk locations from 33 individuals collected between November 2017 and February 2019 (Appendix A).

As my goal was to capture the causal factors driving population distribution and habitat use for elk at the home range and regional scales, I selected a set of predictor variables that have been shown to represent important drivers of elk habitat selection in other studies (Appendix B; Skovlin et al. 2002, Rowland et al. 2018). These variables can be broadly categorized as pertaining to forage availability, predation risk, or energetic

cost of movement. I included eight predictor variables in the RSF, seven of which were GIS-based measurements. I used a land cover layer that assigned each pixel as belonging to one of eight land cover types (CalFire 2018). I used a forest cover change layer to account for changes in forage availability due to timber production and wildfire (Hanson et al. 2013). I used distance to nearest forest edge layer, since the forest edge is an important transition zone between forage (outside the forest) and shelter/safety (inside the forest) (USGS GAP 2011). I calculated distance to nearest road, as elk populations exposed to human hunting pressure will avoid roads due to perceived predation risk (US Bureau of the Census 2018). The road shapefile included all primary, secondary, rural, and private roads, including vehicular trails. I used a digital elevation model to calculate terrain slope in ArcMap, measured in degrees above horizontal, since steeper terrain is energetically demanding to use (NASA 2001). I also calculated two complementary layers to capture the effects of topographic aspect: "northness" and "eastness" (sin and cosine of aspect * π/180, respectively). I included a single non-GIS measurement – "fear score" – to account for differences in human disturbance tolerance between the distinct elk groups. Elk were considered part of the same group if home ranges had considerable spatial overlap (i.e., >50%). I assigned each group a rating based on the elk group's flight initiation distance in response to human presence. Elk behavior was assessed from observations of each group during research and management field work (i.e., captures, calf survival monitoring, mortality investigations, census counts, opportunistic sightings, etc.) by myself and the California Department of Fish and Wildlife's regional elk

management personnel. Fear scores ranged between 0-3, with a score of 0 being the least fearful (i.e., most tolerant of human presence) and 3 being the most fearful of human presence (i.e., least tolerant of human presence) (Appendix C).

RSF design

I created RSFs by measuring and comparing a set of environmental predictor variables found at each elk use location to those found at available locations (Manly et al. 2002). Available locations were randomly drawn from two spatial scales corresponding to the 2nd and 3rd orders of selection (Johnson 1980), which I refer to as the landscape scale and home range scales, respectively. I defined the landscape range as the 100% minimum convex polygon created using the full set of elk locations, with a 700 m buffer (Figure 1.2). This buffer reflects average 4-hour movement distance reported from 7 separate elk movement studies (Strohmeyer and Peak 1994). Within the landscape scale, I randomly sampled a number of available locations equal to the number of use locations. The home range scale was defined as the 95% isopleth of a time-local convex (T-LoCoH) hullset, where V_{max} was the greatest distance between two consecutive points and the *s*-value was set to 0.5 to provide equal weight to time and spatial distance between points, for each individual elk's set of locations ('tlocoh' package in program R; Lyons et al. 2013). Within each elk's individual home range area, I randomly sampled a number of available locations equal to the number of used locations collected for that individual elk.

I excluded locations from one individual from the landscape scale dataset due to anomalous results caused by the highly linear shape of its home range (Elk.ID 44046, Group.ID Gold Bluff Beach). Since this elk's movements were constrained to a narrow strip of beach, assumptions about habitat availability in relation to distance-to-feature measurements could not be met. After censoring available locations that occurred in areas missing environmental predictor data, this resulted in 79,223 available locations within a landscape scale of 4,230 km^2, and 94,089 available locations within a home range scale of 322 km^2. I developed a set of RSFs at both scales using mixed-effects logistic regression models with a binomial distribution and logit-link function to estimate response coefficients for each environmental predictor variable (Manly et al. 1993, Boyce et al. 2002).
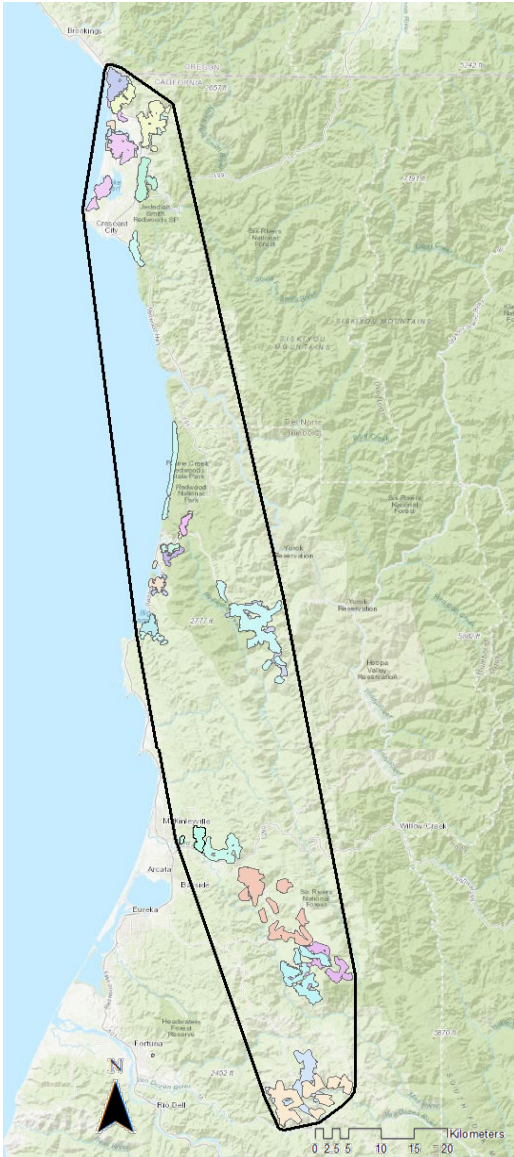
Figure 1.2: Map showing the distribution of collared elk home ranges in northwestern California, USA. The black polygon represents the landscape scale. The home range scale was the collection of individual home ranges.

I built a set of 11 models with predictive variables included as fixed effects and either Group ID or Individual ID as a random effect, for both spatial scales. I also ran the same 11 models as only fixed-effect models, for a total of 33 total models at each scale. I tested for collinearity between each variable and did not include predictors in the same model if ($|r| > .70$). The most parsimonious model within < 2 AIC of the lowest scoring model was selected as the best model for each spatial scale (Arnold 2010).

Potential abundance estimates

I used a habitat-based ratio estimator to estimate the potential population size of Roosevelt elk in the study area following the principles and methods reported in Boyce and McDonald (1999) and Hebblewhite et al. (2011). Fundamentally, my ratio-estimator approach was based on extrapolating the observed density ratios (i.e., number of elk / unit of habitat) across the entire study area using minimum group count data, group home ranges, and the relative probability of use values from the RSFs. The formula for the ratio-estimator is expressed in the following equation:

$$\hat{N}_{North\ Coast} = \frac{\left(\sum \hat{w}_{North\ Coast}(x)_i \right) * \hat{N}_{study}}{\sum \hat{w}_{study}(x)_i}$$

Where N_{study} is the population estimate for elk in the study groups, $\sum \hat{w}_{study}(x)_I$ is the sum of the relative probabilities from the RSF of the study group ranges and $\sum \hat{w}_{North\ Coast}(x)_I$

is the sum of the relative probabilities from the RSF of the entire North Coast region (see Appendix D for graphical interpretation of habitat-based ratio estimator). For the study group count data, I used the highest cow-calf count observed for each group during the study period (CDFW 2019, unpublished data). I excluded elk that did not have reliable count data (n = 4, Group ID = "Goodman" and "Grizzly Creek / Kneeland"). The group ranges were created by merging each collared elk's 95% minimum convex polygon (MCP). I used MCPs for each group instead of T-LoCoH hullsets since MCPs are more inclusive and therefore better account for the possibility that un-collared elk within a group may use nearby areas not included in a collared individual's home range.

I defined a "habitat suitability" threshold based on RSF values in order to exclude the large amount of habitat unlikely to be used by elk. As no previous studies have attempted to use a habitat-based ratio estimator for elk, I tested a total of five threshold methods to assess the effect changing the threshold had on final population size estimates. One threshold was set at the RSF value of 0 (corresponding to 0% relative probability of use). The other thresholds were set at the RSF values that captured 95%, 90%, 75%, and 50% of use-locations.

To test the effect of variable human tolerance on potential population abundance and the amount of available elk habitat, I divided the data based on fear score and created two additional RSFs using location data from either bold or shy elk only (total of three RSFs: "combined", "bold", "shy"). I defined bold elk as those with fear scores of 0 or 1 and shy elk as those with fear scores of 2 or 3. I created scenario-specific RSFs using the

top landscape scale model from the combined data. The thresholds based on RSF values of elk-use location were specific to their respective scenarios (i.e., only bold elk locations used to determine habitat suitability thresholds for the bold RSF). I calculated the density relationship using the combined elk abundance counts and group ranges with scenario-specific RSFs. While density estimates would ideally be based on scenario-specific group counts and ranges, this was precluded by the wide variance in group sizes and small number of groups for each scenario.

Results

Landscape scale

The top model included the full set of variables, with interactions between fear score and forest edge distance and between fear score and road distance, with Elk.ID included as a random variable (Table 1, see Appendix E for complete landscape scale model selection results). Relative probability of elk presence was greater closer to forest edge, further from roads, on gentler slopes, and in areas that had lost forest cover more recently (Figure 1.3). Herbaceous and agricultural areas were the most strongly selected land cover types (Figure 1.4). Greater fear scores resulted in stronger selection for areas closer to forest edge and further from roads (Figure 1.5, Figure 1.6). The top model was used to predict relative probability of use across the North Coast (Figure 1.7).

Table 1.1: Partial/Top Model selection results from set of mixed effects models explaining landscape level habitat selection patterns of Roosevelt elk in northwestern California. Top model contained 10 fixed effect terms: Land cover type, distance to forest edge, distance to road, years since forest loss, slope, northness, eastness and fear score, as well as interaction terms between fear score with road distance and fear score with edge distance. Elk ID was included as a random effect.

Model Description	df	logLik	AICc	ΔAIC	weight
Full, Elk.ID random	18	-76351.80	152739.6	0.00	1.0000
(-) Fear_Score:road_dist, Elk.ID random	17	-76386.27	152806.5	66.95	0.0000
Full, Group.ID random	18	-76416.16	152868.3	128.73	0.0000
(-) Fear_Score:road_dist, Group.ID random	17	-76448.21	152930.4	190.81	0.0000
(-) Fear_Score:edge_dist, Elk.ID random	17	-76585.20	153204.4	464.81	0.0000
(-) Fear_Score:edge_dist + Fear_Score:road_dist	16	-76634.89	153301.8	562.18	0.0000
(-) Fear_Score, Elk.ID random	15	-76646.76	153323.5	583.92	0.0000
(-) Fear_Score:edge_dist, Group.ID random	17	-76648.96	153331.9	592.33	0.0000
(-) Fear_Score:edge_dist + Fear_Score:road_dist, Group.ID random	16	-76695.87	153423.7	684.14	0.0000
(-) Fear_Score, Group.ID random	15	-76703.63	153437.3	697.66	0.0000
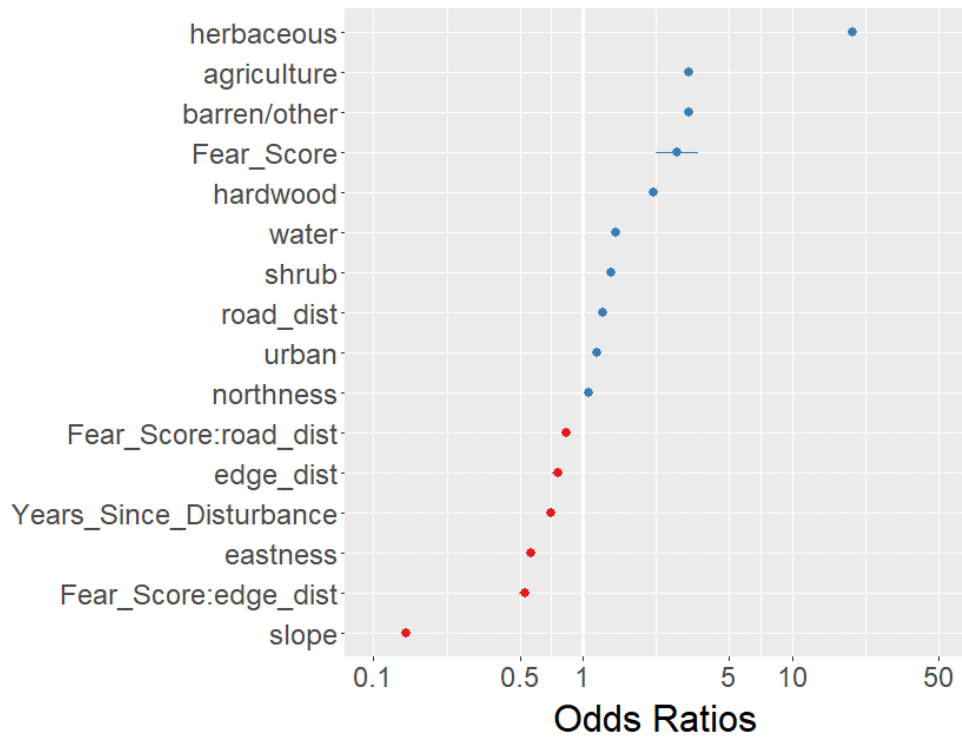
Figure 1.3: Standardized beta values of the fixed effects terms of top model explaining 2nd order habitat selection patterns of Roosevelt elk in northwestern California. Values above 1 (blue) and below 1 (red) represent positive and negative effects, respectively. Top model contained elk ID as random effect. Conifer was the reference class for the land cover terms. Error bars represent 95% confidence intervals.
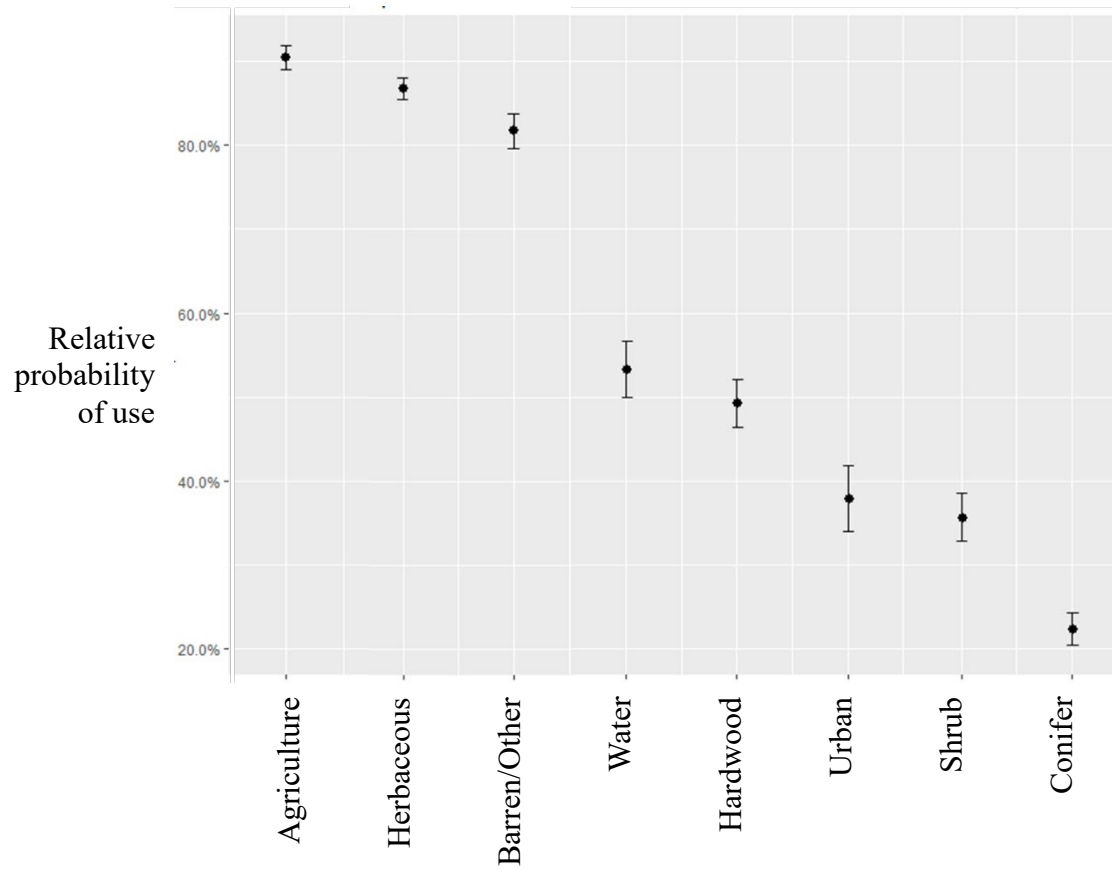
Figure 1.4: Marginal effects plot showing response of Roosevelt elk to land cover at the landscape scale. California, USA. Error bars represent 95% confidence intervals.
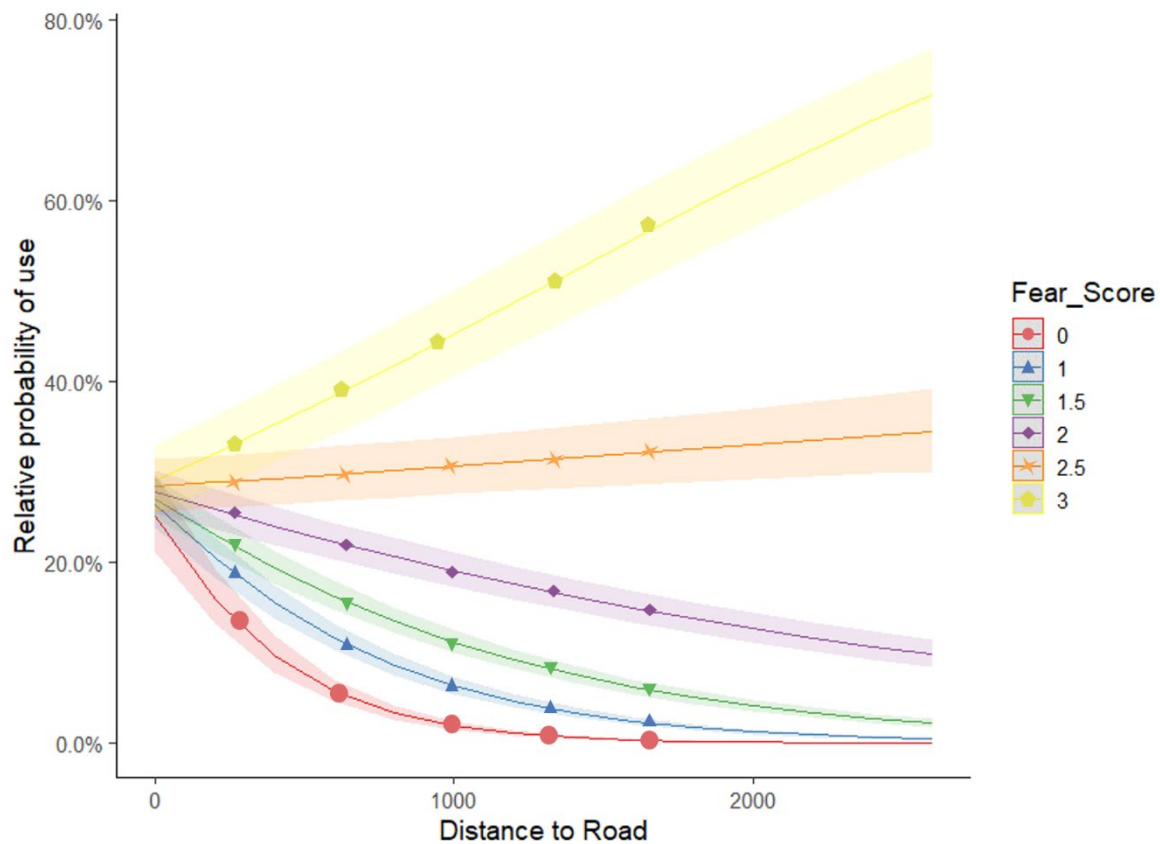
Figure 1.5: Interaction plot showing how 2nd order habitat selection changes in response to distance to roads depending on fear score. Greater fear scores correspond to lower tolerance to human disturbance for Roosevelt elk in northwestern California. Shaded areas represent 95% confidence intervals.
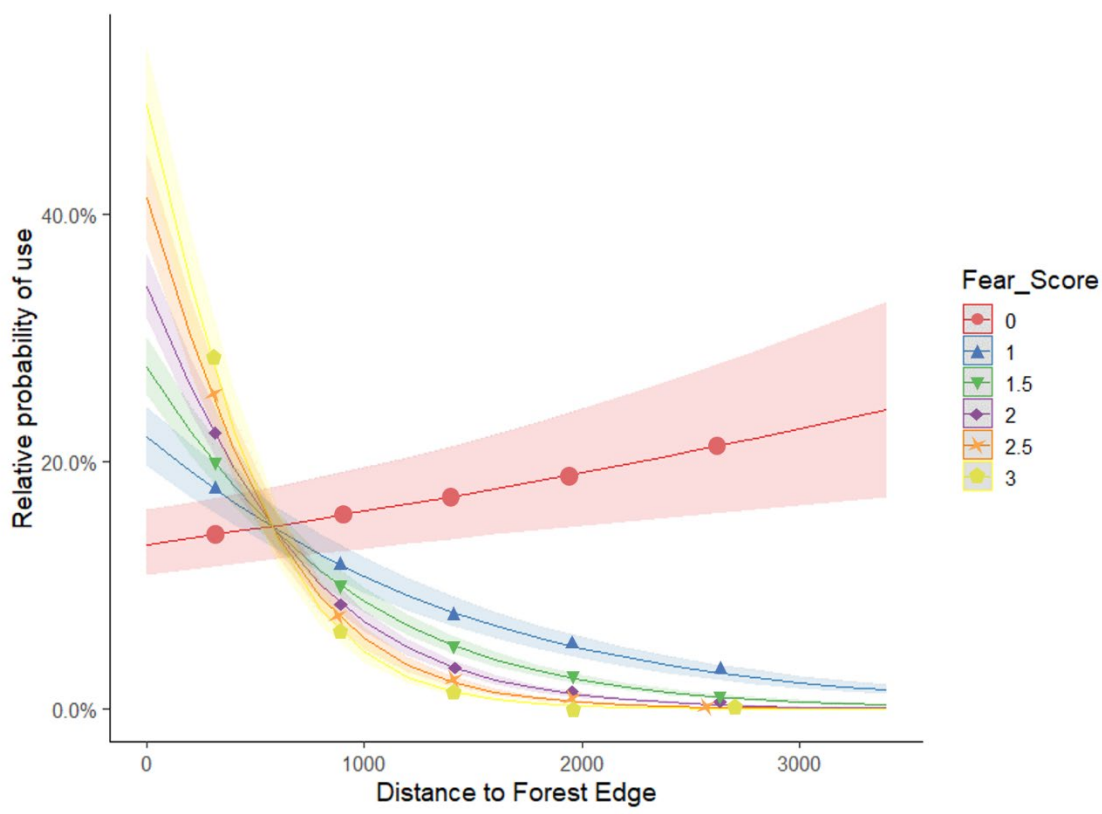
Figure 1.6: Interaction plot showing how 2nd order habitat selection changes in response to distance to forest edge depending on fear score. Greater fear scores correspond to lower tolerance to human disturbance for Roosevelt elk in northwestern California. Shaded areas represent 95% confidence intervals.

High Suitability

Low Suitability

N

km
0 5 10   20   30   40
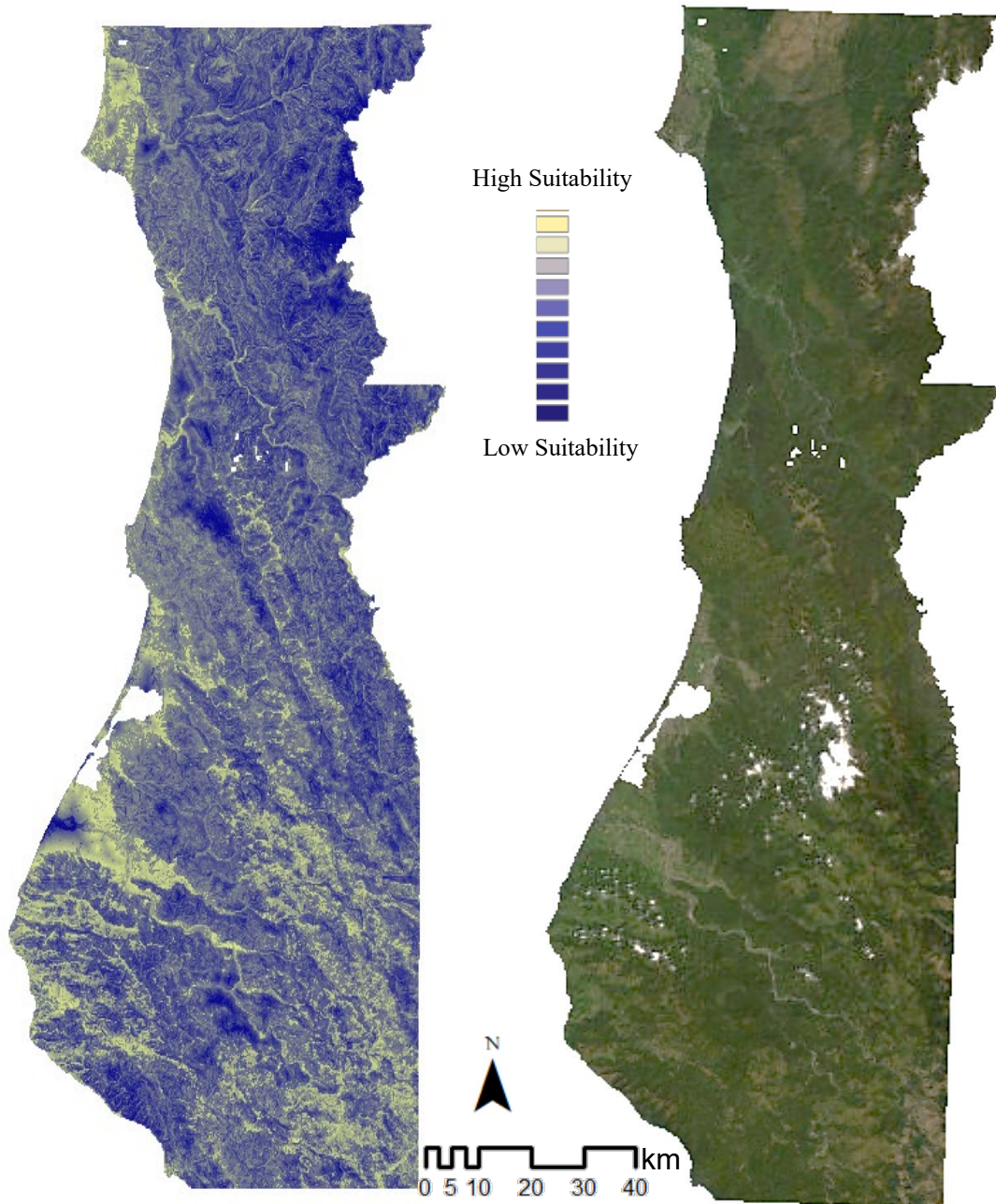
Figure 1.7: A) Habitat suitability for Roosevelt elk in the North Coast Elk Management
Unit in northwestern California created using the top model from a resource
selection function analysis of all elk locations (n= 33 individuals). B) A true color
image of the North Coast Elk Management Unit, California.

Home range scale

The top model for the home range level selection included the full set of environmental variables, with interactions between fear score with distance to forest edge and nearest road and Group.ID included as a random effect (Table 2, see Appendix F for complete home range scale model selection results). The distance to road term was the only term to overlap 0 in the 95% confidence interval; however, the interaction term of distance to road with fear score did not overlap 0. At the home range scale, elk selected for areas further from forest edge and roads, with gentler slopes and areas that had more recently lost forest cover (Figure 1.8). Selection for land cover classes followed a similar pattern to the landscape scale with herbaceous and agriculture land cover as the two most strongly selected cover types, and with conifer and shrub being the least strongly selected (Figure 1.9). The interaction terms showed that groups of elk with higher fear scores selected for areas closer to forest edge and further from roads while elk with the lowest fear scores selected for greater distance to forest edge and had no response to roads (Figure 1.10, Figure 1.11).

Table 1.2: Model selection results from set of mixed and fixed effects models explaining home range level habitat selection patterns of Roosevelt elk in northwestern California. Top model included 9 fixed effect terms: land cover type, distance to forest edge, distance to road, time since forest loss, slope, eastness and fear score, as well as interactions between fear score with road distance and fear score with edge distance. Elk ID was included as a random effect.

Model Description	df	logLik	AICc	delta	weight
Full, Group.ID random	18	-128209	256454.8	0	0.9975
Full, Elk.ID random	18	-128216	256467.8	12.99	0.0015
(-) northness + eastness, Group.ID random	16	-128219	256469.2	14.39	0.0007
(-) Fear_Score:road_dist, Group.ID random	17	-128219	256471.9	17.04	0.0002
(-) Fear_Score:road_dist, Elk.ID random	17	-128225	256483.6	28.80	0.0000
(-) northness + eastness, Elk ID random	16	-128226	256484.2	29.35	0.0000
(-) slope, Group.ID random	17	-128250	256533.2	78.37	0.0000
(-) slope, Elk.ID random	17	-128255	256544.4	89.55	0.0000
(-) Fear_Score:edge_dist, Group.ID random	17	-128287	256608.6	153.72	0.0000
(-) Fear_Score:edge_dist + Fear_Score:road_dist, Group.ID random	16	-128292	256616.8	162.00	0.0000
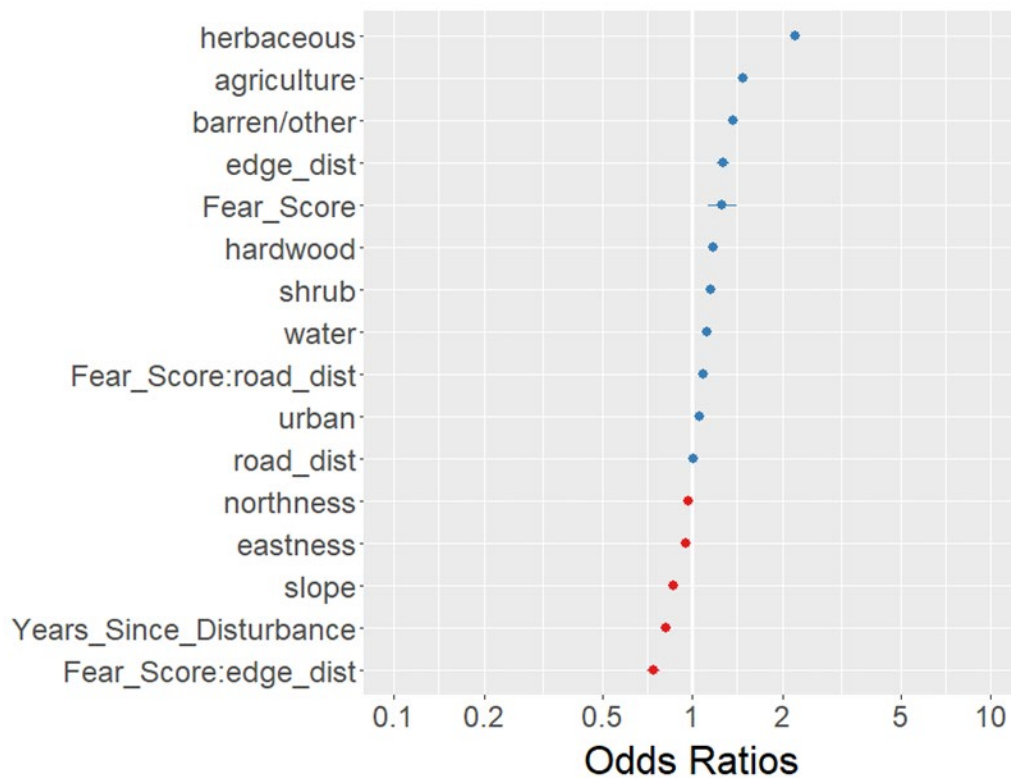
Figure 1.8: Standardized beta values of the fixed effects terms of top model explaining 3rd order habitat selection patterns of Roosevelt elk in northwestern California. Values above 1 (blue) and below 1 (red) represent positive and negative effects, respectively. Top model contained Group.ID as random effect. Conifer was the reference class for the land cover terms. Error bars represent 95% confidence intervals.
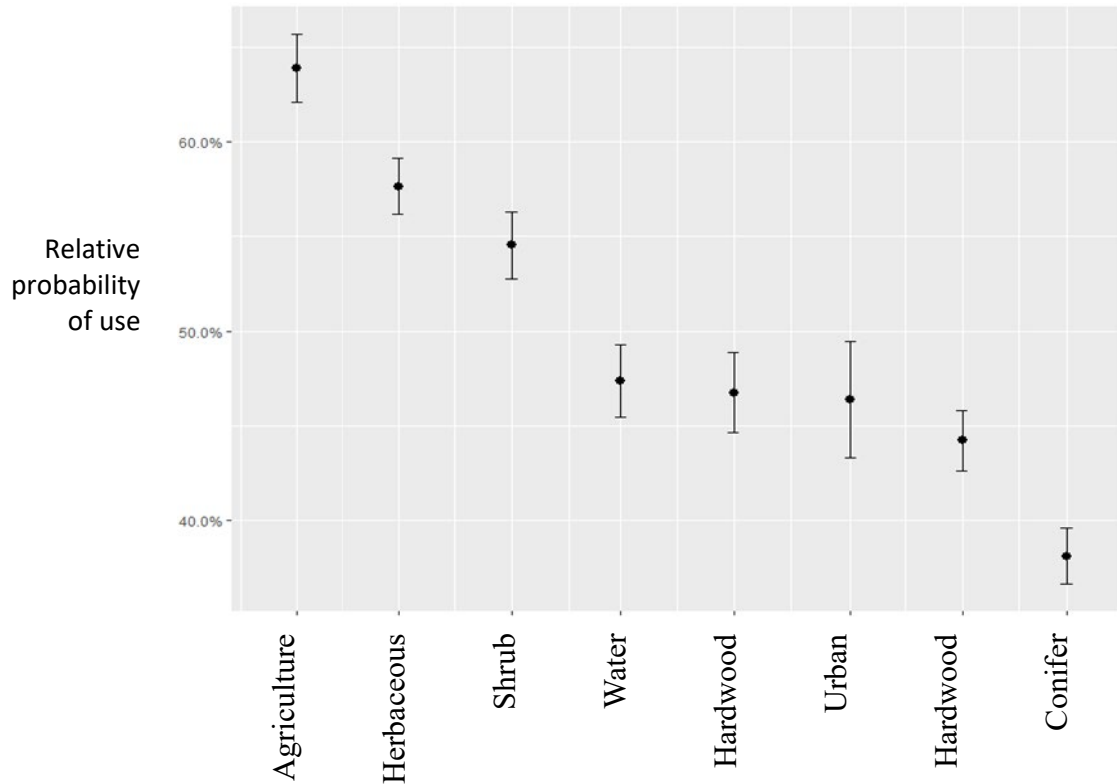
Figure 1.9: Marginal effects plot showing response of Roosevelt elk to land cover at the home range scale. California, USA. Error bars represent 95% confidence intervals.
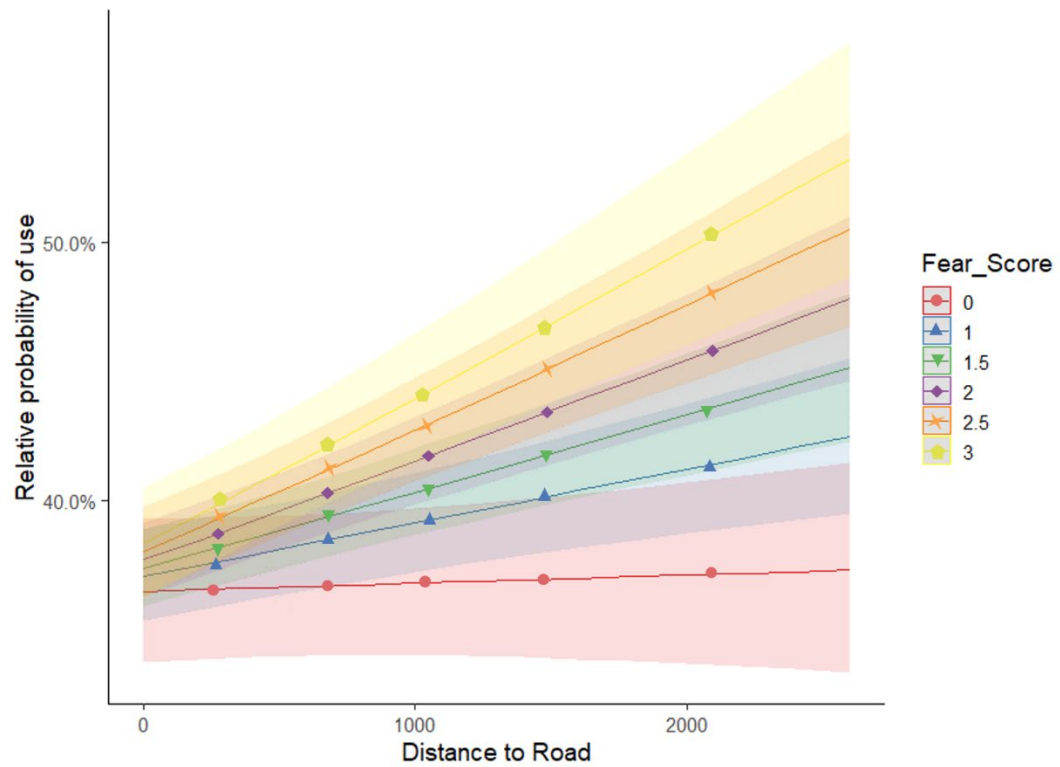
Figure 1.10: Interaction plot showing how 3rd order habitat selection for Roosevelt elk in northwestern California changes in response to distance to road depending on fear score. Greater fear scores correspond to lower tolerance to human disturbance. Shaded areas represent 95% confidence intervals.
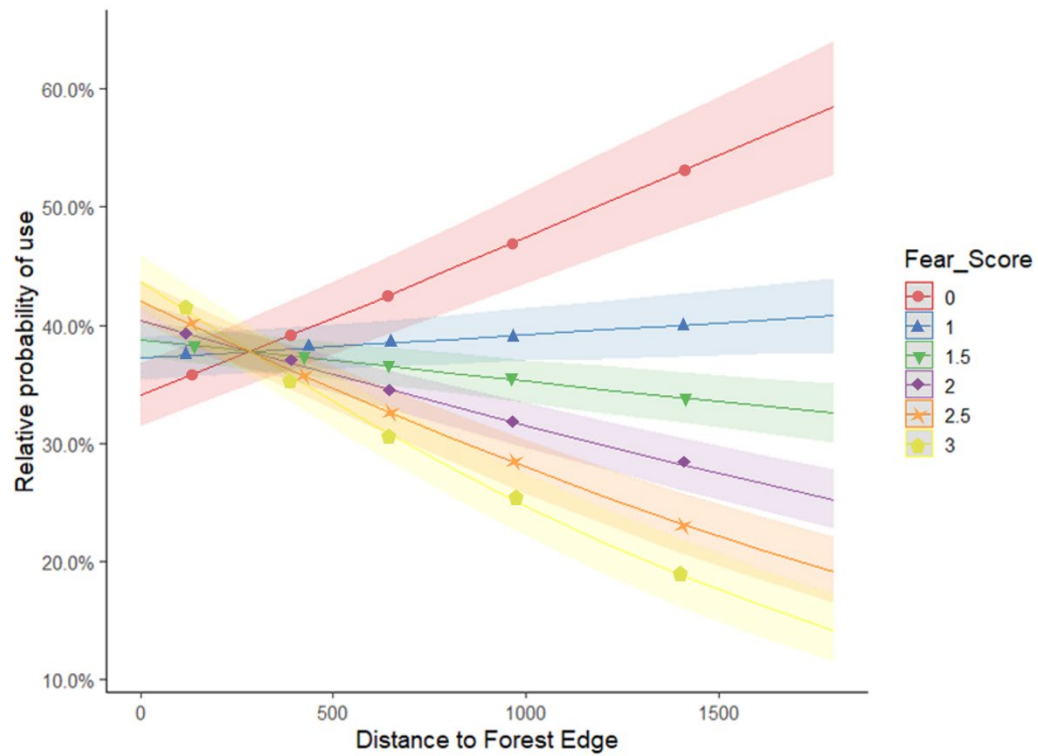
Figure 1.11: Interaction plot showing how 3rd order habitat selection changes in response to distance to forest edge depending on fear score. Greater fear scores correspond to lower tolerance to human disturbance for Roosevelt elk in northwestern California. Shaded areas represent confidence intervals.

<u>Abundance estimates</u>

   The amount and composition of predicted suitable elk habitat differed between the three RSF scenarios (Figure 1.12, Figure 1.13). The size and consistency of potential abundance estimates varied based on the RSF and threshold method (Figure 1.14). The bold RSF scenario showed the most consistency, with an inter-method range of between 12,286-14,337 individuals. Estimated population sizes were least consistent for the shy scenario ranging between 8,518-18,827 individuals (average = 14,904 individuals), which were the two most extreme population estimates. The combined scenario estimates were relatively consistent, ranging between 10,480-15,683 individuals, and had a similar average compared to the bold scenario (13,485 vs. 13,784 individuals, respectively). The amount of suitable habitat predicted by each RSF varied by threshold method but was generally consistent between RSFs. For each given threshold, the shy RSF predicted the greatest amount of suitable habitat and the bold RSF predicted the least amount of suitable habitat (Figure 1.15; Appendix G).
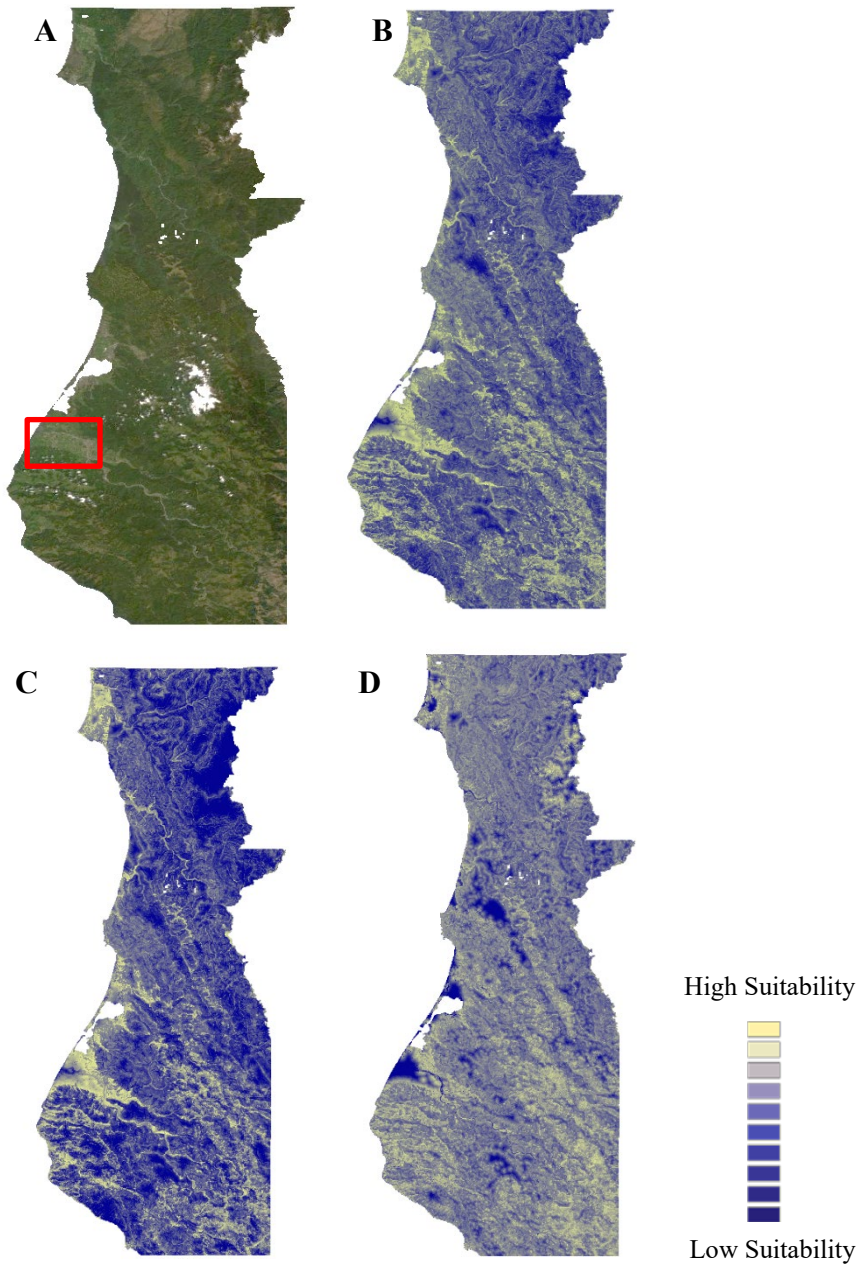
Figure 1.12: Comparison of the three scenarios' RSFs predicted across the study area. A) True color satellite image of the study area. B) RSF created using the full location dataset. C) RSF created with bold elk locations. D) RSF created with shy elk locations. Area highlighted in red in 1.12A is shown in detail in Figure 1.13.
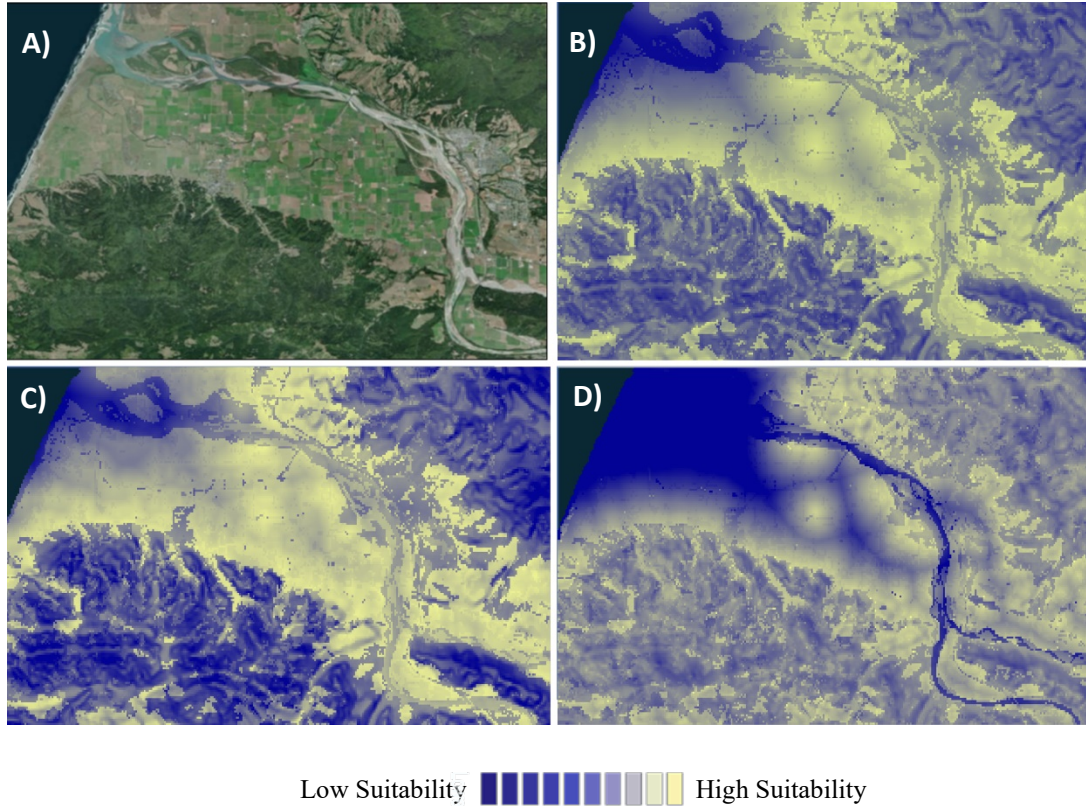
Figure 1.13: Detail comparison of the three RSFs shown in Figure 1.12. A) True color satellite image of the study area. B) RSF created using the full location dataset. C) RSF created with bold elk locations. D) RSF created with shy elk locations. B) and D) show relative probability of use is negatively correlated with distance to forest edge, with bold elk more likely to use areas at greater distance to forest edge than in the shy scenario.
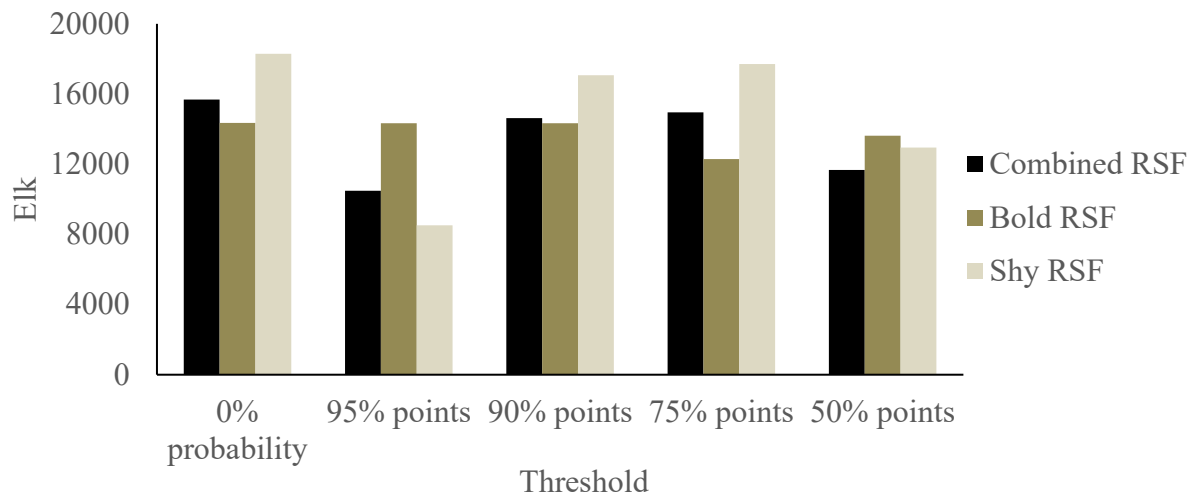
Figure 1.14: Potential population size estimates for Roosevelt elk in northwestern California, USA, calculated under three management scenarios. Potential population size was calculated using a scenario-specific resource selection function (RSF) and a habitat-based ratio estimator. Minimum habitat suitability thresholds were set either by excluding all areas that fell below 0% relative probability of use, or by using the RSF value corresponding to the highest x% of elk-use locations.
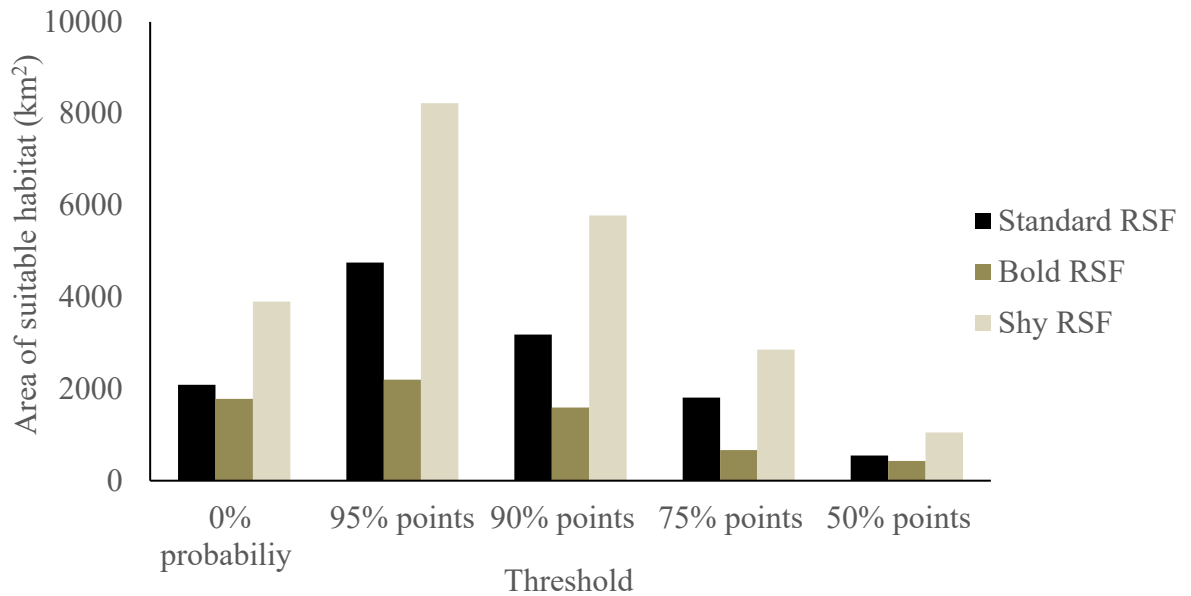
Figure 1.15: Amount of suitable habitat for Roosevelt elk in northwestern California, USA, calculated under three scenarios. Suitable habitat was calculated using a scenario-specific resource selection function (RSF) and a habitat-based ratio estimator. Minimum habitat suitability thresholds were set either by excluding all areas that fell below 0% relative probability of use, or by using the RSF value corresponding to the highest x% of elk-use locations.

Discussion

Human predation risk perception played a key role in structuring elk habitat selection patterns. Bold and shy elk selected habitat differently, which had consequences for predicted regional habitat suitability and population size. Shy elk remained closer to forest edge and further from roads compared to bold elk. Estimates of potential population size were relatively consistent between thresholds for the bold RSF scenario, and to a lesser extent for the combined RSF, but varied widely for the shy RSF. Regardless of human-tolerance, optimal elk habitat in the study area was represented by areas with open land cover types, in close proximity to forest edge, further from roads, and with gentle terrain. Management decisions should be made at the level of individual elk groups whenever possible, as decisions that affect a group's human tolerance impacts habitat selection patterns and potential abundance.

Risk perception was a key factor in habitat selection patterns as shy elk avoided areas with higher perceived human predation risk. The best-supported models showed fear score interacted with distance to road and forest edge at both spatial scales and for all three RSFs. At the landscape scale, the combined model showed that elk avoided roads and selected areas near forest cover; however, these patterns varied with an individual's response to human disturbance. Shy elk selected areas further from roads and closer to forest cover compared to bold elk (Figure 1.5, Figure 1.6, Figure 1.10, Figure 1.11). These results align with previous studies that have found perceived risk elicits changes in spatio-temporal distribution patterns as individuals avoid areas with greater chance of

encountering predators and select areas near predation refugia (Frid and Dill 2002, Creel et al. 2008, Cleveland et al. 2012). Forest cover is a common predation refugia for elk in heterogeneous landscapes, and roads represent areas with higher risk of encountering or being disturbed by humans (Czech 1991, Creel et al. 2005, Frair et al. 2005, Hernández and Laundré 2005). In this study, selection was positively correlated with distance to forest edge at the home range scale – a result that would be difficult to interpret without accounting for behavioral variation in the population (Figure 1.8, Figure 1.11). Individual behavioral patterns have been found to correspond with a variety of aspects in ungulate life-history, including diel activity patterns, usage of risky habitats, and migration (Bonnot et al. 2013, Found and St. Clair 2016). The large differences in elk selection patterns observed in this study provide further support for including behavioral variability in habitat selection modeling.

To be clear, this study did not assess individual animals on the spectrum of shy to bold in the traditional sense as developed by behavioral ecologists (*in situ* Wilson et al. 1994, Found and St. Clair 2016); rather, I assigned this trait to behavior at the group level. In other words, while shyness and boldness were observable phenomena at the group level, these traits are by necessity emergent properties of the combined decisions of every individual member of that group. Nonetheless, my assessment of group behavior was consistently measurable and repeatable over the timeframe of this study. Further, the differences in group-level behavior explained a substantial portion of the group's selection of habitat. In fact, my findings are in accordance with the "grazing personality

model" recently described by Garcia et al. (2020). The grazing personality model,
defined as "suites of traits of different nature (e.g., behavioral, cognitive, physiological,
and morphological), which… result in specific grazing patterns displayed consistently
across contexts and over time", accounts for the role of individual behavioral variation in
the collective foraging decisions of large herbivore groups. This model has particular
relevance to elk management as a range of herd personalities may maximize productivity
and ecosystem services in areas with a diversity of habitats (Garcia et al. 2020). Elk and
other social species would benefit immensely from further research into the interplay
between this individual and group-level behavior.

Underlying most habitat suitability modeling is the premise that animals select
habitat based on its quality, that is, animals should spend more time in areas that
contribute to an individual animal's fitness. However, this study demonstrated that
habitat selection differs between groups identified as shy and those identified as bold.
Bold behavior entails a trade-off between greater access to resources, such as foraging or
mating opportunities and greater risk of mortality (Ward et al. 2004). For ungulates, bold
behavior increases individual's mortality risk from anthropogenic sources, such as human
predation (Cuiti et al. 2012), and can increase disease transmission risk from contact with
domestic livestock (Richomme et al. 2006). While this study did not explicitly address
how bold and shy strategies related to fitness, there were no obvious disparities in
mortality between the bold and shy elk, with mortality sources of collared individuals
being: hunter harvest (3 bold individuals, 2 shy), unknown (2 bold, 2 shy), and vehicle

collision (1 bold, 1 shy). Ultimately, there was a fairly tight correlation between density and habitat suitability in the group home ranges, indicating that, at least at the home range level, fitness and behavior were linked. Future work examining the link between behavior and fitness in this population should explore recruitment rates and juvenile mortality between the bold and shy strategies.

Competition for available forage may be the ultimate cause driving habitat selection for bold elk. Energetically-stressed individuals incur greater risk for foraging opportunities (Sih 1980, Sweitzer and Berger 1992), a phenomenon that has been suggested as one of the mechanisms behind the growing number of habituated elk populations in North America (Thompson and Henderson 1998). Long-term monitoring of the habituated groups in Redwood National and State Parks has shown population growth was density dependent and linked to forage availability (Weckerly 2017), and some groups have expanded their home ranges in tandem with a reduction in palatable forage in traditional grazing areas (Weckerly, pers. comm. 2020). Future work that quantifies the effect of human tolerance on energetic availability, such as measuring giving-up densities and vigilance behavior in relation to road and forest cover distance, would improve our understanding of the fitness implications of bold behavior and establishing long-term population goals.

An alternative mechanism for bold group's human tolerance – the "human shield" hypothesis – was not well-supported as elk did not show risk avoidance behavior at the home range scale, and are unlikely to be responding to landscape scale patterns of

mountain lion presence. Mountain lions in the study area avoid primary roads (Meinke 2004), yet bold elk did not select for areas closer to roads at the home range scale, as would be expected if elk were responding to fine-scale patterns of predation risk. While bold elk did select areas closer to roads at the landscape scale, it is problematic to interpret this as evidence of risk avoidance behavior since overall mountain lion density would be similar across elk group home ranges due to ubiquity of mountain lion presence throughout the study area and the large size of mountain lion territories. Mountain lion home ranges around Redwood National and State Parks averaged 147 and 621 km^2 for females and males, respectively (Meinke 2004), dwarfing elk group home ranges in the same area, which averaged 11 km^2 in this study. Future research that more directly addresses the influence of non-human predation risk on elk behavior should include a fine-scale temporal component to account for daily variation in human disturbance and mountain lion activity.

Management Implications

The areas most likely to be selected by Roosevelt elk, regardless of human tolerance, were comprised of open land cover (i.e., herbaceous and agriculture) in close proximity to forest edge, and with lower slope (Figures 1.4, 1.9, see Appendix H for land comparison of land cover selection between bold vs. shy elk). The agricultural areas selected by elk were typically composed of pasture land used by livestock, rather than row crop production. The importance of open cover types and selection for areas that had recently lost forest cover indicate that forage availability was a primary driver of habitat selection in the population. This would also explain the strong selection for the barren/other land cover class observed at the landscape scale, as a herbaceous area heavily used by one group (Red School House) was incorrectly classified as barren/other in the land cover layer (Appendix I).

The results suggest that human predation risk perception should factor into elk management decisions. While the mechanisms controlling human tolerance in ungulates are complex (Thompson and Henderson 1998, Blumstein 2016), management actions can influence tolerance and its component behaviors. In ungulate populations, changes in hunting pressure, disturbance frequency and disturbance type affect habituation, habitat selection and disturbance response (Cassier and Freddy 1992, Bender et al. 1999, Stankowich 2008, Naylor et al. 2009). Accordingly, management decisions that decrease human tolerance could inhibit elk expansion into unoccupied areas. Whether or not to promote the growth of a given population should be dependent on situation-specific

context, such as high potential for human-wildlife conflict or the proximity to suitable but unoccupied areas. For example, in areas with high potential for human-elk conflict, targeted management action towards nearby elk groups could deter population expansion. Management practices which emphasize disturbance, such as extended hunting seasons or aversive conditioning with dogs, may help deter tolerance behavior and conflict better than numerical reduction alone (Bateson and Bradshaw 1997, Cromsigt et al. 2013). Conversely, practices that prioritize tolerance may facilitate dispersal to suitable habitat through human-disturbed areas and increase elk viewing opportunities for non-consumptive uses such as tourism. Formal establishment of tolerance goals into management plans may be helpful for transparency in managing non-consumptive uses and human-elk conflicts. Elk behavior is highly variable; even neighboring groups can have differing human tolerance. Elk management decisions should therefore be made at as small of spatial scales and on a group-by-group basis whenever possible (Sevigny et al. 2018).

The habitat-based ratio-estimator technique I used demonstrated utility as a management tool. I took a basic approach and implementation was straightforward. Results were consistent across threshold methods and illustrative of population-level response to differing tolerance scenarios. While estimates of its accuracy are unknown, it was useful to gauge relative differences between alternative management actions. This approach could have practical applications for two management scenarios, or for giving a basic idea of population size a given area of habitat could support. This may help identify

areas for habitat conservation and restoration and guide management plan

implementation under specific tolerance scenarios.

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Appendix A

Appendix A: Table of each collared elk's number of points, group membership, and size
of their group.

Elk.ID	Number of Points	Group.ID	Group Size
42732	13188	Tolowa	200
42733	12912	Tolowa	200
42727	12678	Tolowa	200
44526	2466	Tolowa	200
44891	6360	Tolowa	200
42735	13287	Big Lagoon	40
44049	8076	Big Lagoon	40
44044	12216	CBEC	100
42737	13071	Davison	65
44048	7962	Davison	65
42729	11181	Gilbert	45
44054	4467	Gilbert	45
44046	12564	Gold Bluff Beach	30
44057	6276	Goodman	NA**
44056	6378	Goodman	NA**
44897	6588	Grizzly	NA**
42728	12504	Hastings	40*
44051	6378	Kneeland	NA**
42731	4653	Lincoln	30
44894	5295	Lincoln	30
44042	6474	Bald Hills	250
44045	7794	Bald Hills	250
42736	11145	Bald Hills	250
44043	6447	Maple Creek	35
42726	12726	McAdams	70
42738	3276	Orick	110
44052	7914	Orick	110
42730	3171	R. Ranch	40
44896	6384	R. Ranch	40
42725	7347	Rowdy	40*
42734	13218	Red School House	65
44047	7953	Red School House	65
42724	12675	Timmons	20

*Hastings + Rowdy are considered the same group for population counts

** NA = Not available. Groups without reliable count data were excluded from
   abundance estimate calculations.

Appendix B

Appendix B: Detail for each variable used in the model selection and habitat suitability mapping process.

Predictor Variable	Name in Model	Product/Source	Year	Resolution	Note
Land Cover	*life_form*	Fveg 15.1	2018	30m	
Distance to Road	*road_dist*	2017 TIGER/Line Shapefile	2017	30m	
Distance to Edge	*edge_dist*	USGS –AP–- Ecotone	2017	30m	
Slope	*slope*	ArcMap calculation	2001	90m	Slope calculated from digital elevation model with Spatial Analyst Extension
Northness	*northness*	Cosine of aspect * pi/180)	2001	90m	Aspect calculated from digital elevation model in ArcMap with Spatial Analyst Extension
Eastness	*eastness*	Sin of aspect * pi/180	2001	90m	Aspect calculated from digital elevation model in ArcMap with Spatial Analyst Extension
Years since forest loss	*years_since_loss*	Global Forest Cover Change 2000-2018	2018	30m	
Fear Score	*fear_score*	Field observations of study groups	2018	-	See Appendix C

Appendix C

Appendix C: Fear Score Assessment Criteria: Fear Scores were assessed based on field observations of disturbance response in the collared study groups. The distance at which elk were disturbed (i.e., became vigilant or initiated flight) was assessed in relation to two disturbance types, humans on foot and vehicles. Groups that fell in between two categories were given the average score (i.e,. 0.5, 1.5, 2.5).

Fear Score	Human on foot	Vehicle
0	<25 m	Minimal / none
1	25-50 m	Minimal / none
2	>50 m	25-50 m
3	>50 m	>50 m

Appendix D

Appendix D: Graphical representation of the habitat-based ratio estimator approach used to estimate the potential population size of Roosevelt elk in the study area based on the density relationship between RSF scores and number of elk in a given area. The potential abundance of elk in the study area (*iv*) is proportional to the number of elk in the collared study groups (*i*) multiplied by the sum of RSF values of suitable habitat in the study area (*ii*), divided by the sum of RSF values of the group study areas (*iii*).
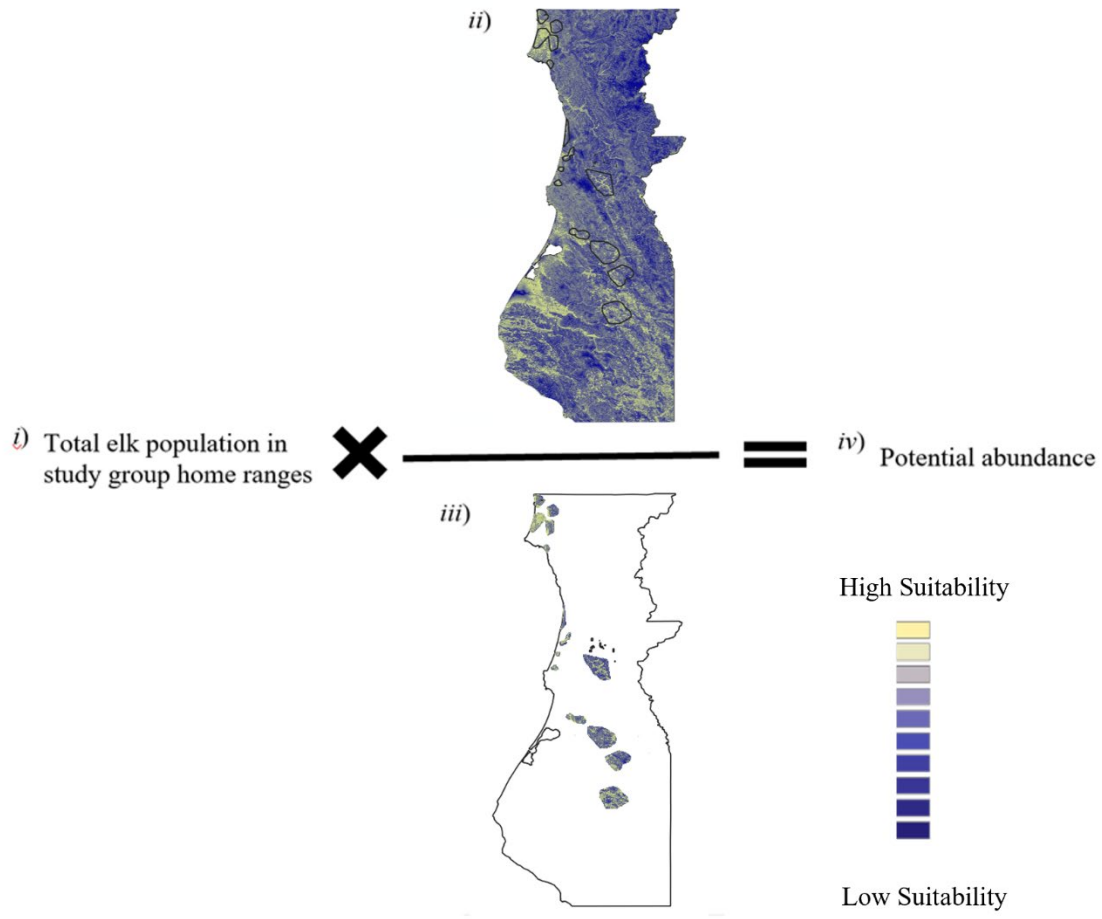
Appendix E

Appendix E: Complete model selection results tab–es - Landscape scale.

Description	logLik	AICc	delta	weight
Full*, Elk.ID random	-76291.53	152619.07	0.00	1.00
(-) Fear_Score:road_dist, Elk.ID random	-76327.10	152688.21	69.14	0.00
Full*, Group.ID random	-76353.06	152742.12	123.06	0.00
(-) Fear_Score:road_dist, Group.ID random	-76386.14	152806.28	187.22	0.00
(-) Fear_Score:edge_dist, Elk.ID random	-76497.60	153029.21	410.15	0.00
(-) Fear_Score:edge_dist + Fear_Score:road_dist	-76546.36	153124.71	505.65	0.00
(-) Fear_Score, Elk.ID random	-76558.44	153146.88	527.81	0.00
(-) Fear_Score:edge_dist, Group.ID random	-76559.05	153152.11	533.05	0.00
(-) road_dist, Fear_Score:edge_dist, Elk.ID random	-76563.36	153156.73	537.66	0.00
(-) Fear_Score:edge_dist, Fear_Score:road_dist, Group.ID random	-76605.04	153242.08	623.01	0.00
(-) Fear_Score, Group.ID random	-76612.92	153255.85	636.78	0.00
(-) edge_dist, Fear_Score:road_dist, Group.ID random	-76624.31	153278.61	659.55	0.00
(-) years_since_loss, Elk.ID random	-76751.42	153536.84	917.77	0.00
(-) years_since_loss, Group.ID random	-76831.11	153696.22	1077.15	0.00
(-) eastness, northness, Elk.ID random	-76866.67	153765.35	1146.28	0.00
(-) eastness, northness, Group.ID random	-76930.08	153892.16	1273.10	0.00
Full*	-77155.72	154345.45	1726.39	0.00
(-) Fear_Score	-77241.89	154515.79	1896.72	0.00
(-) Fear_Score:edge_dist	-77318.81	154669.62	2050.56	0.00
(-) Fear_Score:edge_dist, Fear_Score:road_dist, Elk.ID random	-77421.18	154872.37	2253.30	0.00
(-) road_dist, Fear_Score:edge_dist, Group.ID random	-77482.15	154992.30	2373.24	0.00
(-) years_since_loss	-77706.56	155445.12	2826.05	0.00
(-) edge_dist, Fear_Score:road_dist, Elk.ID random	-77835.80	155701.60	3082.54	0.00
(-) edge_dist, Fear_Score:road_dist, Group.ID random	-77913.06	155856.12	3237.06	0.00
(-) eastness, northness	-77959.19	155948.39	3329.32	0.00
(-) Fear_Score	-78706.66	157441.32	4822.26	0.00
(-) edge_dist, Fear_Score:road_dist	-79093.16	158214.31	5595.25	0.00
(-) slope, Elk.ID random	-81926.68	163887.35	11268.29	0.00
(-) slope, Group.ID random	-82003.80	164041.59	11422.53	0.00
(-) slope	-82771.41	165574.82	12955.75	0.00
(-) life_form, Group.ID random	-98002.89	196027.78	43408.71	0.00
(-) life_form, Elk.ID random	-98014.48	196050.96	43431.90	0.00
(-) life_form	-98993.40	198006.79	45387.73	0.00

Full* = northness + eastness +life_form + Years_Since_Disturbance + Fear_Score*road_dist + Fear_Score*edge_dist

Appendix F

Appendix F: Complete model selection results tables- home range scale.

Description	logLik	AICc	delta	weight
Full*, Group.ID random	-128209.42	256454.83	0.00	0.997545
Full*, Elk.ID random	-128215.91	256467.82	12.99	0.0015075
(-) eastness, northness, Group.ID random	-128218.61	256469.23	14.39	0.0007478
(-) Fear_Score:road_dist, Group.ID random	-128218.94	256471.88	17.04	0.0001988
(-) Fear_Score:road_dist, Elk.ID random	-128224.82	256483.63	28.80	5.56E-07
(-) eastness, northness, Elk.ID random	-128226.09	256484.18	29.35	4.23E-07
(-) slope, Group.ID random	-128249.60	256533.21	78.37	9.56E-18
(-) slope, Elk.ID random	-128255.19	256544.38	89.55	3.58E-20
(-) Fear_Score:edge_dist, Group.ID random	-128287.27	256608.55	153.72	4.17E-34
(-) Fear_Score:edge_dist, Fear_Score:road_dist, Group.ID random	-128292.42	256616.83	162.00	6.63E-36
(-) Fear_Score:edge_dist, Elk.ID random	-128293.18	256620.36	165.53	1.13E-36
(-) Fear_Score, Group.ID random	-128296.97	256623.93	169.10	1.90E-37
(-) Fear_Score:edge_dist + Fear_Score:road_dist	-128297.78	256627.56	172.72	3.11E-38
(-) edge_dist, Fear_Score:road_dist, Group.ID random	-128299.97	256629.94	175.11	9.45E-39
(-) edge_dist, Fear_Score:road_dist, Group.ID random	-128301.25	256632.50	177.67	2.63E-39
(-) road_dist, Fear_Score:edge_dist, Elk.ID random	-128304.71	256639.43	184.59	8.23E-41
(-) Fear_Score, Elk.ID random	-128305.04	256640.08	185.25	5.93E-41
(-) edge_dist, Fear_Score:road_dist, Elk.ID random	-128305.13	256640.27	185.44	5.40E-41
(-) Fear_Score	-128414.21	256860.41	405.58	8.48E-89
Full*	-128413.97	256861.95	407.11	3.94E-89
(-) years_since_loss, Group.ID random	-128424.91	256883.81	428.98	7.03E-94
(-) years_since_loss, Elk.ID random	-128428.26	256890.52	435.68	2.46E-95
(-) slope	-128445.48	256922.95	468.12	2.23E-102
(-) eastness, northness	-128450.74	256931.49	476.65	3.13E-104
(-) Fear_Score:edge_dist, Fear_Score:road_dist	-128453.42	256936.84	482.01	2.15E-105
(-) Fear_Score:edge_dist	-128452.56	256937.12	482.29	1.87E-105
(-) road_dist, Fear_Score:edge_dist, Group.ID random	-128482.58	256993.16	538.32	1.27E-117
(-) edge_dist, Fear_Score:road_dist	-128519.72	257067.44	612.61	9.38E-134
(-) Fear_Score	-128556.24	257140.49	685.65	1.29E-149
(-) years_since_loss	-128671.30	257374.61	919.78	1.87E-200
(-) life_form, Group.ID random	-130207.41	260436.82	3981.99	0
(-) life_form, Elk.ID random	-130226.41	260474.82	4019.98	0
(-) life_form	-130335.52	260691.03	4236.20	0

Full* = northness + eastness + life_form + Years_Since_Disturbance + Fear_Score*road_dist + Fear_Score*edge_dist

Appendix G

Appendix G: Table showing estimated potential cow-calf abundance in the study area, amount of predicted suitable habitat (km^2) and density (elk / km^2) as predicted with 5 different thresholds for the three RSFs.

Combined RSF

Threshold	Population	Area	Density
0% probability	15,683	2,091	7.5
95% points	10,481	4,753	2.2
90% points	14,631	3,183	4.6
75% points	14,958	1,810	8.3
50% points	11,672	552	21.1
Average	13,485	2,478	5.4

Bold RSF

Threshold	Population	Area	Density
0% probability	14,347	1,783	8
95% points	14,332	2,198	6.5
90% points	14,337	1,594	9
75% points	12,286	667	18.4
50% points	13,620	427	31.9
Average	13,784	1,334	10.3

Shy RSF

Threshold	Population	Area	Density
0% probability	18,288	3,906	4.7
95% points	8,519	8,225	1
90% points	17,063	5,778	3
75% points	17,707	2,859	6.2
50% points	12,945	1,049	12.3
Average	14,904	4,364	3.4

Appendix H

Appendix H: Marginal effects plots from the bold and shy RSF showing response of Roosevelt elk to land cover at the landscape scale. California, USA. Vertical bars represent confidence intervals.
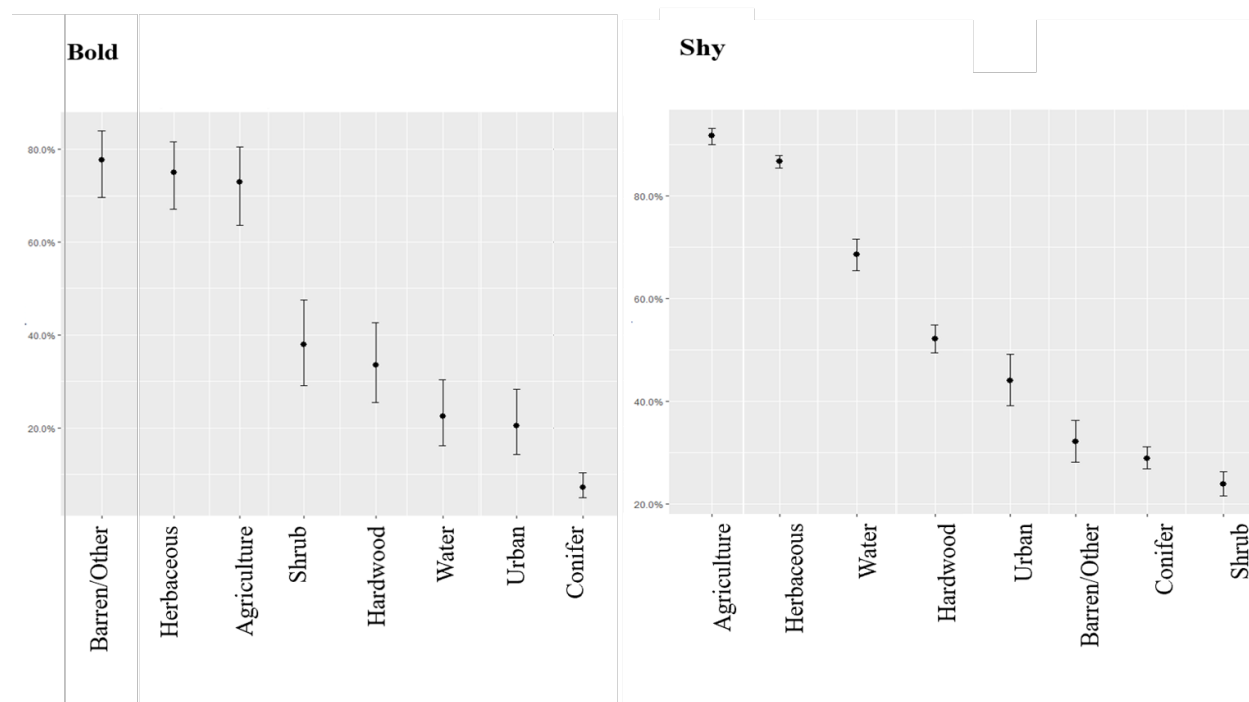
Appendix I

Appendix I: Image panel showing how a misclassificaiton in the land cover layer of an herbaceous area likely caused an over-estimation of selection for the barren/other land cover class. Panel A shows a land cover classification and home range for one elk from the Red School House group (Elk.ID 42734). The black points in Panel B depicts the elk locations. Panel C shows a satellite image of the area in Panels A and B. Panel D shows a detailed view of the area classified as Barren/Other instead of Herbaceous.
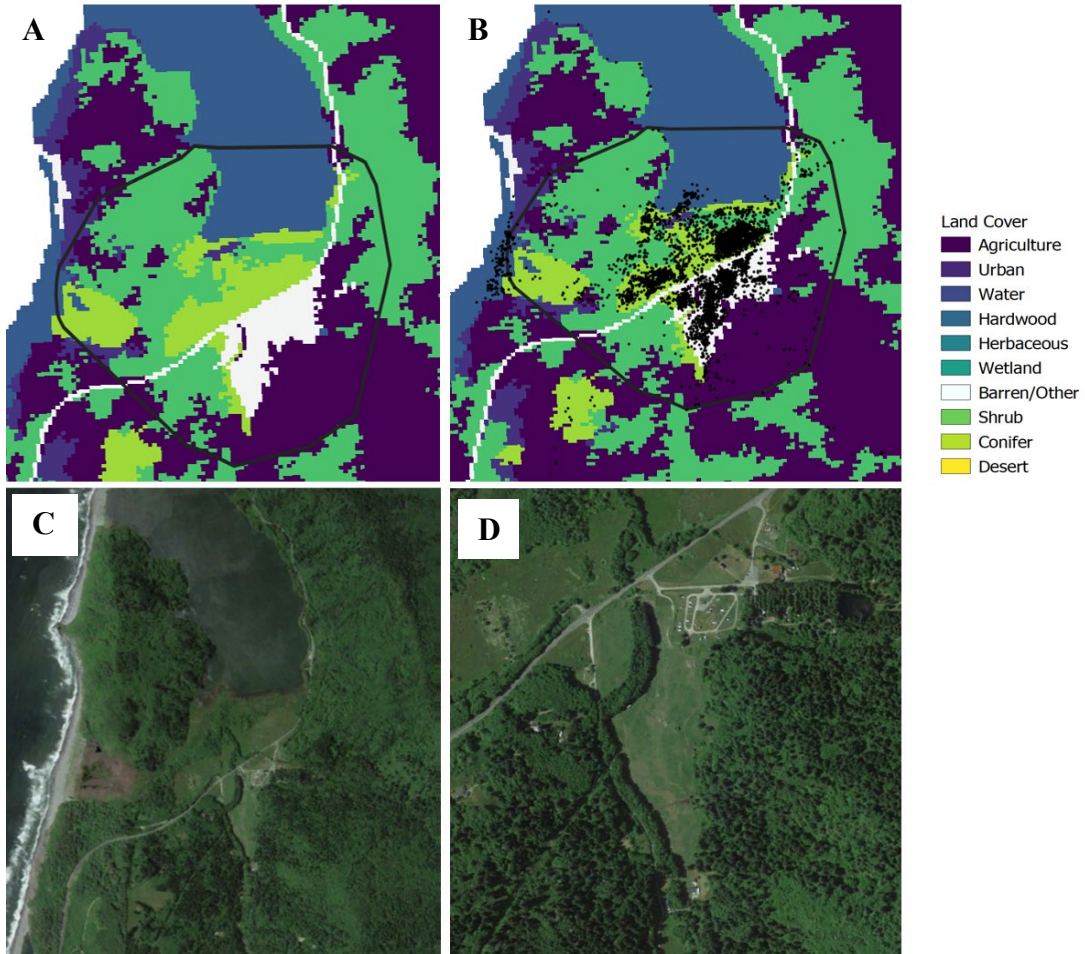
Intermission

While the mild, coastal climates along the North Coast means Roosevelt elk experience relatively consistent resource availability throughout the year, elk habitat selection varies temporally, with populations responding to annual changes in resource availability in their environment (Green and Bear 1990, Skovlin et al. 2002). As tule elk have evolved in arid ecosystems with unpredictable resource landscapes, these highly variable environments present a considerable challenge for habitat selection models due to unmet assumptions regarding resource availability. Fortunately, advances in our ability to collect spatial data now allow us to measure changes in resource availability at increasingly fine spatial and temporal scales. Simultaneously, the use of GPS collars can provide insight into animal response to these resources at similar scales. These technological improvements have enabled us to examine habitat selection in unpredictable environments in unprecedented detail.

CHAPTER 2: SEASONAL WATER DEPENDENCE AND FORAGE DYNAMICS DRIVES HABITAT SELECTION BY TULE ELK

Abstract

Climate change is expected to affect arid-system ungulate populations by altering the availability of critical resources, such as forage and water sources, and by increasing the frequency and severity of drought. The habitat selection patterns of the tule elk, a subspecies endemic to the Mediterranean climate regions of California, may provide insight into the behavioral adaptations which will allow affected ungulate populations to remain in their current geographic ranges. I used location data from GPS-collared tule elk to model their response to different environmental covariates including water sources, forage dynamics, human disturbance, and drought, across the wet and dry seasons. I found that tule elk behaved as central place foragers around water sources during the dry season, and that this behavior was likely tied to forage moisture content. During the wet season, elk appeared to be water independent and selected for high quality forage sources. These patterns were mediated by drought, as severe drought resulted in elk selecting for areas closer to water sources in the dry season and further from water sources in the wet season. My findings will help inform management decisions regarding artificial water source allocation and minimizing the effect of human disturbance on resource availability.

Introduction

Climate change is altering historic patterns of resource availability by affecting precipitation, phenology, temperature and drought (Parmesan and Yohe 2003, Trenberth 2011, Trenberth et al. 2014). Many wildlife populations will need to adapt their behaviors to persist in their current ranges as conditions change (Van Buskirk et al. 2012, Beever et al. 2017). These changes are expected to negatively impact terrestrial herbivore populations, particularly ungulates, due to their effects on the availability of forage (Post and Stenseth 1999) and water resources. Ungulates in arid regions are especially vulnerable, as many populations are at the limits of their physiological tolerances in these climates and experience seasonal resource shortages, which are exacerbated by drought (Duncan et al. 2012). The behavioral adaptations of arid system ungulates to persist in their challenging environments contain lessons for their continued resiliency and could provide valuable insight for ungulate management and conservation efforts in areas facing a warmer, drier future.

The adaptive behaviors wildlife use to increase fitness can be observed through their habitat selection patterns. Examining habitat selection can elucidate the factors affecting resource use across multiple spatial and temporal scales and provide insight into population distribution and growth (Fortin et al. 2008). Ungulates select habitat that allow them to access resources and avoid predation risk in an energetically efficient manner (Laundré et al. 2001, Skovlin 2012). For arid system ungulates, balancing these competing demands is complicated by the unpredictable availability of forage and water

resources in time and space. To understand how arid system ungulates have adapted to their dynamic resource landscapes, it is necessary to examine their habitat selection in relation to forage, water, and risk.

Foraging behavior is fundamental to understanding how herbivores acquire the energetic reserves necessary to survive periods of scarcity. Forage dynamics – changes in the quality and abundance of available forage – are an important factor in ungulate forage selection (Fryxell 1991, Bischof et al. 2012, Merkle et al. 2016). Ungulates face trade-offs between selecting forage sources of higher quality or greater abundance (Fryxell 1991, Bergman et al. 2001). At earlier growth stages, forage has lower fiber content, shorter passage times and higher nutritional content, but low biomass entails greater forage effort. Conversely, forage at later growth stages has lower nutritional content and takes longer to digest, but the greater biomass allows individuals to quickly achieve rumen-fill and devote more time to ruminating, acquiring other resources, or vigilance. Many ungulate populations track forage dynamics across the landscape by exploiting heterogeneity in forage phenology (Merkle et al. 2016, Aikens et al. 2017). These forage selection patterns vary between species and populations and likely reflects adaptation based on physiology, life-history, and available habitat. For example, a Rocky Mountain elk (*Cervus canadensis nelsonsoni*) population in British Columbia contained a mixture of forage selection strategies, with migratory individuals selecting for forage quality and non-migratory individuals selecting forage abundance (Hebblewhite et al. 2008). However, forage growth stage only accounts for foraging behavior during the growing season. Ungulates will alter their diet selection in response to forage senescence; this

often entails a switch from utilizing primarily herbaceous vegetation to woody browse, as browse contains higher protein and moisture content (Kutilek 1979). These diet selection decisions are particularly important for arid system ungulates as forage selection decisions are interconnected with forage moisture and the availability of water sources.

The availability of surface water and a species' level of water dependence mediate ungulate behavior in time and space. How often individuals must visit a water source is a function of forage moisture content, ambient temperature, and a species' physiological adaptations to conserve water (Cain et al. 2006). Water dependence concentrates ungulate activity around available water sources, especially during the dry season when water demands are high and forage moisture is low. In ungulates, this localization behavior can result in central place foraging dynamics and accompanying effects on foraging behavior, predation risk, and population dynamics (Coppolillo 2001, Rozen-Rechels et al. 2015). Critically, the gradual depletion of forage around the water source imposes limits on arid system herbivores' energetic returns and ultimately population growth (Western 1975, Owen-Smith 1996, Chamaillé-Jammes et al. 2009, Landman et al. 2012). While there is a growing recognition of the myriad effects of water availability and central place foraging behavior in herbivore communities, there has been comparatively little examination of these aspects outside of Africa. Relationships between arid system ungulates and their water sources is central to understanding the population-level impacts of drought and enabling informed management decisions regarding artificial water source allocation.

Predation risk further complicates ungulate foraging decisions. For ungulates, the effects of human activity as disturbances are especially important. Human disturbance

functions as a form of perceived predation risk (Frid and Dill 2002, Northrup et al. 2015) and elicits risk-mediation strategies such as flight and temporal or spatial avoidance (Stankowich 2008, Gaynor et al. 2018). Ungulates minimize disturbance by avoiding areas where human activity is concentrated, such as trails, roads, dwellings and energy production sites (Rowland et al. 2000, Sawyer et al. 2006, Weir et al. 2007, Brook 2010). In this manner, human disturbance reduces habitat suitability (Northrup et al. 2015), and can ultimately result in decreased fitness due to restricted access to critical resources (Dwinnell et al. 2019).

One species that can provide insight into the behavioral adaptations of arid-system ungulates is the tule elk (*Cervus canadensis nannodes*). Tule elk are a subspecies of the North American elk, a widely-distributed species evolved to cope with harsh winters and resource-abundant summers. Tule elk are endemic to the Mediterranean climate regions of California, which are characterized by large seasonal fluctuations in forage and water availability as well as frequent interannual drought. This subspecies has adapted both physiologically and behaviorally to cope with hot, dry summers when resources are scare, and cool, wet winters when resources are more abundant. In fact, despite the harsh conditions, including a historically severe drought across their range between 2012-2017, tule elk populations have grown steadily in the modern era (Griffin and Anchukaitis 2015, CDFW 2018). For these reasons, tule elk offer unique insight into habitat selection strategies to mitigate the challenges of arid systems on sensitive ungulates. Accordingly, I investigated tule elk habitat selection patterns within their dynamic resource landscapes in relation to season and drought. I hypothesized that forage

quality and water dependence would be the main drivers of selection in the wet and dry seasons, respectively, and that drought would amplify patterns of water dependence. I tested the prediction that elk would track forage green-up during the wet season and behave as central place foragers around water sources during the dry season. Because drought engenders greater water dependence and lower forage availability, I predicted that central place foraging behavior would increase with greater drought severity, and that the effect of drought would differ between the wet and dry seasons. I also hypothesized human disturbance would affect selection in all seasons and spatial scales. Specifically, I tested the prediction that elk would avoid roads and other landscape features associated with human presence.

Materials and Methods

<u>Study area</u>

The study area was located in San Luis Obispo, California (~ 35° 12'N, 119° 55'W), in and around the Carrizo Plain National Monument (Figure 2.1). The study area was comprised of a mixture of state, federal and private land ownership. The climate was semi-arid with an average annual precipitation of ca. 200 mm, most of which comes in the form of winter and spring rains. Summer temperatures averaged a high of 36°C while winter temperatures averaged 18°C (National Climate Data Center 2017). Elevations ranged between 450-1550 m. Vegetation varied across the study area, with California prairie, Piñon-juniper, oak-woodland, and chaparral being the most abundant vegetation communities (Buck-Diaz and Evens 2011). Cattle grazing occurred in some parts of the state and federal lands and throughout the adjacent private ranchlands, but usage of specific grazing allotments varied between years. Between 2012-2017, livestock numbers fell and many grazing allotments on public land were unused (B. Stafford, pers. comm., 2018). Potential elk predators in the study area included mountain lions (*Puma concolor*), black bears (*Ursus americanus*), bobcats (*Lynx rufus*), and coyotes (*Canis latrans*). The study region is managed as part of the La Panza Elk Management Unit. Elk hunting permits are allocated each year by the California Department of Fish and Wildlife (CDFW) and various hunting seasons with different regulations (i.e., general draw, Private Lands Management tags) occur between August and early December each year.

The amount of hunting pressure varied between the sub-herds due to differences in

ownership and public access restrictions.
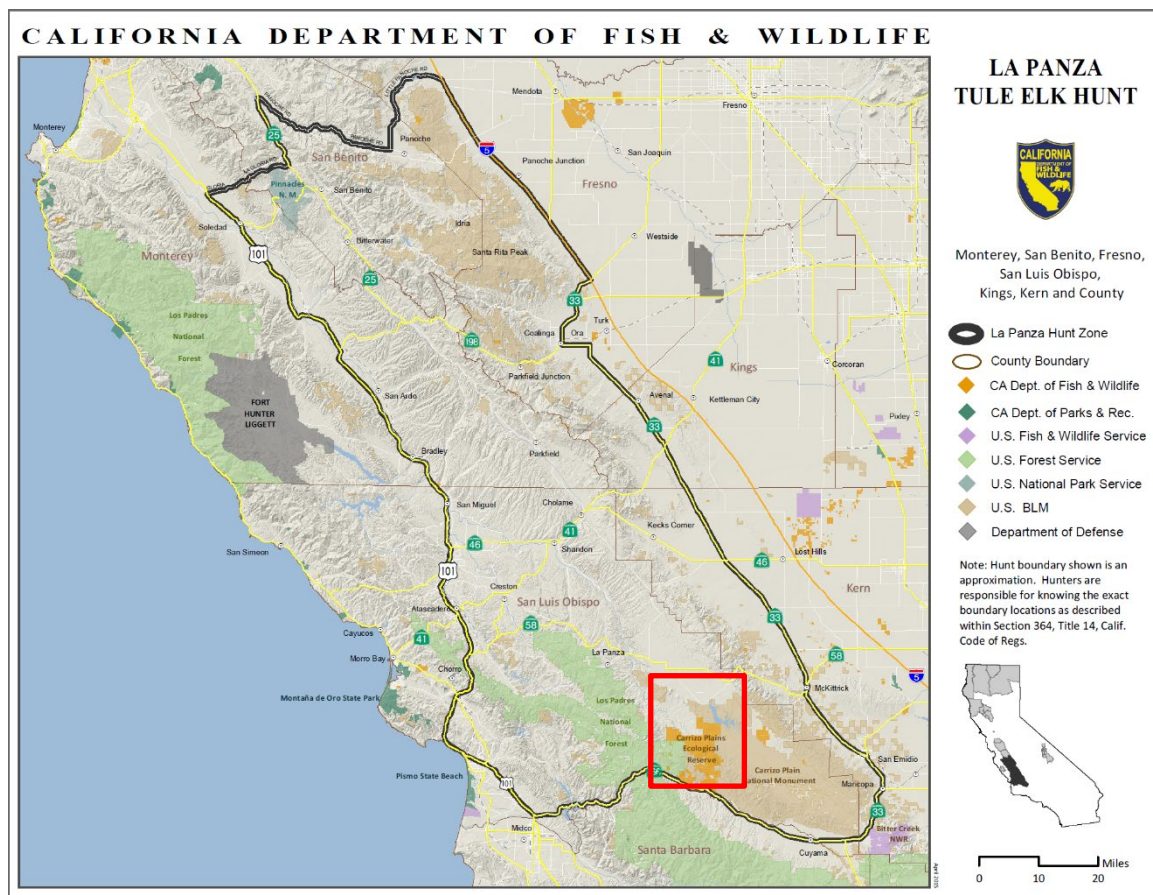
Figure 2.1: The study area was located within the La Panza Elk Management Unit, California, USA (Map credit: CDFW 2018). Highlighted area represents general location of the study area within the management unit.

<u>Data</u>

Between 2005 and 2017 location data were collected using GPS collars deployed on 36 tule elk (23 cows, 13 bulls) captured using helicopter net-capture. This time period contained a mixture of wet and dry years, but the majority (n = 24) of collars were deployed in 2015 during the severe drought that occurred between 2012-2017. Collars were distributed amongst four sub-herds historically recognized by CDFW ("California Valley", "American", "Chimineas", "Cedar Canyon"), with the sub-herd designation referring to geographic areas of the management unit. These sub-herds' home ranges differ in relation to land cover composition, proximity to human development, and property ownership (Figure 2.2). Collars were programmed to record a location every 13 hours and monitored for the duration of the collar's battery life or until the elk died. All captures were conducted independent of HSU by California Department of Fish & Wildlife and followed internal animal use protocols. *Post hoc* data analysis for this chapter was approved under HSU IACUC #16/17.W.94-E. A total of 30,667 elk location points were used in the habitat selection analysis, with a range of 115 – 1406 locations collected for each individual elk (Appendix J).
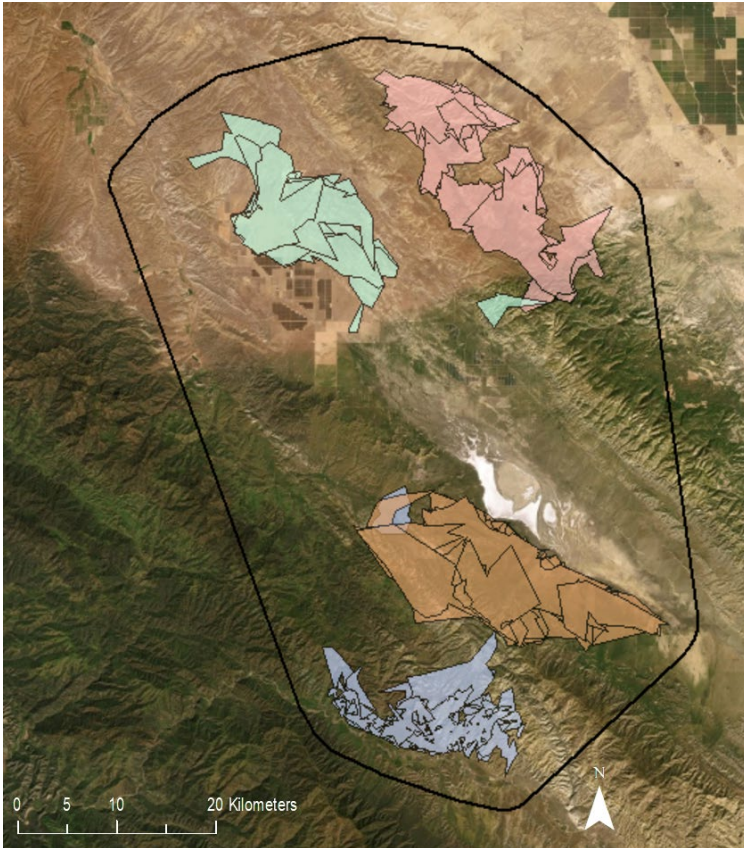
Figure 2.2: The distribution of collared elk in four distinct sub-herds in the study area in San Luis Obispo County, California, USA. The home range scale was the collection of individual home ranges. The black polygon represents the landscape scale.

I selected 13 raster-based predictor variables related to resource availability, risk and energy expenditure (Appendix K), which were known drivers of elk habitat selection in other populations or potential influences on habitat selection in this system (Skovlin et al. 2002). I used a land cover layer (*life_form*) that assigned each pixel as belonging to one of 10 land cover types (MLRC 2011). Distance to nearest road layer (*road_dist*) was included to account for human disturbance (US Bureau of the Census 2018). A digital elevation model was used to calculate terrain slope in ArcMap (Environmental Systems Research Institute, Inc., Redlands, CA, USA, Version 10.6.1), (*slope*) and topographic position in R (*TPI*, NASA 2001). Topographic aspect was measured using two complimentary layers: "northness" and "eastness" (*northness*, *eastness*; sin and cosine of aspect * $\pi/180$, respectively). The quantity and quality of available forage was estimated using the normalized difference vegetation index (*NDVI*) and the instantaneous rate of green-up (*IRG*), respectively (NASA 2018, see Appendix L for background and processing details). I conducted an extensive mapping effort to locate available water sources – both natural and man-made – on the landscape using a combination of satellite and aerial imagery (see Appendix M for full water source availability methodology). From this, I calculated distance to nearest water source for each location (*water_dist*). I also included distance to nearest solar production site, transmission-line and permitted cannabis production site to test for the possibility these activities and infrastructures represent an additional disturbance to elk (*solar_dist*, *power_dist*, *cannabis_dist*). The Palmer Drought Severity Index (PDSI) was used to account for the effects of drought,

measured monthly at the geographic center of the study area (Abatzoglou et al. 2017). I

included a term to account for differences between the sub-herds (*Herd*).

<u>RSF design</u>

I employed a use-available design in a resource selection function (RSF)

framework (Manly et al. 2002) to model the effects of the environmental predictor

variables on habitat use. Available locations were randomly drawn from two spatial

scales corresponding to the 2nd and 3rd orders of selection (Johnson 1980), which I refer

to as the population range and home range scales, respectively. I defined the population

range as the 100% minimum convex polygon with a 2,300 m buffer, created using the

full set of elk locations (Figure 2.2). This buffer reflected a mean 13-hour movement

distance as calculated from seven elk studies that reported average hourly elk movement

rates (Strohmeyer and Peak 1994). Within the population range, I randomly sampled

available locations equal to the number of use locations. The home range scale was the

collective set of individual elk home ranges, defined as the 95% isopleth of a time-local

convex (T-LoCoH) hullset where V$_{max}$ was the greatest distance between two consecutive

points, hulls were constructed with the nearest 15 locations, and the *s*-value was set to 0.5

to provide equal weight to time and spatial distance between points ('tlocoh' package in

program R; Lyons et al. 2013). Within each elk's individual home range area, I randomly

sampled a number of available locations equal to the amount of used locations collected

for that elk. Each available point matched the date when the use location was collected. I

censored use and available locations that occurred in areas missing environmental

predictor data (n=873).

At both spatial scales, I ran three sets of models based on the date each used point

was collected: full year, wet season, and dry season. I defined the wet season as

November 16 – May 15 and the dry season as May 16 – November 15. These two periods

were chosen in order to align with characteristic seasonal resource availability conditions

(i.e., the period of higher forage and water availability after the arrival of the first rains,

which typically occurs in November, and the period of lower resource availability after

vegetation senesces in the late spring and early summer).

I developed RSFs using mixed-effects logistic regression models with a binomial

distribution and logit-link function to estimate response coefficients for each

environmental predictor variable. In an RSF framework, habitat selection can be

quantified using a logistic regression model (logistic discriminant function) to provide a

relative probability of use for a resource unit (Johnson et al. 2006, Lele et al. 2013). For

each spatial scale, I built three sets of 17 logistic regression models with the same set of

variables included as fixed effects (see Appendix N for model descriptions), but which

differed in their included interaction terms. The competing models and differing

interaction terms were designed to test my hypotheses regarding the influence of water,

forage, roads and drought on selection. Each set of models had either Group ID as a

random effect, Individual ID as a random effect, or Group ID as a fixed effect, for a total

of 51 models tested. I tested for collinearity between each variable and did not include

predictors in the same model if $|r| > 0.60$. Three variables, distance to solar, distance to

cannabis, and distance to powerline, were all correlated with each other. I chose to consider only distance to solar in the model, as the other two variables were also correlated with distance to road. The most parsimonious model within < 2 AIC of the lowest scoring model was selected as the best model for each spatial scale (Arnold 2010). I then used the top models from the landscape scale to create maps of relative probability of use in the study region.

Results

Seasonal differences in habitat selection

The top dry season home range scale model included interactions between
distance to water with NDVI, IRG, distance to road, and PDSI, with Herd included as a
fixed effect (Table 2.1, Figure 2.3, see Appendix N for all model selection results).
Confidence intervals of coefficients overlapped 1 for the PDSI, distance to road, and
distance to road:distance to water interaction terms. Of the 10 land cover classes,
confidence intervals overlapped 1 for the barren/other, wetland, and water land cover
classes.

Table 2.1: Top models explaining habitat selection patterns at the landscape scale (2nd
order selection) and home range scale (3rd order selection) in a population of tule
elk in California, USA.

Model	Description	df	logLik	weight
Home range - full year	Full* (-water_dist*PDSI). Herd ID fixed	29	-41758	0.8
Home range - dry season	Full* (-NDVI*road_dist, -IRG*road_dist). Herd ID fixed	27	-21713	0.45
Home range - wet season	Full*. Elk ID random	27	-19878	0.99
Landscape - full year	Full* (-IRG*road_dist, water_dist*-PDSI). Elk ID random	26	-38282	0.55
Landscape - dry season	Full* (-water_dist*PDSI). Herd ID fixed	28	-19861	0.45
Landscape - wet season	Full*(-IRG*road_dist). Elk ID random	26	-18086	0.53

*Full = Water_Distance + road_dist + NDVI + IRG + Water_Distance + PDSI+ TPI + slope+ Northness +
Eastness + Solar_Distance + Water_Distance*NDVI + Water_Distance*IRG+ Water_Distance*road_dist
+Water_Distance*PDSI + NDVI*road_dist+ IRG*road_dist
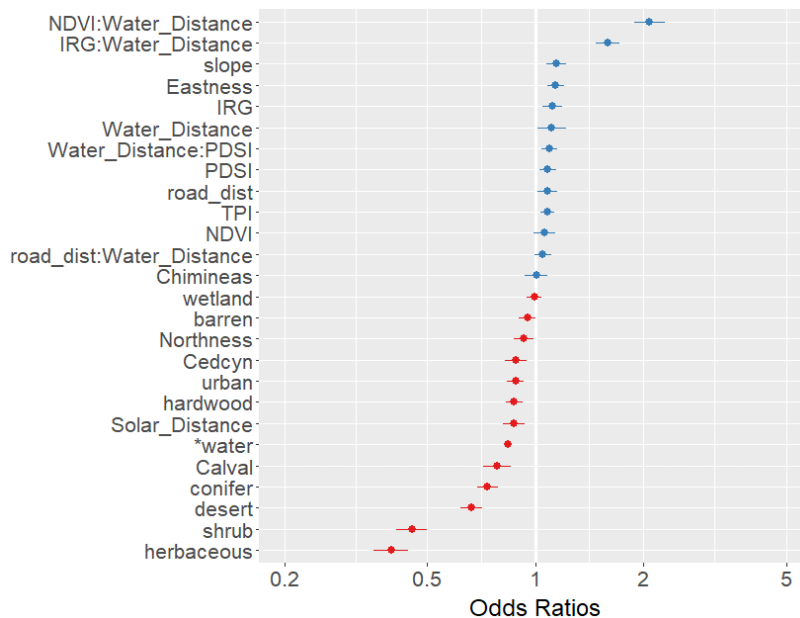
Figure 2.3: Standardized beta values of the fixed effects terms of top model explaining dry season habitat selection patterns at the home range scale (3rd order selection) in a population of tule elk in California, USA. Values above 1 (blue) and below 1 (red) represent positive and negative effects, respectively. Horizontal lines represent confidence intervals, asterisk indicates confidence interval too wide to plot. Agriculture was the reference class for the land cover terms.

The top wet season home range scale model included interactions of distance to
water with IRG, NDVI, distance to road and PDSI, with Herd as a fixed effect (Figure
2.4, see Appendix N for model selection results). Confidence intervals overlapped 1 for
the eastness, PDSI, TPI terms and for the barren/other, urban wetland, and water land
cover classes.

Figure 2.4: Standardized beta values of the fixed effects terms of top model explaining
    wet season, 3rd order habitat selection patterns in a population of tule elk in
    California, USA. Values above 1 (blue) and below 1 (red) represent positive and
    negative effects, respectively. Horizontal lines represent confidence intervals,
    asterisk indicates confidence interval too wide to plot. Agriculture was the
    reference class for the land cover terms.

The wet and dry season models showed contrasting patterns of selection in response to distance to water (Figure 2.5), the interactions between distance to water and NDVI (Figure 2.6, Figure 2.7), as well as the interaction between distance to water and PDSI (Figure 2.8). Selection for the forage metrics NDVI and IRG also differed between the wet and dry seasons (Figure 2.9). Land cover selection patterns were generally similar across season, though selection for agriculture, hardwood, and conifer was slightly higher while selection for shrub was slightly lower in the dry season (Figure 2.10). Elk strongly avoided roads in the wet season, but avoidance was weaker in the dry season (Figure 2.11). Similarly, elk strongly selected steeper slopes in the wet season but not during the dry season (Figure 2.12).
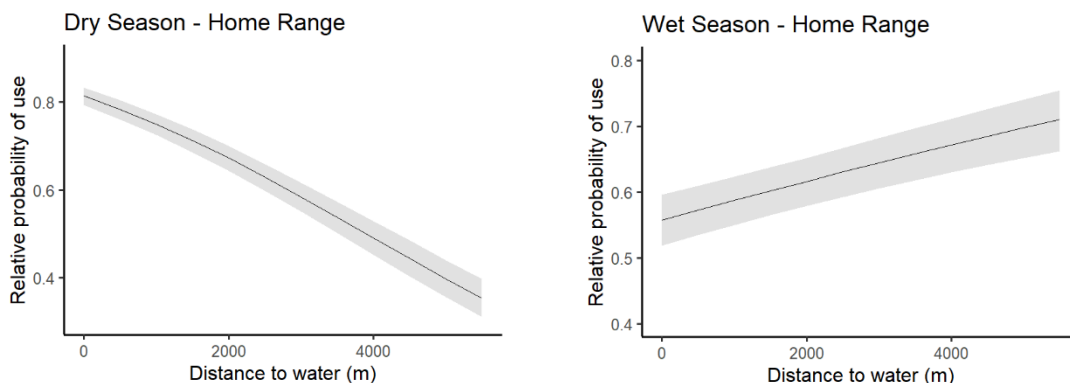
Figure 2.5: Response plots showing seasonal differences in 3rd order habitat selection for water sources for a population of tule elk in California, USA. Shaded areas represent confidence intervals.
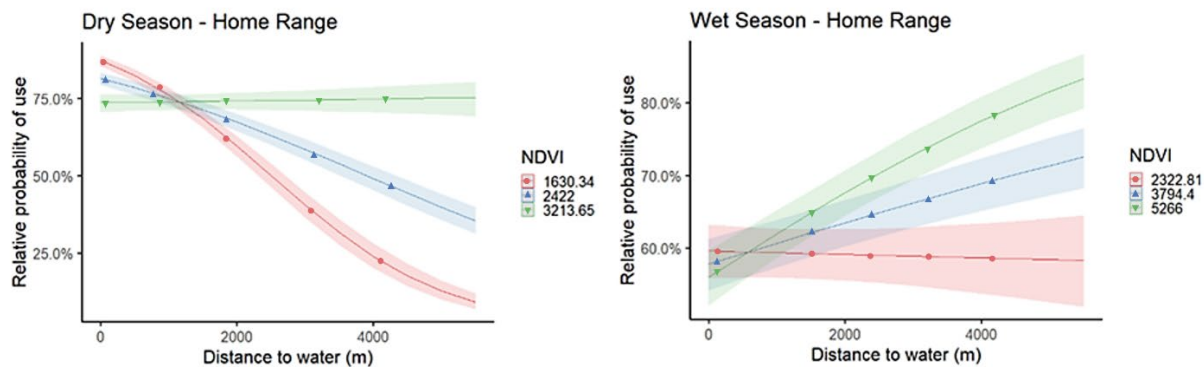
Figure 2.6: Interaction plots showing seasonal changes in 3ʳᵈ order habitat selection for water sources changes in response to forage availability (NDVI) for a population of tule elk in California, USA. Higher NDVI score corresponds to greater forage availability. Shaded areas represent confidence intervals.
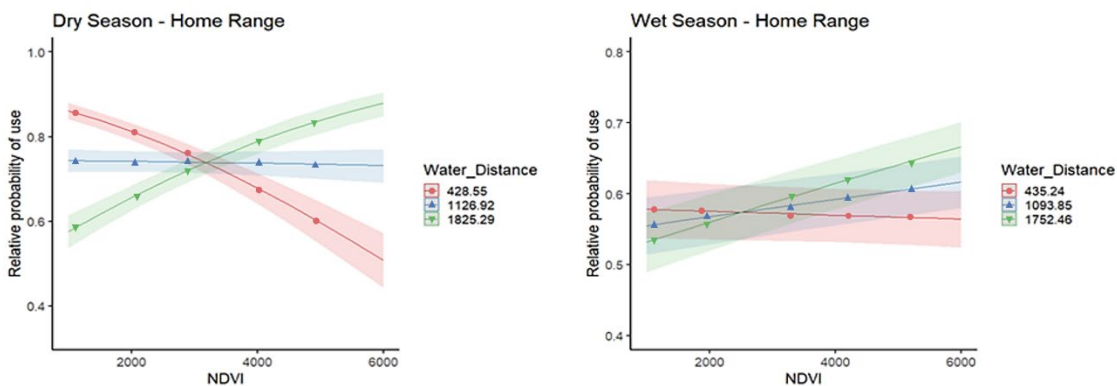
Figure 2.7: Interaction plots showing 3ʳᵈ order habitat selection for forage availability (NDVI) changes in response to water availability for a population of tule elk in California, USA. Higher NDVI score corresponds to greater forage availability. Shaded areas represent confidence intervals.
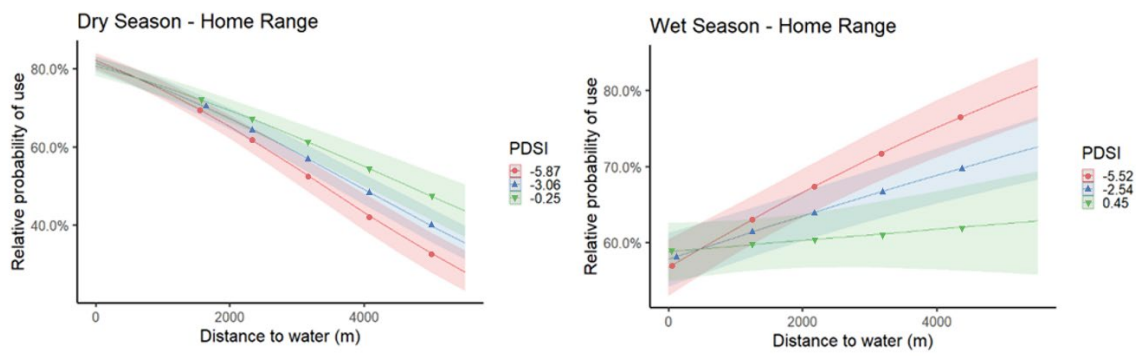
Figure 2.8: Interaction plot showing seasonal patterns of 3rd order habitat selection for water sources changes in response to drought severity (PDSI) for a population of tule elk in California, USA. Lower PDSI score corresponds to greater drought severity. Shaded areas represent confidence intervals.
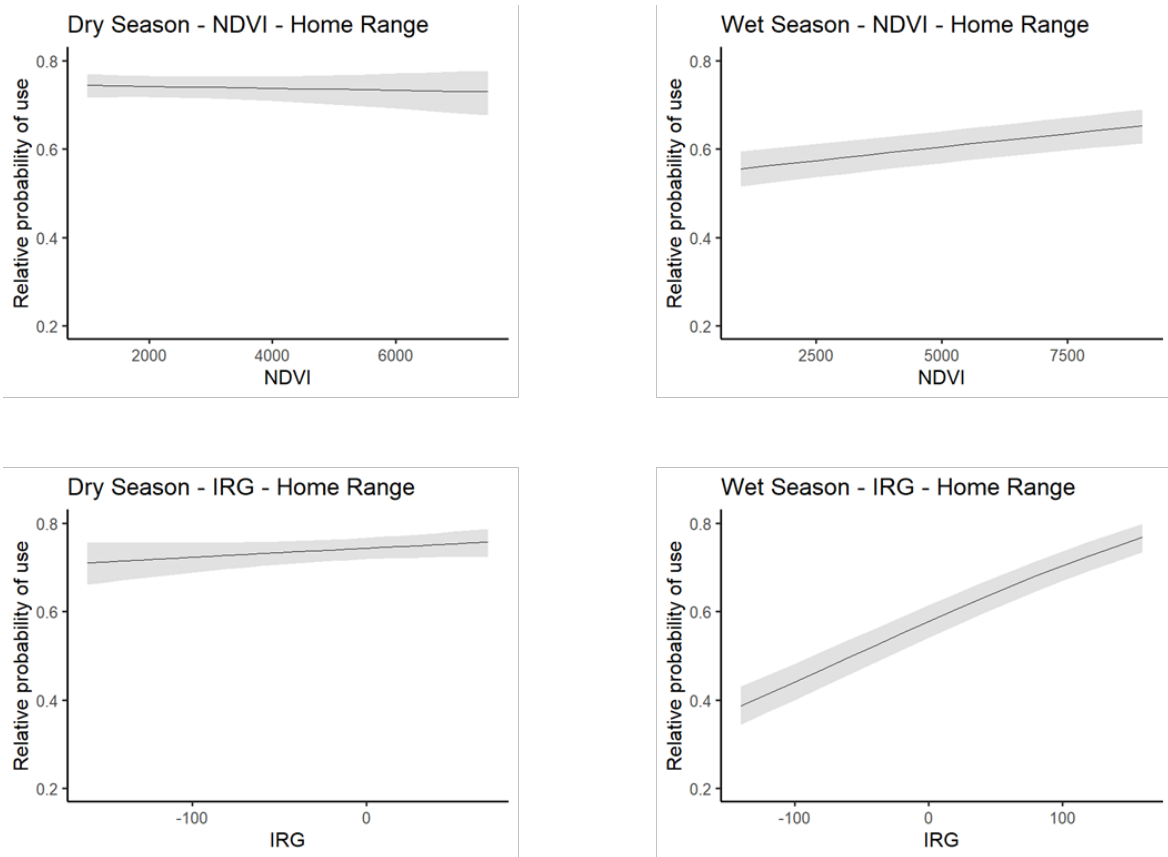
Figure 2.9: 3rd order habitat selection response to forage abundance (NDVI) and forage quality (IRG) in the wet and dry season for a tule elk population in California, USA. Shaded areas represent confidence intervals.
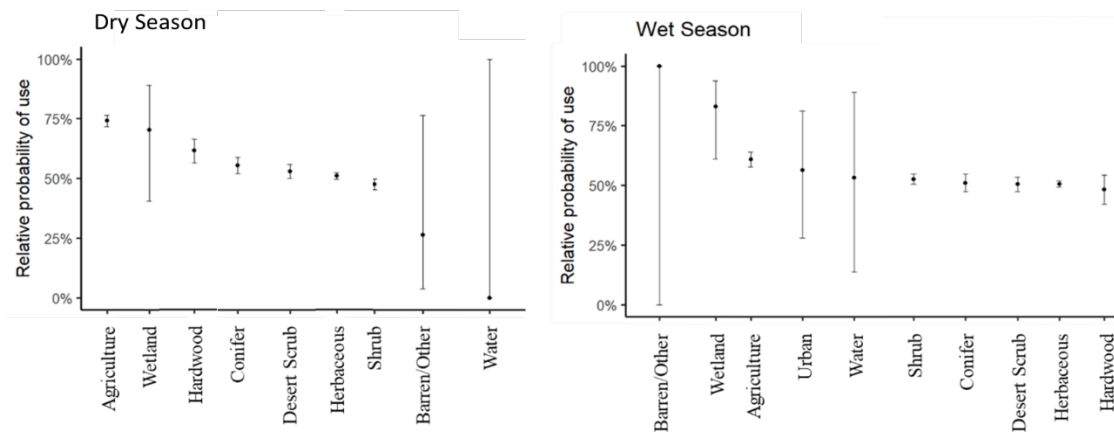
Figure 2.10: Marginal effects plots showing 3rd order habitat selection response of tule elk to land cover in the wet and dry season in the Carrizo Plain region, California, USA. Bars represent confidence intervals.
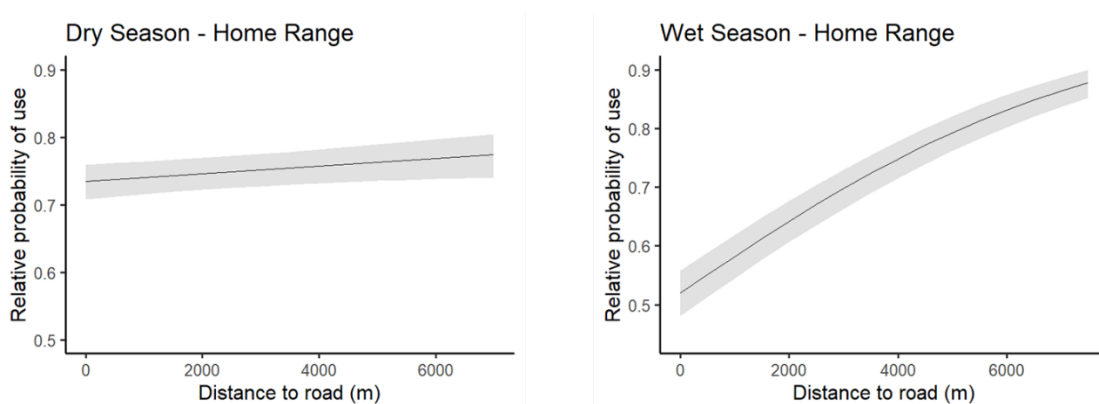
Figure 2.11: Response plots showing seasonal differences in 3rd order habitat selection in relation to roads for a population of tule elk in California, USA. Shaded areas represent confidence intervals.
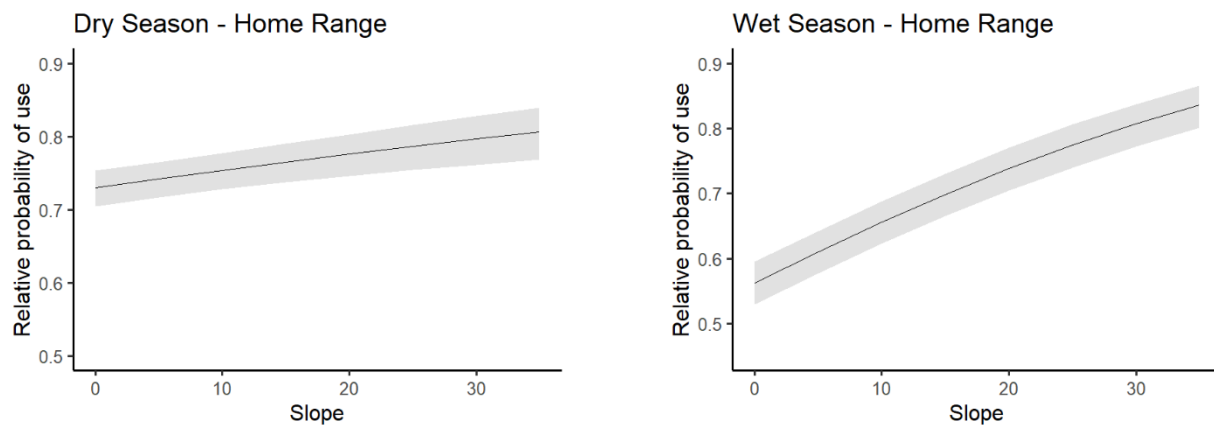
Figure 2.12: Variable response from top 3rd order habitat selection models showing tule elk response to slope in the wet and dry season in the Carrizo Plain region, California, USA. Shaded areas represent confidence intervals.

The top home range scale model included interactions between distance to water with NDVI, IRG and distance to road, as well as interactions between distance to road with NDVI and IRG, with Elk.ID as a random effect (Figure 2.13, see Appendix N for model selection results). Confidence intervals overlapped 1 for the PDSI term and the water, wetland, and barren/other land cover classes for the home range scale model.
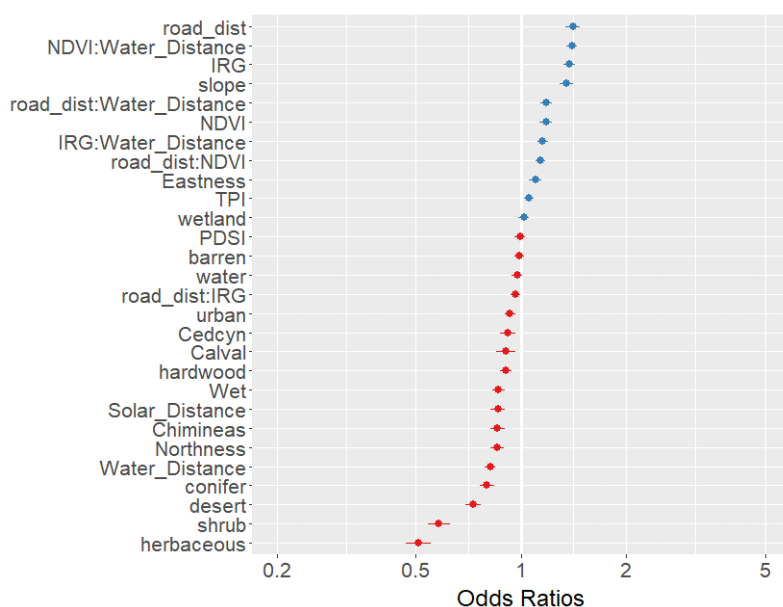
Figure 2.13: Standardized beta values of the fixed effects terms of top model explaining year-round, 3rd order habitat selection patterns in a population of tule elk in California, USA. Values above 1 (blue) and below 1 (red) represent positive and negative effects, respectively. Horizontal lines represent confidence intervals. Agriculture was the reference class for the land cover terms.

The top landscape scale model included interactions between distance to water with NDVI, IRG, and distance to road, as well as the interactions between distance to road and NDVI with Herd as a fixed effect (Figure 2.14, see Appendix O for 2nd order wet and dry season selection results). Confidence intervals overlapped 1 for the TPI, PDSI and interaction between the distance to road and distance to water terms.
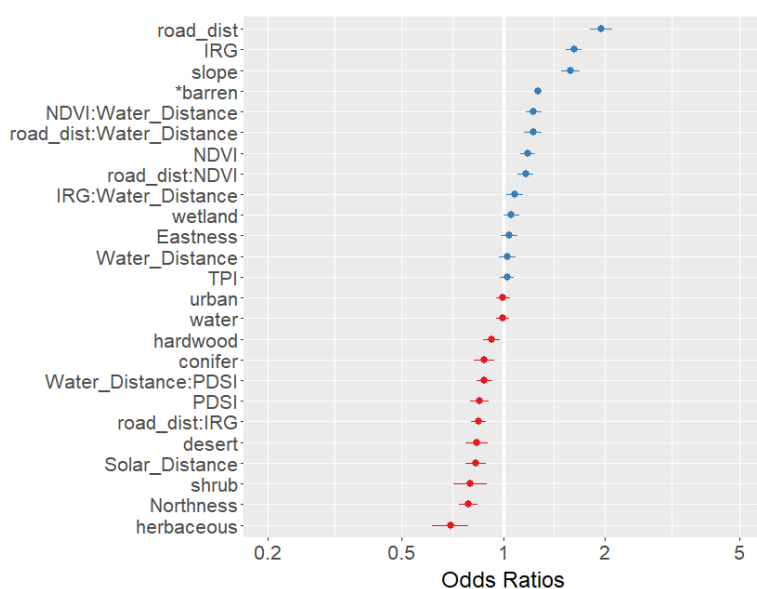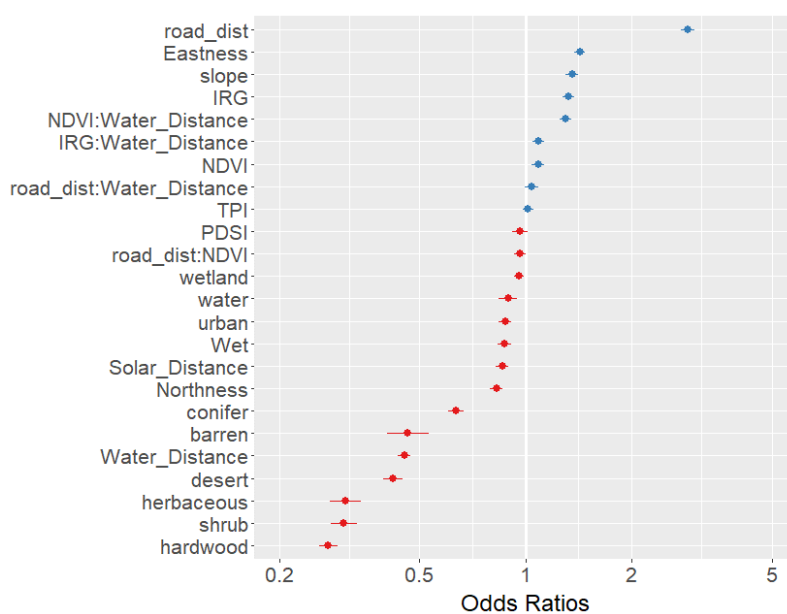

Figure 2.14: Standardized beta values of the fixed effects terms of top model explaining year-round, 2nd order habitat selection patterns in a population of tule elk in California, USA. Values above 1 (blue) and below 1 (red) represent positive and negative effects, respectively. Horizontal lines represent confidence intervals. Agriculture was the reference class for the land cover terms.

Over the course of the full year, both the landscape and home range scale models showed that elk selected areas closer to water sources, further from roads, closer to solar production sites, and with greater NDVI and IRG values. Patterns of selection in response to land cover were generally similar at both spatial scales, with agriculture being the most highly selected land cover type; however, selection for hardwood was higher at the home range scale compared to selection for these land cover classes at the landscape scale. Elk utilized similar areas before and after solar farm construction (Appendix P) and did not appear to avoid solar production sites, as evidenced by the negative coefficient for both the landscape and home range scale models. The top models of 2nd order selection in the wet and dry season were used to create maps of predicted habitat suitability across the region (Appendix Q).
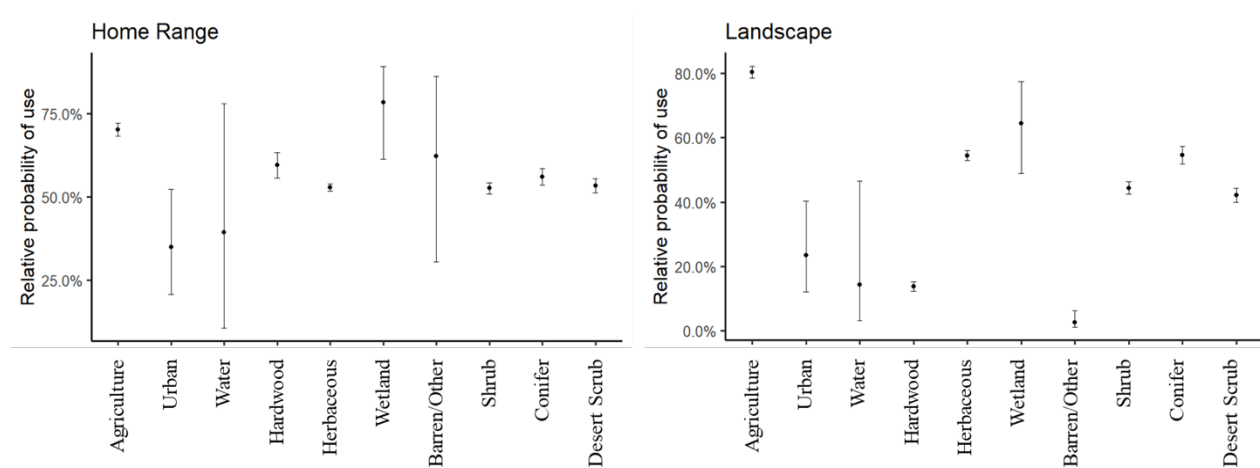
Figure 2.15: Marginal effects plot showing 2nd (Landscape) and 3rd (Home Range) order habitat selection response of tule elk to land cover in the Carrizo Plain region, California, USA. Bars represent confidence intervals.

Discussion

Water source selection

Tule elk selection patterns were reflective of seasonal changes in forage conditions and dependence on water sources. These patterns were consistent with the expectation that tule elk are water dependent and behave as central place foragers around water sources in the dry season. Elk showed a strong, negative selection response to water source distance in the dry season (Figure 2.5). Selection response during drought was also consistent with central place foraging behavior, as elk responded to greater drought severity by selecting areas further from water in the wet season (Figure 2.8). For large herbivores, central place foraging causes a gradient in forage availability due to concentrated foraging activity near water sources (Andrew 1988). This forage gradient can lead to a "humped" distribution as ungulates select areas at intermediate distance to water sources (Ogutu et al. 2014). Severe drought in the wet season, such as occurred in the study area 2012-2016, would correspond with depleted forage conditions and push elk to forage at increasingly greater distance from water sources. In contrast to selection patterns in the dry season and during drought, tule elk appeared to avoid water sources during the wet season (Figure 2.5). A similar, bimodal selection pattern has been observed in African herbivore communities characterized by concentration around water sources in the dry season and dispersal away from these sources in the wet season (Western 1975, Ogutu et al. 2014).

Selection for water sources was closely linked to forage conditions. NDVI was negatively related to distance to water in both the wet and dry season (Figure 2.6), likely because the higher moisture content of photosynthetically active plants reduced water dependence. Forage moisture is a main factor in ungulate water budgets (Cain et al. 2006) and dependence on water sources has been associated with lower forage moisture content for arid system ungulates in Africa (Jarman 1973) and Rocky Mountain elk in New Mexico (Harris et al. 2015). Although the coarse resolution of elk location intervals and water source availability data prevents more precise descriptions of the tule elk's water dependence, such as water source visitation rates, the inflection between positive and negative selection for water sources was roughly approximate in both seasons (occurring at a raw NDVI value of ~3000; Figure 2.6, Figure 2.7). This may serve as a rough approximation of the forage conditions necessary for tule elk to transition out of central place foraging behavior.

Forage dynamics

In contrast to the localization around water sources seen during the dry season, elk appeared to track forage quality across their home ranges during the wet season, as seen in the positive selection response to IRG. Response to IRG was stronger and had greater certainty in the wet season than dry season (Figure 2.9). The strong response to IRG in the wet season matches the expectations of the Forage Maturation Hypothesis, that herbivores select forage at intermediate growth stages to maximize energy gain (Fryxell

1991). Previous studies have reported migratory ungulates track IRG across elevation gradients (Bischof et al. 2012, Merkle et al. 2016, Aikens et al. 2017), although non-migratory populations can track IRG as well (Hebblewhite et al. 2008). While the elk in this study were non-migratory, their large home ranges (~45-120 km^2) may have provided enough green-up heterogeneity due to differences in elevation, aspect, rainfall and forage species, to allow them to exploit fine scale differences in forage quality over the course of the wet season. 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). The importance of tracking high quality forage would also explain why elk selected areas further from water sources in the wet season (Figure 2.5) and when NDVI (and forage moisture) was high (Figure 2.6).

As discussed previously, tule elk appeared less dependent on surface water when forage conditions were favorable; however, the positive selection response suggests an additional mechanism causing elk to forage at greater distance to water sources. While forage depletion near water sources is an expected effect of central place foraging, the apparent avoidance of water sources could also be a side-effect of water source placement in the broader landscape. For example, elk may be tracking high quality forage areas with fewer water sources, such as in areas of rugged terrain. Rugged terrain experiences more heterogeneity in green-up timing due to topographic complexity and elevational gradients, which subsequently provide elk longer access to forage in its most nutritious growth stages. Indirect evidence for the role of rugged terrain in elk foraging patterns was seen in their selection for greater slope in the wet season than in the dry

season (Figure 2.12). Alternatively, water source avoidance could be a consequence of human disturbance, as water sources are typically located near roads and subject to human visitation. Whether this behavior is driven by forage selection or disturbance avoidance is a salient area for future research.

Elk in this study did not exhibit a strong seasonal shift in land cover selection. This result contrasted with expectations that elk would show strong selection for browse during the dry season. While there was moderately higher selection for hardwood land cover in the dry season (Figure 2.10), selection for hardwood was low compared to its availability at the landscape scale (Figure 2.15). Furthermore, shrub land cover, a potential source of browse, had lower selection in the dry season than in the wet season (Figure 2.9, Figure 2.10). This result contrasts with other studies that have noted tule elk switched between herbaceous vegetation in the wet season and browse in the dry seasons (McCullough 1969, O'Connor 1988, Cobb 2010). In fact, two of the four sub-herds were almost entirely reliant on herbaceous and agricultural land cover for the duration of the study (Appendix R). As the use of agricultural land cover increased in the dry season, agriculture may have been an important resource during periods when natural forage sources were unavailable or insufficient.

Response to human disturbance

Human disturbance was an important driver of tule elk habitat selection at both spatial scales, as evidenced by the strong avoidance of roads (Figure 2.13, Figure 2.14).

The relative lack of vegetation structure in the Carrizo Plain may have contributed to the elk's road avoidance. A lack of vegetation structure, which is used for predator avoidance and escape cover, can cause ungulates to increase vigilance and result in flight responses at greater distances to potential danger (Stankowich 2008). Interestingly, elk were less responsive to roads in the dry season (Figure 2.3). This could be due to the stronger dependence on artificial water sources, which are typically near roads in the study area, or poor forage conditions resulting in greater risk-taking (Sih 1980). Alternatively, human disturbance levels could be lower in the dry season due to lower human visitation to the study area, or elk may be more nocturnal to avoid higher ambient temperatures and thus encounter humans less frequently.

Management Implications

The allocation of free water for ungulates is a common management practice, although it is a subject of debate (Broyles 1996, Rosenstock et al. 1999, Krausman et al. 2006). While artificial water sources increase forage availability for ungulates during the dry season, a high density of water sources can lead to over-exploitation of the forage base (Walker et al. 1987, Illius and O'Connor 2000) and ultimately result in high mortality in the event of drought (Walker et al. 1987, Illius and O'Connor 2000, Owen-Smith 2004). In this regard, areas of low water availability act as grazing refugia and therefore serve as critical sources of reserve forage (Gaylard et al. 2003, Fensham and Fairfax 2008). For ungulates, central place foraging around water source mediates population growth by imposing physiological constraints on energy gain (Western 1975, Owen-Smith 1988, Landman et al. 2012). Accordingly, short-term drought impacts ungulate populations primarily by reducing recruitment rates rather than increased adult mortality (Ogutu et al. 2008). As central place foragers, tule elk populations will likely be more resilient to future droughts if managers incorporate heterogeneity into water allocation decisions. Future research on forage utilization in relation to water sources and elk recruitment rates would help establish best-practices for water source allocation.

Additionally, managers should consider the effects of competition and predation around water sources when making water allocation decisions. A species' degree of water dependence is an important mechanism structuring herbivore communities in semi-arid southern Africa (Shannon et al. 2009, Smit and Grant 2009, Cain et al. 2012), with lower

water dependence acting as a competitive advantage (Western 1975). Artificial water sources can also increase predation risk, as predators utilize water sources for drinking and for hunting prey (Davidson et al. 2013, Harris et al. 2015). Seasonal reductions in artificial water allocation, especially during the wet season when tule elk are less dependent on water sources, could reduce potential competition with invasive feral pigs (*Sus scrofa*) and predation risk from mountain lions.

Human disturbance could negatively impact tule elk populations by interfering with the availability of water sources and high-quality forage. Human disturbance, in addition to causing greater stress and energy expenditure (White 1983, Seip et al. 2007), 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 cows must build sufficient energy stores in the wet season to sustain themselves and a calf through the dry season. Disturbance could push tule elk into areas with lower quality forage and water availability. 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). Management actions that 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.

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Appendix J

Appendix J: Table of each collared elk's ID, sex, number of points, group membership.

Elk.ID	Sex	Number.of.Points	Subherd
200	F	562	California Valley
250	F	855	Cedar Canyon
300	F	1406	American
350	F	1340	Cedar Canyon
377	F	1081	Cedar Canyon
397	F	1189	California Valley
528	M	817	Chimineas
562	M	782	Chimineas
582	M	1099	American
592	M	785	American
650	F	1297	Chimineas
9000	F	695	American
9020	F	146	California Valley
9040	F	617	Cedar Canyon
9060	F	1344	American
9080	F	1260	California Valley
9100	F	599	Cedar Canyon
9120	F	848	American
9137	F	1064	American
9140	F	128	California Valley
9160	F	959	American
9180	F	999	California Valley
9220	F	826	Cedar Canyon
9223	F	1587	California Valley
9298	F	1284	Chimineas
9320	F	1248	American
9420	M	667	American
9440	M	767	California Valley
9460	M	1358	Cedar Canyon
9480	M	250	California Valley
9499	F	665	Chimineas
9500	M	472	Cedar Canyon
9520	M	247	American
9540	M	804	California Valley
9560	M	777	Cedar Canyon
9580	M	116	American

Appendix K

Appendix K: Table of predictor variables

Predictor Variable	Name in Model	Source	Temporal Resolution	Spatial Resolution	Note
Land Cover	*life_form*	NLCD	2011	30m	-
Distance to Road	*road_dist*	TIGER/Line Shapefile	2017	-	-
NDVI	*NDVI*	NASA	8-day	250m	Transformed to daily values (Appendix B)
IRG	*IRG*	NASA	8-day	250m	Interpolated to daily values (Appendix B)
Distance to Water Source	*water_dist*	Multiple	Monthly	-	Appendix C
Slope	*slope*	DEM	2000	90m	Slope with Spatial Analyst Extension in ArcMap
Topographic Position Index	*TPI*	DEM	2000	90m	Calculated in rStudio with spatialEco package using 5x5 pixel window
Northness	*northness*	DEM	2000	90m	Aspect calculated with ArcMap with Spatial Analyst Extension. Northness = Cosine of aspect * pi/180
Eastness	*eastness*	DEM	2000	90m	Aspect in ArcMap with Spatial Analyst Extension. Eastness = Sin of aspect * pi/180
Distance to Solar Farm	*solar_dist*	CDFW provided shapefile	2017	-	Calculated with Euclidean Distance tool in ArcMap

Predictor Variable	Name in Model	Source	Temporal Resolution	Spatial Resolution	Note
Distance to Cannabis site	*cannabis_dist*	CDFW provided shapefile	2017	-	Calculated with Euclidean Distance tool in ArcMap
Distance to Transmission Line	*power_dist*	CDFW provided shapefile	2017	-	Calculated with Euclidean Distance tool in ArcMap
Drought Severity	*PDSI*	Western Regional Climate Center	Monthly	-	PDSI = Palmer Drought Severity Index
Sub-herd membership	*Herd*	CDFW	-	-	-

Appendix L

Appendix L: Background on the use of Normalized Difference Vegetative Index (NDVI) and Instantaneous Rate of Green-up (IRG) to estimate forage quantity and quality.

NDVI is a measure of the photosynthetic activity occurring in a given pixel of satellite imagery. NDVI is correlated with primary productivity and vegetation biomass and widely used metric for estimating available forage for herbivores (Ryan et al. 2012) (Pettorelli et al. 2005, Pettorelli et al. 2011). Previous research has shown that the rate at which NDVI increased over the course of the growing season was correlated with peak fecal protein, a measure of forage quality (Hamel et al. 2009). Therefore, a metric for forage quality, IRG, can be estimated using the rate of change of a given pixel's NDVI (Bischoff et al. 2012).

I performed a series of steps to retrieve NDVI and IRG values for each elk and available location over the course of the study, following the methods outlined in Bischoff et al. (2012). Briefly, the steps were i) download every MOD09Q1 product collected over the course of the study and extract the NDVI values for each pixel. The MOD09Q1 product gives surface reflectance values with a 250-meter spatial resolution, with each pixel representing the highest quality observation available over an 8-day time period. ii) Remove all pixels classified as low quality. iii) Apply a moving three-window median filter to remove spikes in the time series. iv) Interpolate NDVI values over the course of a year using a curve fitting function. v) Calculate IRG using the first-derivative. vi) Extract NDVI and IRG value for the specific day each used location was recorded.

My methodology differed from Bischoff et al. (2012) and other similar studies (e.g.,

Merkle et al. 2016) in that I used a spline method to interpolate values instead of a double

logistic function in order to better capture the variable timing and rate of vegetation

growth patterns in Mediterranean climates, and I did not scale each pixel's NDVI values

between 0 and 1 to better capture differences in forage abundance between pixels.

Appendix M

Appendix M: Background on how water sources were located in the study area.

I attempted to locate all water sources within the study area using a combination of methods. The primary method was using Google Earth imagery to "fly" evenly spaced transects across the study area and locate water sources visually. After locating a water source, I attempted to determine when water was available. I first looked through Google Earth historical imagery catalog to see when water was first visible and then estimated its availability over the course of the study. Images dated back to the early 2000s, with a new image available generally every ~ 2 years. After 2013, imagery was of higher spatial resolution (< 1m resolution), which made identification of water presence in small features like cattle troughs easy. Pre-2013 imagery varied between ~1-5m resolution and made identification of water presence in cattle troughs at these resolutions difficult, and I relied more on spatial context (i.e., appearance of bare earth and trails around a trough) to estimate water availability. To estimate availability between images I considered water sources as falling into two categories, natural (i.e., seeps, rivers, ponds, etc.) or artificial (i.e., cattle troughs, stock ponds, etc.). I considered an artificial water source permanent if it contained water in each high-resolution image and had indications of use pre-2013 (i.e., worn-down area, trails leading to water trough, etc.). If an artificial water source was missing water in a single image I either: A) considered it permanent if the appearance of the earth around the water source remained bare and worn in the absent image (i.e., the

water source was in use until recently); or B) if the area around the water source made it appear like it had not been used recently, I averaged availability before and after the imagery date when water was absent (e.g., if water was present in an image taken January 1st 2012 and water was present on an image taken January 1st 2016, but not January 1st 2014, water would be considered unavailable from January 1st 2013 to January 1st 2015). If an artificial water source was missing water in two or more consecutive images then I similarly averaged availability around the date when water was absent.

Most natural water sources displayed seasonality in availability, with water present during the wet season and absent during the dry season. To estimate these water sources' availability, I created a basic calculation to estimate monthly availability using the monthly precipitation data for the Carrizo region and a "Persistence Score" (ranging between 0-5) which I estimated based on how many months a water source appeared to hold water after a significant monthly rainfall amount (which I defined as 3.8 cm of rainfall in one month). Therefore, a Persistence Score of 0 meant a water source only had water if it had rained more than 3.8 cm of rain that month, while a Persistence Score of 5 corresponds to holding water five months after the last significant rainfall. After closely observing the patterns of water availability, it was apparent that periods of drought were affecting how long water was lasting into the dry season for water sources with Persistence Scores of 4 and 5, likely since annual rainfall totals were low. To account for this, I included a "Wet Year Effect", such that these water sources received an additional +1 to their Persistence Score in years of above average rainfall.

After water availability had been calculated for each water source for each month over the duration of the study, I measured the distance to the closest available water source for each used and available location.

Appendix N

Appendix N: Model selection results for all scales and seasons

Model descriptions:
*Full = Water_Distance + road_dist + NDVI + IRG + Water_Distance + PDSI+ TPI + slope+ Northness + Eastness + Solar_Distance + Water_Distance*NDVI + Water_Distance*IRG+ Water_Distance*road_dist +Water_Distance*PDSI + NDVI*road_dist+ IRG*road_dist

**Fixed variables = Water_Distance + road_dist + NDVI + IRG + Water_Distance + PDSI+ TPI + slope+ Northness + Eastness + Solar_Distance

Full model
Full*. Herd ID random
Full*. Elk ID random
Full*. Herd ID fixed

Fixed variables** + Water interactions
Full*(-IRG*road_dist, -NDVI*road_dist). Herd ID random
Full*(-IRG*road_dist, -NDVI*road_dist). Elk ID random
Full*(-IRG*road_dist, -NDVI*road_dist). Herd ID fixed

Fixed variables** + Water interactions except drought
Full*(-IRG*road_dist, -NDVI*road_dist, -water_dist*PDSI). Herd ID random
Full*(-IRG*road_dist, -NDVI*road_dist, -water_dist*PDSI). Elk ID random
Full*(-IRG*road_dist, -NDVI*road_dist, -water_dist*PDSI). Herd ID fixed

Fixed variables** + forage interactions
Full*(-water_dist*road_dist, -water_dist*PDSI). Herd ID random
Full*(-water_dist*road_dist, -water_dist*PDSI). Elk ID random
Full*(-water_dist*road_dist, -water_dist*PDSI). Herd ID fixed

Fixed variables** + road interactions
Full*(-IRG*water_dist, -NDVI*water_dist, -water_dist*PDSI). Herd ID random
Full*(-IRG*water_dist, -NDVI*water_dist, -water_dist*PDSI). Elk ID random
Full*(-IRG*water_dist, -NDVI*water_dist, -water_dist*PDSI). Herd ID fixed

Fixed variables** + water & forage quality interactions except drought
Full*(-NDVI*road_dist, -water_dist*PDSI). Herd ID random
Full*(-NDVI*road_dist, -water_dist*PDSI). Elk ID random
Full*(-NDVI*road_dist, -water_dist*PDSI). Herd.ID fixed

Fixed variables** + water & forage quality interactions
Full*(-NDVI*road_dist). Herd ID random
Full*(-NDVI*road_dist). Elk ID random
Full*(-NDVI*road_dist). Herd.ID fixed

Fixed variables** + water & forage quantity interactions except drought
Full*(-IRG*road_dist, -water_dist*PDSI). Herd ID random
Full*(-IRG*road_dist, -water_dist*PDSI). Elk ID random
Full*(-IRG*road_dist, -water_dist*PDSI). Herd.ID fixed

Fixed variables** + water & forage quantity interactions
Full*(-IRG*road_dist). Herd ID random
Full*(-IRG*road_dist). Elk ID random
Full*(-IRG*road_dist). Herd.ID fixed

Fixed variables** + forage quantity and road interactions
Full*(-IRG*water_dist, -water_dist*PDSI). Herd ID random
Full*(-IRG*water_dist, -water_dist*PDSI). Elk ID random
Full*(-IRG*water_dist, -water_dist*PDSI). Herd ID fixed

Fixed variables** + forage quality and road interactions
Full*(-NDVI*water_dist, -water_dist*PDSI). Herd ID random
Full*(-NDVI*water_dist, -water_dist*PDSI). Elk ID random
Full*(-NDVI*water_dist, -water_dist*PDSI). Herd ID fixed

Home range scale, full year:

Model Description	df	logLik	AICc	delta	weight
Full* (-water_dist*PDSI). Herd ID fixed	29	-41758	83574.04	0	0.80
Full* (-IRG*road_dist, -water_dist*PDSI). Herd ID fixed	28	-41760.5	83577.03	2.99	0.18
Full* (-water_dist*PDSI). Elk ID random	27	-41764.3	83582.65	8.61	0.01
Full* (-IRG*road_dist, -water_dist*PDSI). Elk ID random	26	-41766.8	83585.63	11.59	2.46E-3
Full* (-water_dist*PDSI). Herd ID random	27	-41765.9	83585.89	11.85	2.15E-3
Full* (-IRG*road_dist, -water_dist*PDSI). Herd ID random	26	-41768.4	83588.89	14.86	4.78E-4
Full*. Herd ID fixed	29	-41783.6	83625.2	51.16	6.24E-12
Full* (-NDVI*road_dist, -water_dist*PDSI). Herd ID fixed	28	-41786.9	83629.88	55.84	6.01E-13
Full* (-IRG*road_dist). Herd ID fixed	28	-41787.1	83630.17	56.13	5.21E-13
Full*. Elk ID random	27	-41789.8	83633.67	59.63	9.03E-14

*Full = Water_Distance + road_dist + NDVI + IRG + Water_Distance + PDSI+ TPI + slope+ Northness + Eastness + Solar_Distance + Water_Distance*NDVI + Water_Distance*IRG+ Water_Distance*road_dist +Water_Distance*PDSI + NDVI*road_dist+ IRG*road_dist

Home range scale, dry season

Model Description	df	logLik	AICc	delta	weight
Full* (-NDVI*road_dist, -IRG*road_dist). Herd ID fixed	27	-21713	43480.3	0	0.45
Full* (-IRG*road_dist, -water_dist*PDSI). Herd ID fixed	28	-21713	43481.5	1.19	0.25
Full* (-NDVI*road_dist, -water_dist*PDSI). Herd ID fixed	28	-21713	43482.3	2	0.16
Full*. Herd ID fixed	29	-21712	43482.6	2.3	0.14
Water interactions (-water_dist*PDSI). Herd ID fixed	26	-21720	43491.9	11.59	1.36E-03
Full* (-IRG*road_dist, -water_dist*PDSI). Herd ID fixed	27	-21720	43493.3	13	6.68E-04
Water interactions. Herd ID random	25	-21722	43493.5	13.21	6.04E-04
Full* (-NDVI*road_dist, -water_dist*PDSI). Herd ID fixed	27	-21720	43493.9	13.58	5.01E-04
Full* (-water_dist*PDSI). Herd ID fixed	28	-21719	43494.4	14.05	3.96E-04

*Full = Water_Distance + road_dist + NDVI + IRG + Water_Distance + PDSI+ TPI + slope+ Northness + Eastness + Solar_Distance + Water_Distance*NDVI + Water_Distance*IRG+ Water_Distance*road_dist +Water_Distance*PDSI + NDVI*road_dist+ IRG*road_dist

Home range scale, wet season:

Model Description	df	logLik	AICc	delta	weight
Full*. Elk ID random	27	-19878.4	39810.95	0.00	0.99
Full* (-NDVI*road_dist). Elk ID random	26	-19888.1	39828.15	17.20	1.84E-04
Full* (-IRG*road_dist). Elk ID random	25	-19890.9	39831.85	20.90	2.90E-05
Full*(-water_dist*PDSI). Elk ID random	26	-19890.4	39832.81	21.85	1.80E-05
Full*. Herd ID fixed	29	-19889.1	39836.27	25.32	3.18E-06
Full*(-NDVI*road_dist, -water_dist*PDSI). Elk ID random	25	-19899.2	39848.36	37.41	7.54E-09
Full*. Herd ID random	27	-19899.3	39852.58	41.63	9.12E-10
Full*(-IRG*water_dist, -water_dist*PDSI). Herd ID fixed	27	-19899.6	39853.29	42.34	6.39E-10
Full*(-water_dist*PDSI). Herd ID fixed	28	-19899.3	39854.62	43.67	3.29E-10
Full*(-NDVI*water_dist). Herd ID fixed	28	-19899.3	39854.69	43.74	3.17E-10

*Full = Water_Distance + road_dist + NDVI + IRG + Water_Distance + PDSI+ TPI + slope+ Northness + Eastness + Solar_Distance + Water_Distance*NDVI + Water_Distance*IRG+ Water_Distance*road_dist +Water_Distance*PDSI + NDVI*road_dist+ IRG*road_dist

Landscape scale, full year:

Model Description	df	logLik	AICc	delta	weight
Full* (-IRG*road_dist, -PDSI). Elk ID random	26	-38282.4	76616.8	0	0.55
Full* (-PDSI). Elk ID random	27	-38282.2	76618.4	1.65	0.25
Full* (-NDVI*road_dist, -IRG*road_dist, -PDSI). Elk ID random	25	-38285.5	76621.0	4.19	0.07
Full* (-NDVI*road_dist, -PDSI). Elk ID random	26	-38284.5	76621.0	4.25	0.07
Full*. Elk ID random	27	-38284.3	76622.6	5.82	0.03
Water and forage quality x roads, no drought. Elk ID random	26	-38285.4	76622.7	5.96	0.03
Full* (-NDVI*road_dist, -IRG*road_dist). Elk ID random	25	-38287.5	76624.9	8.12	0.01
Full* (-NDVI*road_dist). Elk ID random	26	-38287.3	76626.6	9.81	0.0041
Full* (-water_dist*road_dist). Elk ID random	26	-38291.1	76634.1	17.31	9.63E-05
Full* (-IRG*road_dist). Elk ID random	26	-38292.6	76637.1	20.34	2.12E-05
Full* (-water_dist*road_dist, -road_dist*IRG, -water_dist*NDVI). Elk ID random	24	-38301.8	76651.6	34.84	1.50E-08

*Full = Water_Distance + road_dist + NDVI + IRG + Water_Distance + PDSI+ TPI + slope+ Northness + Eastness + Solar_Distance + Water_Distance*NDVI + Water_Distance*IRG+ Water_Distance*road_dist +Water_Distance*PDSI + NDVI*road_dist+ IRG*road_dist

Landscape scale, dry season:

Model Description	df	logLik	AICc	delta	weight
Full* (water_dist*-PDSI). Herd ID fixed	28	-19861.3	39778.61	0	0.45
Full*(-water_dist*road_dist). Herd ID fixed	27	-19862.5	39779.03	0.42	0.36
Full*. Herd ID fixed	29	-19861.2	39780.36	1.75	0.19
Full*(-PDSI). Herd ID random	26	-19870.2	39792.44	13.83	4.44E-05
Full*(-water_dist*road_dist). Herd ID random	25	-19871.4	39792.85	14.24	3.62E-04
Full*. Herd ID random	27	-19870.1	39794.19	15.58	1.86E-04
Full*(-NDVI*road_dist, water_dist-PDSI). Herd ID fixed	27	-19871	39796.03	17.42	7.40E-05
Full* (-NDVI*road_dist). Herd ID fixed	28	-19870.9	39797.8	19.19	3.05E-05
Full* (-IRG*road_dist, -water_dist*PDSI). Herd ID fixed	27	-19872.6	39799.27	20.66	1.46E-05
Full* (-IRG*road_dist). Herd ID fixed	28	-19872.5	39801	22.39	6.17E-06
Full*(-IRG*road_dist, -NDVI*road_dist, -water_dist*PDSI. Herd ID fixed	26	-19874.6	39801.25	22.64	5.44E-06

*Full = Water_Distance + road_dist + NDVI + IRG + Water_Distance + PDSI+ TPI + slope+ Northness + Eastness + Solar_Distance + Water_Distance*NDVI + Water_Distance*IRG+ Water_Distance*road_dist +Water_Distance*PDSI + NDVI*road_dist+ IRG*road_dist

Landscape scale, wet season:

Model Description	df	logLik	AICc	delta	weight
Full*(-IRG*road_dist). Elk ID random	26	-18086.31	36225	0.00	0.53
Full*. Elk ID random	27	-18085.43	36225	0.24	0.47
Full*(-IRG*road_dist, -NDVI*road_dist). Elk ID random	25	-18097.91	36246	21.19	1.32E-05
Full*(-NDVI*road_dist). Elk ID random	26	-18097.49	36247	22.36	7.38E-06
Full*(-IRG*road_dist, -water_dist*road_dist, -water_dist*PDSI). Elk ID random	25	-18106.30	36263	37.98	3.00E-09
Full*(-IRG*road_dist, -water_dist*PDSI). Elk ID random	25	-18107.15	36264	39.67	1.29E-09
Full*(-water_dist*PDSI). Elk ID random	26	-18106.28	36265	39.95	1.12E-09
Full*(-IRG*water_dist, -IRG*road_dist, -water_dist*road_dist, -water_dist*PDSI). Elk ID random	23	-18113.12	36272	47.61	2.43E-11
Full*(-water_dist*road_dist, -water_dist*PDSI). Elk ID random	25	-18112.21	36274	49.79	8.18E-12
Full*(-IRG*road_dist, -NDVI*road_dist, -water_dist*PDSI). Elk ID random	24	-18119.20	36286	61.77	2.04E-14

*Full = Water_Distance + road_dist + NDVI + IRG + Water_Distance + PDSI+ TPI + slope+ Northness + Eastness + Solar_Distance + Water_Distance*NDVI + Water_Distance*IRG+ Water_Distance*road_dist +Water_Distance*PDSI + NDVI*road_dist+ IRG*road_dist
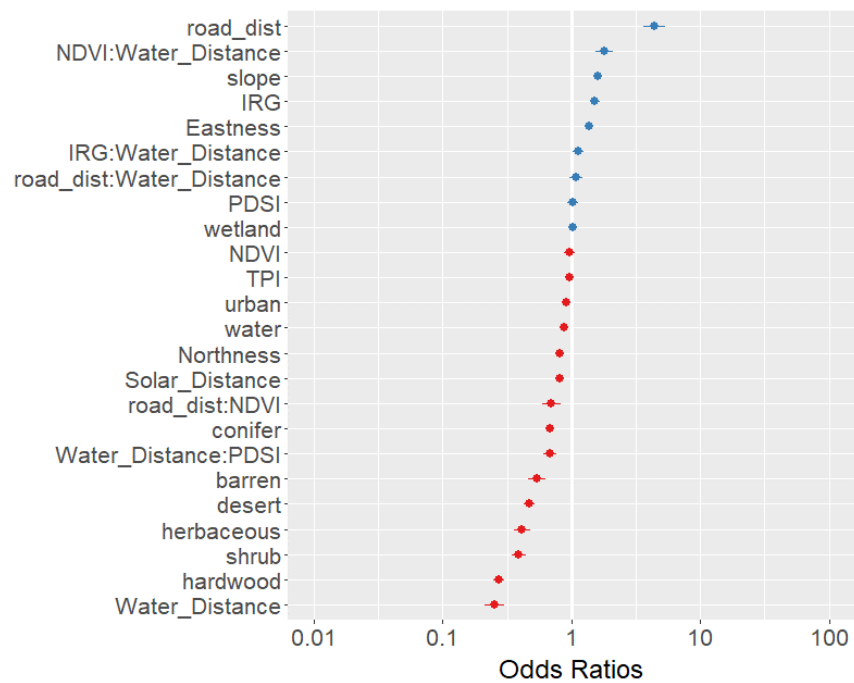
Appendix O

Appendix O: Standardized beta values of the top selection models explaining seasonal 2nd order
habitat selection for a population of tule elk in California, USA. Values above 1 (blue)
and below 1 (red) represent positive and negative effects, respectively. Agriculture was
the reference class for the land cover terms. Error bars represent confidence intervals.
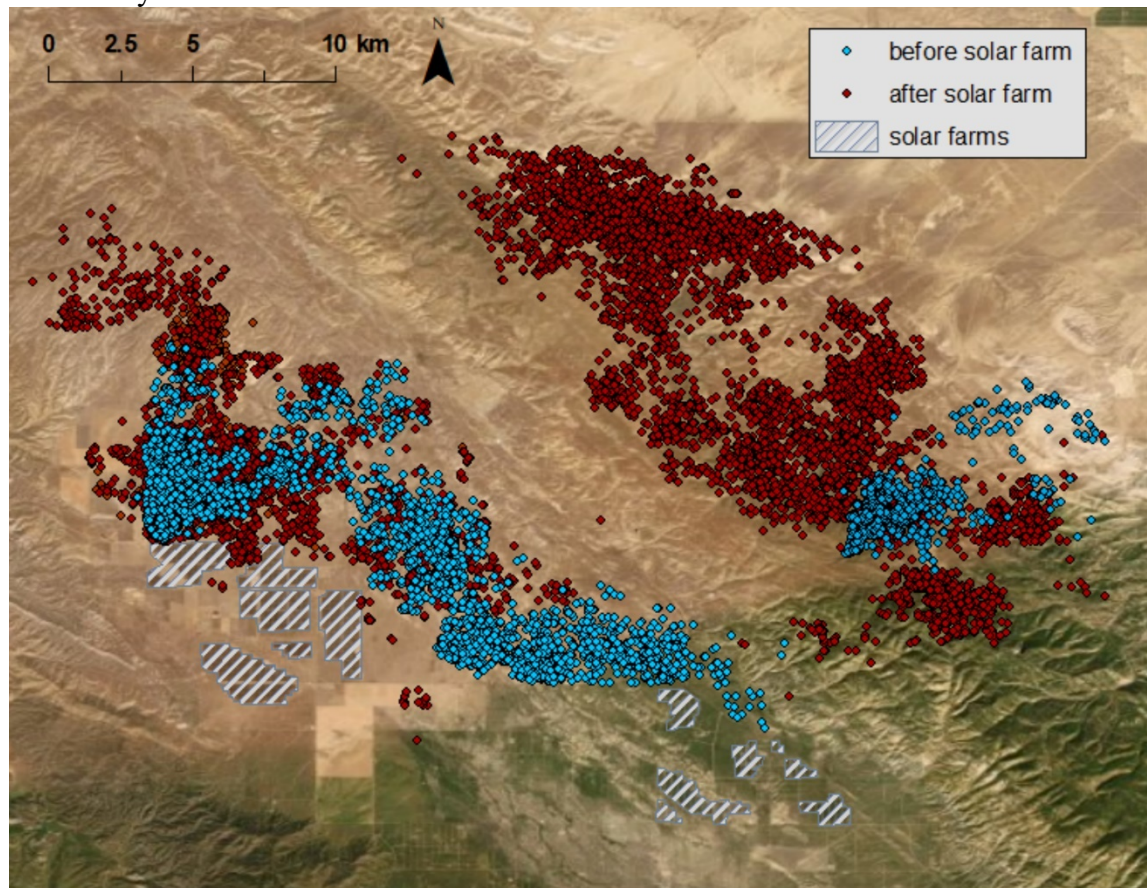
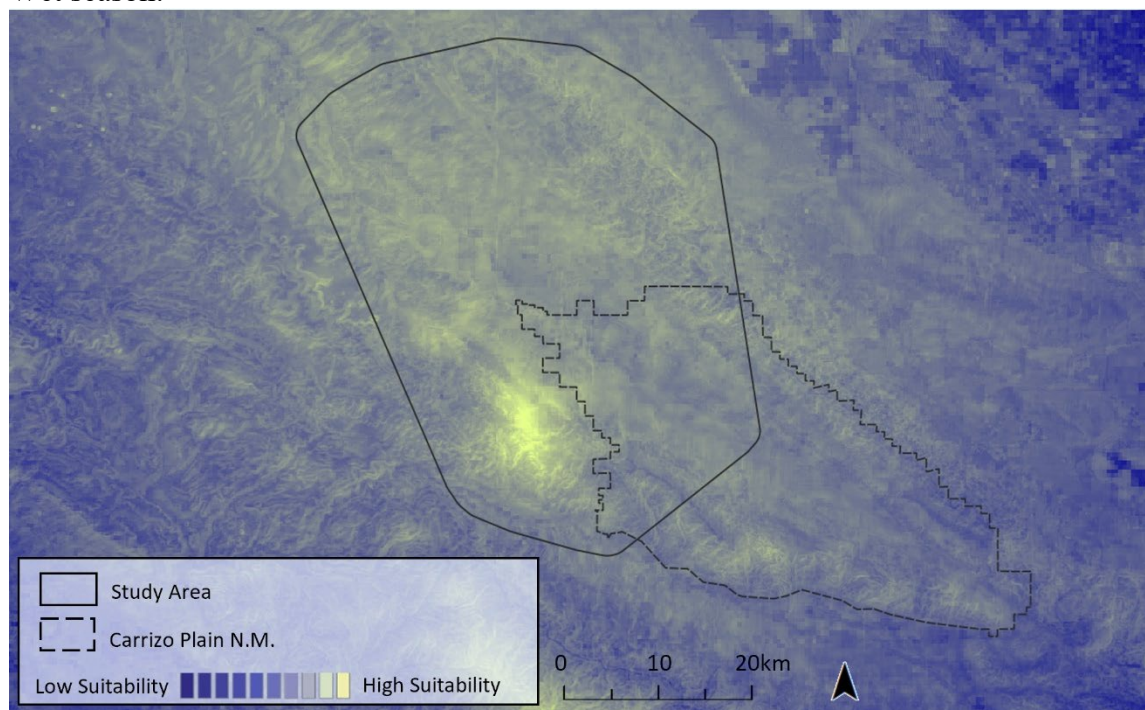Dry Season:
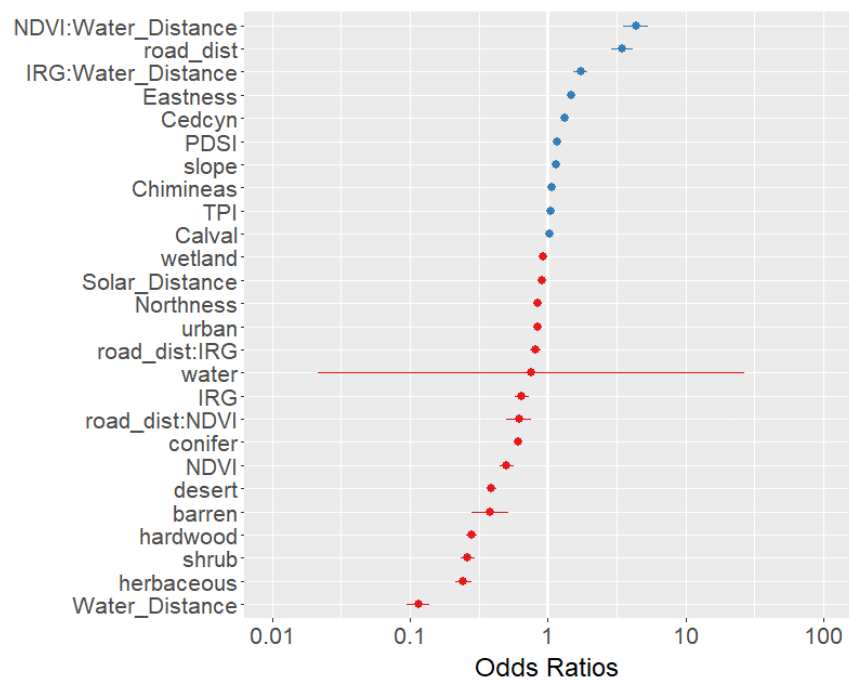
Wet Season:

Appendix P

Appendix P: Map showing locations from collared individuals in the California Valley and
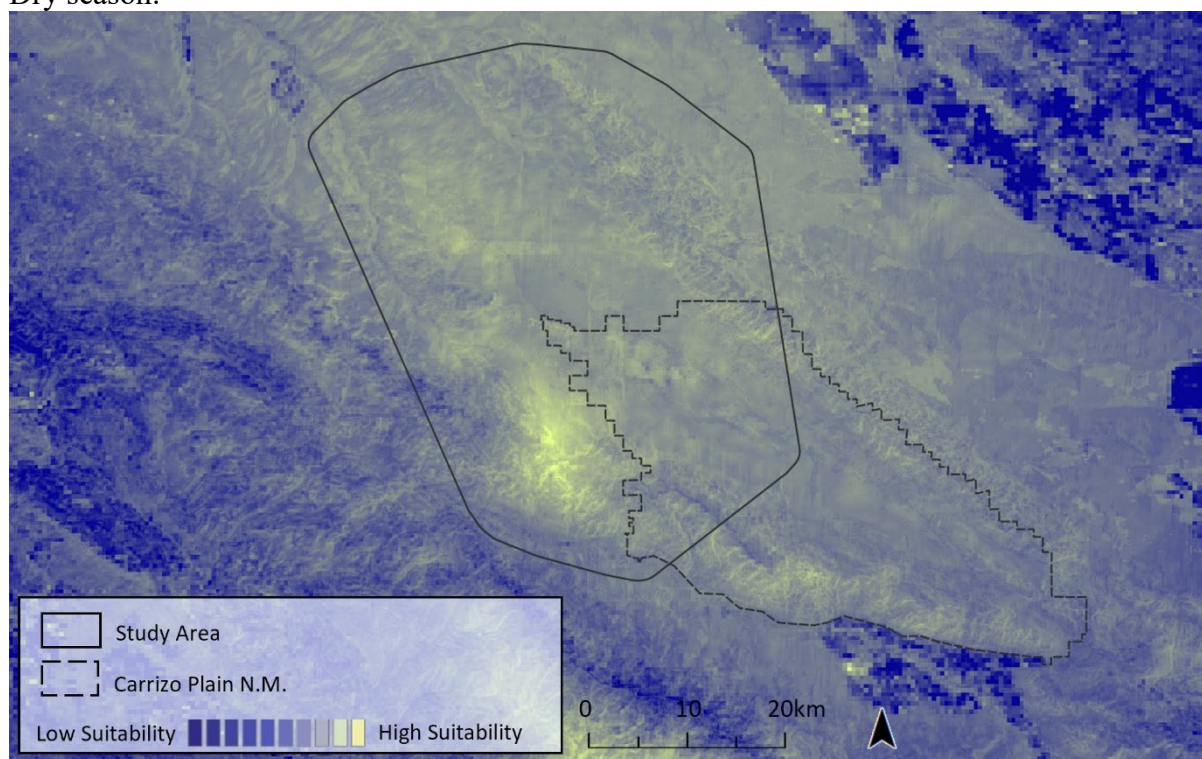Cedar Canyon subherds before and after solar farm construction.

Appendix Q

Appendix Q: Habitat suitability maps created using the top landscape scale model for each season. The values for distance to water, NDVI, and IRG were calculated by averaging across December – April for the wet season and July-October for the dry season.

Wet season:

Dry season:

Appendix R

Appendix R: Land cover map of the study area with each individual elk's home range overlaid.