Predicting mountain lion resource selection and abundance in North America

William Connor O'Malley

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PREDICTING MOUNTAIN LION RESOURCE SELECTION AND ABUNDANCE IN NORTH AMERICA

By

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Bachelor of Science, Colorado State University, Fort Collins, CO, 2008

Thesis

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Predicting mountain lion resource selection and abundance in North America

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ABSTRACT

The relationship between habitat quality and density is well documented in lower trophic levels but to what extent it can be extended to higher trophic levels is unknown. I tested the relationship between habitat quality, home-range size and density using a wide-ranging, well-studied, top carnivore, the mountain lion (Puma concolor). First, I created a second-order resource selection function (RSF) for mountain lions in their current North American range using GPS collar data from 476 individuals in 20 study sites and remotely-sensed landscape data. I used the RSF and home range estimates derived from collared animals to quantify mountain lion habitat and possible densities across North America. Secondly, I explored the relationship of the RSF model, home-range size, and density based on 142 published density estimates toward the goal of testing the justification and/or limitations of using RSF models to project population densities. In addition, I tested whether ‘top-down’ influences such as presence of bears, wolves or human hunting improved the model’s ability to predict local densities. I found strong support for habitat quality driving mountain lion densities as shown by the relationship between the RSF and home range size. I found additional support for habitat quality driving densities in the relationship between the RSF and reference densities. I did not find support for my hypotheses that top-down factors negatively impacted mountain lion densities which may be due to the high variance in traditional density estimation methods.
ACKNOWLEDGEMENTS

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INTRODUCTION

Organisms are expected to expend the minimum amount of energy necessary to meet their survival and reproductive needs (Pyke et al. 1977). As a result, the total area they depend on (i.e. their home range or territory) is expected to be as small as possible (Harestad and Bunnell 1979, Herfindal et al. 2005). As habitat quality increases, total area used decreases and the number of organisms per unit area (density) increases. The correlation between habitat quality and density is well documented in lower trophic levels but whether it can be extended to higher trophic levels is less understood.

If habitat quality proves to be an effective predictor of the populations of higher-trophic level species, it could be a powerful reference on which to base population estimations and later, to integrate into more complex population models that include territoriality, home range overlap, survival, recruitment, hunting and other top-down forces. This would be especially valuable for estimating populations of top carnivores who tend to live at low densities, are difficult to quantify and are more vulnerable to extirpation and extinction (Ripple et al. 2014). Moreover, defining the relationship between habitat quality and density will benefit conservation efforts focused on increasing animal populations from ‘bottom-up’ i.e. habitat restoration approaches.

Ecologists recognized early on that food resources moved upward through trophic levels. Sunlight drives vegetative growth, which becomes food for herbivores, who then become food for predators. Hairston et al. (1960) provided a popular contribution to this subject with their landmark publication which became known as the “Green World” hypothesis. They suggested that predator abundance was driven by prey abundance, and that herbivores were rarely limited by food resources; rather, they were most often
limited by predators. Building off this hypothesis, managers focused their attention on predators as a means of regulating the abundance of prey. This led to a paradigm of predator-limitation which dominated until the early 1990’s (White 2001). More recently, ecosystem management has replaced species level management as our understanding of complex interactions between species and their environment increases (Estes 1996). Managers have shifted to a viewpoint that species persist or decline most often in response to changes in habitat, a more bottom-up perspective. Further, it is not usually feasible to conserve a species any other way than by preserving or restoring its habitat and alleviating threats that result in higher mortality (Estes 1996).

Primary production, the coalescence of carbon from the atmosphere through photosynthesis, is the foundational bottom-up resource that almost all life on Earth is built upon (Lieth and Whittaker 2012). Primary productivity is measured in terms of “greenness” of plants which directly relates to the amount of digestible energy available to herbivores (Garroutte et al. 2016). By using normalized difference vegetation index (NDVI), the greenness of plants can be measured via satellite imagery and thus, be used as a simple but useful metric for herbivore digestible energy, and can be obtained at global scales (Myneni et al. 1995, Pettorelli et al. 2005). Researchers have successfully linked primary productivity to abundance of species at lower trophic levels such as arboreal ants (Pringle et al. 2019), other arthropods (Borer et al. 2012), a variety bird species (Meehan et al. 2004, Matthiopoulos et al. 2019) and white-tailed deer (Odocoileus virginianus; Walters 2001). If, in the absence of other stressors such as habitat fragmentation, hunting, and disease, primary productivity can predict primary producers or prey, and prey in turn can predict predator densities, it should be possible to
predict predator densities based largely on primary productivity.

In the absence of human impacts, carnivore populations are generally regulated by a combination of prey abundance and competition through territoriality. This is well documented in wolves (Canis lupis; Peterson et al. 1998, McRoberts and Mech 2014), polar bears (Ursus maritimus, Rode et al. 2010), and African wild dogs (Lycaon pictus; Creel and Creel 1996). In addition, several wild felids have shown an increase in density correlated to increased prey abundance such as snow leopards (Panthera uncia), leopards (Panthera pardus), African lions (Panthera leo), tigers (Panthera tigris), and cheetahs (Acinonyx jubatus; Fuller and Sievert 2001, Carbone et al. 2011, Logan 2019).

Mountain lions are a low-density species that experiences varied levels of hunting pressure. Unlike other wild felids that have spots or stripes, mountain lions are not uniquely identifiable which further complicates abundance estimates using tools such as remote camera traps. Although some methods of estimating mountain lion abundance have proven effective such as intensive monitoring, genetic mark-recapture, and statistical population reconstruction (Choate 2006, Howard et al. 2020), these methods are expensive, time consuming and often require hard-to-acquire data. In addition, even the best methods for estimating mountain lion populations are often imprecise and biased (Murphy et al. 2022). Therefore, there is a need for other ways to quantify mountain lion populations, especially for large areas and areas with sparse data. Here, I explore if estimates of mountain lion habitat can be used to predict densities.

To tie mountain lion abundance or densities to habitat, habitat must first be defined. One method relies on expert opinion to create a habitat suitability model based on habitat metrics that experts believe are important to mountain lions such as prey
density, rugged terrain, etc. (Hirzel et al. 2006). The Habitat Society of the United States (2017) used this method to estimate mountain lion habitat in the United States.

A more rigorous approach is to use GPS data, which, after two decades of mountain lion research, has accumulated in large quantities, to create a resource selection function (RSF) based on a variety of habitat covariates (Manly et al. 2002). The RSF can then be projected as a map predicting the probability of mountain lion use, and this map can be interpreted as an indicator of mountain lion habitat quality (Boyce and MacDonald 1999).

In statistical modeling one must choose between the distinct goals of inference or prediction (James et al. 2013, Bzdok and Ioannidis 2019). Inference is a case where the goal is low variance whereas prediction seeks to minimize mean squared error (James et al. 2013). Generally, models with high flexibility have lower interpretability and are more suited towards the goal of prediction (Bzdok and Ioannidis 2019). In modeling animal habitat, the difference can be defined as “what” vs “where”. Inference seeks to understand “what” is habitat, i.e. what features of the landscape do animals select for. In contrast, prediction seeks to predict “where” is habitat, i.e. where on the landscape do animals prefer to live. My goal was to create a mountain lion probability map to maximize spatial prediction (i.e. “where” mountain lion habitat is in North America) so that total mountain lion habitat could be quantified and related to abundance and density.

Once mountain lion habitat was defined, the next step was to link habitat to abundance. This can be done directly using reference densities if such data are available. If reference densities are unavailable or insufficient, the link of habitat quality to abundance must be estimated in other ways. Given that the most widely available data on
mountain lions is GPS locations, my approach was to measure the size of their home ranges and compare that to a measure of habitat quality. In less productive regions, mountain lions should have to travel farther to meet all their energetic needs and we should see larger home ranges which should also lead to lower densities. In more productive regions, we should see the opposite effect, smaller home ranges and higher densities.

In Chapter 1, I compared two different methods for creating resource selection functions, performed a rigorous out-of-sample validation and chose the method with the highest predictive performance. I used a variety of covariates that are widely referenced in regional mountain lion resource selection models and examined their positive and negative effects at a continental scale. In Chapter 2, I tested the resource selection function against home range sizes and published estimates of mountain lion density. I provide population estimates for mountain lions in North America from two methods: first, linking the RSF to home ranges and resource availability and second, linking the RSF to reference densities. In addition, I tested whether top-down influences such as presence of bears, wolves or human hunting improved the reference-density model. These models can be used for baseline expectations for mountain lion abundance under different habitat types, bioregions, and management schemes and these analyses provide insight to our overall understanding of the ecology of the species.

REFERENCES


CHAPTER 1: Predicting mountain lion habitat in North America

INTRODUCTION
Habitat use is driven by the selective pressures of survival and reproduction which ultimately drive animal abundance (Mitchell and Powell 2004, Mitchell and Powell 2007). Because habitat use generally indicates habitat quality, the probability that an animal uses specific areas can serve as an indication of the importance of that habitat to the animal’s fitness (Boyce and MacDonald 1999). Understanding an animal’s habitat or resource selection is important for conservation of the species, predicting potential recolonization into extirpated areas, and estimating population numbers from landscape variables.

Resource selection functions (RSF) predict the probability of an animal’s use of different landscape traits such as elevation, terrain ruggedness, or variations in vegetation (Manly et al. 2002). Resource selection functions use randomly generated locations to represent the availability of landscape traits, which are then compared to actual animal locations. The landscape traits that the study animal selects, disproportionately to what is available, can be considered important to the animal’s fitness. Conversely, the habitat traits that an animal avoids indicates a negative impact to the animal’s fitness. Thus, a resource selection function can serve as a valuable habitat quality map to identify areas that are likely to be occupied by a particular species and also areas that are important to their persistence on the landscape (Manly et al. 2002).

Mountain lions are a generalist predator that occupy diverse habitats ranging from mountains, to jungles, to deserts. Their range spans from southern Alaska to the southern tip of South America. As an obligate carnivore, the foremost resource that mountain lions depend on is prey (Lendrum et al. 2014). In North America, the main prey species of mountain lions are predominantly large ungulates such as deer (*Odocoileus* spp.), elk
(Cervus canadensis) and bighorn sheep (Ovis canadensis) (Logan and Sweanor 2001). Mountain lion abundance has been tied to prey abundance (Logan and Sweanor 2001, Laundré et al. 2007, Pierce et al. 2012), but there may also be abiotic landscape traits that affect mountain lion fitness such as rugged terrain; important for rest and thermoregulation (Kusler 2019), or edge habitat where hunting success may be higher (Laundré 2007). As such, analysis of mountain lion resource selection should include abiotic landscape traits alongside metrics that indicate prey abundance such as primary productivity (Walters 2001).

The scale at which resource selection is modeled dictates the inferences that can be made from that model (Boyce et al. 2006, DeCesare et al. 2014). At small scales, a resource selection function can show how an animal uses areas within its home range but that may not translate to how the species uses the larger landscape. Johnson (1980) described four scales of selection. 1st order: the entire range of a species; 2nd order: the range of a population, 3rd order: the home range of an individual; and 4th order: the localized movement of an individual. To model habitat use of mountain lions across North America, I will analyze their 2nd order habitat selection from a use vs available framework. By sampling from multiple study areas in diverse bioregions, I will identify the most robust effects that different landscape traits have on mountain lion resource selection and thus, come to a better understanding of their most important habitat drivers. If mountain lion habitat selection is universal across bioregions (e.g. if they select for the same traits in all landscapes) then this model can be used to accurately identify habitat in unsampled regions where intensive study may not be feasible. Further, if habitat selection
is universal, then this model can be used to predict habitat in currently unoccupied areas (i.e. their historic range such as the eastern United States).

Typically, resource selection functions are performed using generalized linear models but more recently, ecologists have turned to other machine-learning algorithms, namely, a popular technique known as Random Forest (Breiman 2001, Shoemaker et al 2018, Bohnett et al 2020). Random Forest models are not bound by linearity and as such, can detect complex relationships and interactions. This applies well to the habitat selection behavior of wild animals (Shoemaker et al 2018). In the case of prediction, Westphal and Brannath (2020) recommend comparing multiple models and choosing the one with the highest predictive strength. For this reason, I created a classical generalized linear model alongside a Random Forest model and tested the two for predictive strength using out-of-sample validation.

**Study area**

I collected global positioning system (GPS) location data from multiple state agencies, federal agencies, universities, and non-governmental organizations (NGOs) across North America. These data span the desert southwest, montane, and alpine zones of the Rocky Mountains, and the temperate rain forests of the Pacific Northwest, thus my study area is best represented as current North American mountain lion range (figure 1, Hornocker and Negri 2012, Nielsen et al. 2015). Elevations in the study area range from sea level to over 4,200m, precipitation ranges from 13cm in southern California to >500cm in the Pacific Northwest, and land-use varies from highly urban areas to isolated wilderness.

**METHODS**
Data

Early mountain lion studies used triangulation or aerial homing to estimate locations of animals fitted with very high frequency (VHF) collars. Since the early 2000’s, researchers have adopted GPS collars which provide more accurate locations and span the diel period with multiple fixes per animal per day. I obtained 1.3 million location points from 476 animals from 20 different study sites from state agencies and non-government organizations across USA and Canada (table 2). I restricted the data to GPS collar locations from independent adults. Most data did not include position dilution of precision or another measure of precision, therefore I did not remove points based on that metric. I did remove locations that were clearly erroneous (i.e. with single point data errors > 100 miles from the previous point in < 4 hours). Advances in technology have led to decreasing fix intervals in GPS data which increases autocorrelation and can bias parameter estimates (Alston et al. 2022). However, large sample sizes and external validation counteract the problem of autocorrelation, especially in cases where the goal is prediction rather than inference (Northrup et al. 2013). Therefore, I did not filter the data for the purpose of counteracting autocorrelation but instead relied on the large sample size and a rigorous method of external validation. In addition, the bootstrapping step of the Random Forest acts as a thinning mechanism to decorrelate autocorrelated data (Breiman 2001).

Spatial covariates

My goal was to create a predictive resource selection model as opposed to a more traditional test of competing hypotheses in a multi-model context. However, the covariates I tested can be viewed under two main hypotheses regarding what shapes
resource selection: bottom-up vs top-down forces. As stated previously, mountain lions depend on their prey which are tied to primary productivity (Walters 2001) so the main bottom-up driver will be primary productivity as represented by the normalized difference vegetation index (NDVI, Petteroli et al. 2005). NDVI is calculated from the ratio of red to near-infrared (NIR) reflectance (NDVI = (NIR-RED)/(NIR+RED); (Myneni et al. 1995) and measures “greenness” of vegetation which is tied to digestible energy for herbivores (Garrouitte et al. 2016). As an ambush predator that utilizes cover for hunting, structural habitat traits are important to mountain lion’s ability to catch prey (Laundré 2007, Coon et al. 2020). Therefore, I included other bottom-up covariates representing abiotic landscape traits such as slope and elevation. Mountain lions are also impacted by top-down forces such as human alterations of the landscape (Dickson and Beier 2005, Benson et al. 2019) although some human-altered landscapes may be to their benefit (Coon et al. 2019). Therefore, I included covariates measuring human influence including a roads impact layer, human population density, land-use, non-vegetated areas and infrastructure in my candidate variable set (table 1). I converted aspect from degrees to a continuous measure using a cosine transformation.

I used several human impact layers produced by the Wildlife Conservation Society (2022) including roads, land-use, and infrastructure. These layers are a weighted calculation of impact based on multiple factors and utilize an exponential decay function to decrease the value of the impact at distance to the feature. For instance, my roads impact layer included weighted values scaled from the lowest impact which includes footpaths and cycleways to higher impact values for motorized roads and major highways (Wildlife Conservation Society 2022). I used several layers from MODIS (DiMiceli et al. 2019).
2015) including forest, shrub cover and non-vegetated areas. These layer values represent the proportion of the pixel at 250m resolution covered by that vegetation type. I acquired these data from satellite imagery using the Google Earth Engine platform (Gorelick et al. 2017). I standardized all variables using a Z transformation. To reduce the total number of candidate variables and to produce a single candidate set, I first screened variables for significance (p < 0.05) in univariate models (Hosmer and Lemshow 2013). I then screened covariates for collinearity, removing correlated variables |r| > 0.8 from the candidate set based on lower relative univariate r² value. I chose a high correlation threshold because overfitting is less of an issue in cases of prediction, especially when sample size is sufficient (Hawkins 2004, Steyerberg 2019). The result of this screening process was a set of candidate variables that I then used to model resource selection based on two methods (see below).

**Resource selection modeling**

I created resource selection functions using two different methods; generalized linear mixed-effects and Random Forest to create a predictive map at the second order of selection (Johnson 1980). Both methods compare animal locations to available or pseudo absence locations and predict habitat use based on the variables contained in the model. Generalized linear models do this using the maximum likelihood method of logistic regression whereas the less familiar Random Forest classification tallies votes from bootstrapped decision trees. First, a number of trees are created from bootstrapped data (e.g. 500 trees is commonly used), then an observation is predicted by each tree. The number of trees predicting ‘used point’ is divided by the number of trees predicting
‘available point’ to achieve a probability (e.g. 50 votes for ‘used point’ and 450 votes for ‘available point’ would produce an 11% probability of use; Shoemaker et al. 2018).

To model second order selection, habitat traits within an animal’s home range are compared to the surrounding landscape (Johnson 1980). In my model, used points were GPS locations for each mountain lion while available points were randomly generated pseudo absences. I used the adehabitatHR package in R for the following tasks (Calenge 2006, R core team 2021). I set the spatial extent of available points specific to each study site by creating 99% adaptive kernel polygons using the combined GPS locations from all independent mountain lions that were collared in each research project. Because research projects define study sites differently and often in non-biologically relevant ways, it was important to create standardized available habitat for each study. I matched used and available points from each study site at a 1:1 ratio. I used the raster package in R to extract landscape (i.e. covariate) values from the location points (Hijmans 2022, R core team 2021).

Generalized linear mixed model

To account for individual and geographical variation, I included individual animals and study sites as random effects (Gillies et al. 2006). The model took the form for location $i$, animal $j$, and study area $k$:

\[
\text{Logit}\{Pr \ (y_{ij} = 1|\mathbf{x}_{ijk}, \zeta_{jk})\} = \beta_1 + \beta_2 x_{2j} + \beta_3 x_{3ij} + \zeta_{jk}
\]

where $\beta_1$, $\beta_2$, and $\beta_3$ are covariate fixed effects and $\zeta_{jk}$ accounts for random variation at the intercept for individual animals and study areas. I used the lme4 package in R to fit this model (Bates et al. 2015, R core team 2021).
**Random forest model**

I used the randomForest package in R (Liaw and Wiener 2002; R core team 2021) to build a Random Forest model using the same pool of habitat variables and used and available points as for the GLM above. Although Random Forest is well suited for large numbers of highly correlated variables (Breiman 2001), I chose to use the same pool of variables for greater comparability to the GLM. To maximize performance of the model, the number of trees and the pool of variables used at each split may need to be adjusted from their default values provided by the software used (Probst et al. 2019). I tuned the model to 1000 trees and 6 variables at each split using the tuneRF function from the randomForest package.

**Model validation and method comparison**

I validated both models using internal and external methods. I internally validated the models and examined their ability to correctly classify used and available points by calculating area under the receiver operating characteristic (ROC) curve in R (Spackman 1989; R core team 2021). An AUC score of > 0.7 is generally considered acceptable and a score of >0.8 is considered excellent (Hosmer and Lemshow 2013). I tested the variable inflation factor (VIF) to ensure no two variables were excessively correlated (i.e. VIF<5). Ecological data often contain dependence structures (i.e. correlations within individual animals or study sites), therefore non-random, blocked, cross-validation approaches should be used to more rigorously validate the models (Roberts et al. 2017). To accomplish this, I performed a leave-one-out (LOO) external validation by excluding each study site from the model and projecting the model to that same site to measure its predictive ability. I first reclassified the RSF into 10 equal area bins based on probability
of use, and then summed the number of used points in each of 10 bins. I then conducted a Spearman’s rank correlation test to see if the used points fell in the higher probability bins (Fielding and Bell 1997, Boyce et al. 2002). Lastly, I examined the output of the two models by comparing the variable importance for the Random Forest model and scaled and centered effect size for the GLM. Finally, I used the raster package in R to project the top model to all of historic mountain lion range to create a probability map of mountain lion habitat (30m cells; Hijmans 2022, R core team 2021).

RESULTS

After initial screening, my final candidate set of covariates included: distance to water, normalized difference vegetation index, slope, forest, shrub cover, non-vegetation, elevation, aspect, roads impact, land-use, infrastructure, and human population density. In the final multivariate GLM, NDVI, slope, and shrub cover had positive effects on mountain lion resource selection while forest, distance to water, elevation, road impact, infrastructure, non-vegetation, land-use, and population density had negative effects (table 3). The random forest variable plots show similar effects to the GLM with habitat covariates exhibiting positive responses and human-influence covariates generally exhibiting negative responses (figure 5).

The Random Forest outperformed the GLM, with AUC values of 0.68 for the GLM and 0.94 for the Random Forest (figure 2). The mean Spearman’s rho score was 0.65 for the GLM and 0.93 for the Random Forest (figure 3). Therefore, I selected the Random Forest model to create the probability map (figure 6). In the GLM, I found support for all hypothesized effects with the exception of elevation and forest (figure 4). I predicted elevation and forest would show positive effects but both showed negative
effects on probability of use. Random Forest partial dependency variable plots show similar responses to my selected variables (figure 5). Probability of use declines overall with increased elevation. Probability of use increases slightly with forest but declines near the maximum values of percent of forest per pixel. The Random Forest model showed increased probability of use with low impact roads (e.g. footpaths) and lower probability of use with higher impact roads (e.g. highways).

**DISCUSSION**

I found support for both bottom-up and top-down effects on mountain lion resource use in North America. Resource selection was driven by bottom-up factors such as NDVI and shrub cover. Mountain lions also showed a negative selection for all human influence factors including human population density, land-use and infrastructure which indicates top-down forces negatively influence mountain lion habitat selection. Contrary to my hypothesized effect (table 1), the GLM predicted a decline in probability of use with increased percentage of forest per pixel. Although mountain lions are commonly associated with forest, this analysis suggests that they do not prefer homogenous forest and that forest mixed with shrubs or other vegetative types provides higher quality habitat for the species. For example, in heavily forested areas such as the Pacific Northwest or north-facing slopes of the Rockies, mountain lions may prefer clear cuts or edge habitats that are more biologically productive.

I found relative agreement between models in the importance of the various covariates tested (figure 4). Although comparing models in this way is non-traditional, it suggests that NDVI had high importance as measured by both methodologies. This supports the hypothesis that primary productivity, as represented by NDVI, is a major
driver in mountain habitat selection and likely, an important factor in mountain lion fitness.

As expected, the Random Forest model outperformed the GLM. The added flexibility of Random Forest models is valuable in predicting complex interactions as in animal habitat selection. In cases where defining habitat location is the priority (rather than interpreting habitat qualities), non-linear techniques such as Random Forest should be considered. In addition, Random Forest can provide useful interpretability in the variable importance plots and the partial dependency plots as shown here. These plots can add insight to traditional analyses focused on model interpretability such as GLM. For example, where the GLM only revealed a small negative effect from the roads impact covariate, the Random Forest shows a stronger and more complex relationship; showing increased selection for low-impact roads such as footpaths and decreased selection for high-impact roads which includes paved motorways and highways (figure 5).

Random Forest, as with other complex models, bring a risk of overfitting. However, this can be examined with rigorous external validation as performed here with the “leave-one-out” method. As stated previously, ecological data often contain dependence structures so “blocked” external validation is needed; in this case, leaving out each study site, some of which represented entire bioregions. For example, the model performed well at predicting mountain lion habitat use in the desert southwest, even when no data from the desert southwest was included in model building. This suggests that the model did not overfit and is transferable to regions where no data are available. In addition, an advantage of a large-scale analysis such as this is that the problem of overfitting is mitigated by the use of data spanning a range of environmental conditions.
An RSF built from one study site may overfit to unique aspects of that region whereas an RSF built from multiple sites will better capture the true habitat selection behavior of the species and can more confidently be extrapolated to other areas once externally validated.

Finally, this model predicts an abundance of high-quality mountain lion habitat in their historic range, i.e. the eastern portion of the United States. In fact, this work would suggest that portions of the eastern United States are superior habitat in comparison to the west. This is most likely due to NDVI being the strongest driver of mountain lion habitat selection and the eastern U.S. contains very high relative NDVI values. One factor that was not included in this model was connectivity, of which, large highways are an impediment for mountain lions (Ernest et al. 2014). The eastern U.S., with its dense highway system may prove to be an obstacle for mountain lions should they eventually repopulate those areas and may lead to genetic isolation in certain areas as a result.

My analysis has important management implications and can be used to identify areas of potential mountain lion habitat and potential corridors to join habitat areas. This analysis may be used to predict the potential re-occupation of the mountain lion’s historic range and highlights areas where their populations may be most successful. In addition, future research can use this map to quantify mountain lion habitat and link it to potential mountain lion population estimates in their current and historic range.

FIGURES AND TABLES

Figure 1. The study area, defined by historic mountain lion range in Canada and the USA. Study sites represent areas where collar data used was collected from 2002 to 2020 (Nielsen et al. 2015, and Hornocker and Negri 2010).
Figure 2. A comparison of internal validation method using ROC curves for the GLM and Random Forest resource selection models for mountain lions from data collected in North America between 2002 and 2020.
Figure 3. Comparison of leave-one-out external validation of GLM and Random Forest mountain lion resource selection models from 20 separate sites (see also figure 1) 2002 to 2020.

Figure 4. A comparison of variable importance from the Random Forest model with standardized, absolute value, effect size from the GLM for mountain lions for years 2002-2020. The ordering of the variables in the GLM is matched to the Random Forest for comparison.
Figure 5. Random Forest partial dependence variable plots depicting mountain lion resource selection in North American for years 2002-2020.

Figure 6. Random Forest derived resource selection function depicting mountain lion habitat quality in North America for years 2002-2020.
Table 1. Candidate landscape and human impact variables and hypothesized effects on mountain lion resource selection.

<table>
<thead>
<tr>
<th>Covariate</th>
<th>Data source (resolution)</th>
<th>Hypothesized effect on resource selection</th>
<th>Published support of hypothesized effect</th>
</tr>
</thead>
<tbody>
<tr>
<td>Biotic/landscape (bottom-up)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Distance to water</td>
<td>JRC Global Surface Water (30m)</td>
<td>-</td>
<td>Dellinger et al. 2020</td>
</tr>
<tr>
<td>Normalized difference vegetation index</td>
<td>Landsat 8 (30m)</td>
<td>+</td>
<td>Logan and Sweanor 2001, Walters 2001</td>
</tr>
<tr>
<td>Gross primary productivity</td>
<td>Landsat 8 (30m)</td>
<td>+</td>
<td>Logan and Sweanor 2001, Walters 2001</td>
</tr>
<tr>
<td>Precipitation</td>
<td>PERSIANN-CDR</td>
<td>+</td>
<td>Logan and Sweanor 2001, Walters 2001</td>
</tr>
<tr>
<td>Slope</td>
<td>U.S. Geological Survey (30m)</td>
<td>+</td>
<td>Zeller et al. 2017</td>
</tr>
<tr>
<td>Forest cover</td>
<td>MOD44Bv006 (250m)</td>
<td>+</td>
<td>Robinson et al. 2015, Dellinger et al. 2020</td>
</tr>
<tr>
<td>Shrub cover</td>
<td>MOD44Bv006 (250m)</td>
<td>+</td>
<td>Robinson et al. 2015, Dellinger et al. 2020</td>
</tr>
<tr>
<td>-------------</td>
<td>-------------------</td>
<td>---</td>
<td>------------------------------------------</td>
</tr>
<tr>
<td>Non-vegetation</td>
<td>MOD44Bv006 (250m)</td>
<td>-</td>
<td>Zeller et al. 2017, Dellinger et al. 2020</td>
</tr>
<tr>
<td>Elevation</td>
<td>U.S. Geological Survey (30m)</td>
<td>+</td>
<td>Robinson et al. 2015, Dellinger et al. 2020</td>
</tr>
<tr>
<td>Aspect</td>
<td>U.S. Geological Survey (30m)</td>
<td>South preferred</td>
<td>Robinson et al. 2015</td>
</tr>
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</table>

**Human impact/competition (top-down)**

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
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</thead>
<tbody>
<tr>
<td>Land-use impact</td>
<td>Wildlife Conservation Society (100m)</td>
<td>-</td>
<td>Robinson et al. 2015, Zeller et al. 2017</td>
</tr>
<tr>
<td>Infrastructure impact</td>
<td>Wildlife Conservation Society (100m)</td>
<td>-</td>
<td>Robinson et al. 2015, Zeller et al. 2017</td>
</tr>
<tr>
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<td>U.S. Census Bureau (100m)</td>
<td>_</td>
<td>Dellinger et al. 2020</td>
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Table 2. Summary table of GPS location data collected from 476 mountain lions from 20 study sites between the years 2002-2020.

<table>
<thead>
<tr>
<th>Study site</th>
<th>Average fix interval (hours)</th>
<th>Number of animals</th>
<th>Number of fixes</th>
<th>Average fixes per animal</th>
<th>Data timespan</th>
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<tr>
<td>1</td>
<td>4.97</td>
<td>63</td>
<td>193265</td>
<td>3067.7</td>
<td>2009-2020</td>
</tr>
<tr>
<td>2</td>
<td>9.35</td>
<td>12</td>
<td>97543</td>
<td>8128.58</td>
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</tr>
<tr>
<td>3</td>
<td>4.92</td>
<td>8</td>
<td>26311</td>
<td>3288.88</td>
<td>2018-2020</td>
</tr>
<tr>
<td>4</td>
<td>2.05</td>
<td>12</td>
<td>56682</td>
<td>4723.5</td>
<td>2011-2013</td>
</tr>
<tr>
<td>5</td>
<td>3.13</td>
<td>91</td>
<td>338739</td>
<td>3722.41</td>
<td>2002-2016</td>
</tr>
<tr>
<td>6</td>
<td>2.23</td>
<td>14</td>
<td>54174</td>
<td>3869.57</td>
<td>2016-2020</td>
</tr>
<tr>
<td>7</td>
<td>2.13</td>
<td>5</td>
<td>14714</td>
<td>2942.8</td>
<td>2010-2012</td>
</tr>
<tr>
<td>8</td>
<td>0.78</td>
<td>14</td>
<td>228249</td>
<td>16303.5</td>
<td>2017-2020</td>
</tr>
<tr>
<td>9</td>
<td>NA</td>
<td>29</td>
<td>39514</td>
<td>1362.55</td>
<td>2009-2014</td>
</tr>
<tr>
<td>10</td>
<td>7.38</td>
<td>20</td>
<td>23064</td>
<td>1153.2</td>
<td>2004-2008</td>
</tr>
<tr>
<td>11</td>
<td>NA</td>
<td>47</td>
<td>48881</td>
<td>1040.02</td>
<td>2006-2014</td>
</tr>
<tr>
<td>12</td>
<td>5.38</td>
<td>30</td>
<td>68554</td>
<td>2285.13</td>
<td>2012-2017</td>
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Table 3. Beta estimates, standard error, z value and p value for the final general linear model of resource selection of mountain lions from 476 individuals and 20 study sites from years 2002-2020.

<table>
<thead>
<tr>
<th></th>
<th>Est.</th>
<th>S.E.</th>
<th>z val.</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>13</td>
<td>-0.212</td>
<td>0.102</td>
<td>-2.070</td>
<td>&lt;0.039</td>
</tr>
<tr>
<td>14</td>
<td>0.652</td>
<td>0.003</td>
<td>217.272</td>
<td>&lt;0.000</td>
</tr>
<tr>
<td>15</td>
<td>0.100</td>
<td>0.002</td>
<td>65.405</td>
<td>&lt;0.000</td>
</tr>
<tr>
<td>16</td>
<td>-0.160</td>
<td>0.002</td>
<td>-101.574</td>
<td>&lt;0.000</td>
</tr>
<tr>
<td>17</td>
<td>-0.078</td>
<td>0.001</td>
<td>-57.857</td>
<td>&lt;0.000</td>
</tr>
<tr>
<td>18</td>
<td>-0.568</td>
<td>0.003</td>
<td>-170.234</td>
<td>&lt;0.000</td>
</tr>
<tr>
<td>19</td>
<td>-0.032</td>
<td>0.002</td>
<td>-19.049</td>
<td>&lt;0.000</td>
</tr>
</tbody>
</table>

<p>| 20 | -0.032 | 0.002 | -19.049 | &lt;0.000 |</p>
<table>
<thead>
<tr>
<th></th>
<th>Est.</th>
<th>S.E.</th>
<th>z val.</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Forest</td>
<td>-0.093</td>
<td>0.002</td>
<td>-45.160</td>
<td>&lt;0.000</td>
</tr>
<tr>
<td>Infrastructure</td>
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<td>0.002</td>
<td>-29.284</td>
<td>&lt;0.000</td>
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<tr>
<td>Non-vegetated area</td>
<td>-0.163</td>
<td>0.003</td>
<td>-61.577</td>
<td>&lt;0.000</td>
</tr>
<tr>
<td>Shrub cover</td>
<td>0.117</td>
<td>0.003</td>
<td>45.634</td>
<td>&lt;0.000</td>
</tr>
<tr>
<td>Human population density</td>
<td>-0.395</td>
<td>0.007</td>
<td>-57.760</td>
<td>&lt;0.000</td>
</tr>
<tr>
<td>Land-use impact</td>
<td>-0.535</td>
<td>0.002</td>
<td>-238.894</td>
<td>&lt;0.000</td>
</tr>
</tbody>
</table>

**Literature Cited**


Calenge, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecological Modelling, 197, 516-519

Coon, C. A., Mahoney, P. J., Edelblutte, E., McDonald, Z. and Stoner, D.C., 2020. Predictors of puma occupancy indicate prey vulnerability is more important than prey availability in a highly fragmented landscape. Wildlife Biology.


https://CRAN.R-project.org/package=raster


CHAPTER 2: Predicting mountain lion abundance in USA and Canada

INTRODUCTION

Organisms expend the minimum amount of energy necessary to meet their survival and reproductive needs (Pyke et al. 1977, Herfindal et al. 2005). As a result, the total area they depend on (i.e. their home range or territory) will be as small as possible (Harestad and Bunnel 1979). Generally, as habitat quality increases, total area used decreases and the number of organisms per unit area (density) increases. The correlation between habitat quality and density is well documented for species at lower trophic levels including arboreal ants (Pringle et al. 2019), other arthropods (Borer et al. 2012), a variety bird species (Meehan et al. 2004, Matthiopoulos et al. 2019) and white-tailed deer (Odocoileus virginianus; Walters 2001). Whether this relationship can be extended to higher trophic levels is less understood.

There are exceptions to the relationship between habitat quality and density. Van Horne (1983) noted that dispersers of some Rodentia species can accumulate in low-quality habitats and that a relationship between habitat suitability and density in these cases would be misleading. In addition, breeding birds are often territorial which leads to non-breeding birds (known as “floaters”) to accumulate in poor habitat (Krebs 1971, Atwood 1980, Carrick 1963). Of note is that these exceptions occur at small geographic scales. As the scale expands to incorporate a range of habitat quality that includes non-habitat, the generalized trend of habitat quality correlating to density becomes more clear. Nonetheless, a model of density based on habitat quality must first justify the assumption that density is in fact correlated to habitat quality in the species of interest.
The relationship between resource availability and population density has been used successfully for population estimation. Boyce and McDonald (1999) showed that resource selection functions (RSF) could be used to link habitat quality to abundance. By summing the probabilities of use from an RSF projection, a value representing habitat quality can be applied to the landscape. This value can then be linked to reference densities through linear regression and quantified to estimate abundance (Boyce et al. 2016).

If populations of carnivores can be predicted from a habitat quality metric, it would allow for a powerful and cost-effective foundation on which to make population predictions. Abundance of carnivores is often difficult to quantify due to their rare and widespread occupancy of the landscape. Carnivores may also be cryptic, in that some species cannot be identified individually based on stripe or spot patterns (i.e. the mountain lion). A habitat-based population model would be particularly useful for creating abundance estimates for these species.

Traditionally, mountain lion abundance was estimated using intensive capture, ground tracking, and radio telemetry (Rabinowitz 2009). Choate et al (2006) tested multiple population estimation techniques against intensively monitored mountain lion populations and found that Lincoln-Peterson mark-recapture, helicopter survey probability sampling, catch-per-unit-effort, scent station visits, track counts and hunter harvest, all failed to accurately estimate mountain lion abundance. Spatial-capture-recapture (Royle et al. 2009, Royle et al. 2013) has been used to effectively estimate mountain lion populations (Russell et al 2012; Proffitt et al 2015) however it is expensive and not feasible for large scale analyses. Recently, Murphy et al. (2022) found that most
mountain lion population estimates were an overestimate and inadequate for the purposes of conservation or management with 90% of studies having a coefficient of variation $> 0.2$. Howard et al. (2020) used statistical population reconstruction to estimate mountain lion abundance in Arizona by combining age-at-harvest data with survival rates, harvest probabilities and hunter effort. For accurate population models, incorporating mortality and habitat in the form of integrated population modeling is effective (Montana Fish Wildlife and Parks 2018) but relies on quality harvest data which vary greatly by state.

Previous authors have attempted to model mountain lion abundance from landscape data (e.g. Robinson et al. 2015). For this method to be valid there should be a relationship between habitat quality and home range size. Higher quality habitats should relate to smaller home ranges and higher densities. With the expectation that mountain lion abundance is correlated with prey abundance and that prey abundance can be modeled using metrics for primary productivity, Stoner et al (2018) tested mountain lion home range size against primary productivity and found a strong correlation. Higher primary productivity, indicating greater abundance of prey, was correlated with smaller mountain lion home ranges, suggesting higher densities of mountain lions.

The direct relationship between resource availability, home range sizes and population density may be complicated by territoriality, the presence of competitive species, and direct pressure from humans. Mountain lions compete directly with wolves and lose a substantial number of kittens to wolves in co-occupied areas (Elbroch et al. 2015, Elbroch et al. 2020). In addition, mountain lions are a solitary predator that hunts prey larger than itself which leads to high levels of kleptoparasitism. In areas when bears (Ursus spp.) were active, mountain lions exhibited higher kill rates (Elbroch et al. 2014,
Allen et al. 2021). Competition with top predators such as wolves and bears may impact mountain lion fitness and lower densities.

Because mountain lions are a hunted species, home range size may also not reflect true density. Male mountain lions in heavily hunted populations have exhibited expanded home range sizes while the home ranges of females in the same population remained unchanged (Maletzki 2014). This may be due to male mountain lions being primarily driven by seeking access to females, while females are primarily driven by resources (Lendrum et al. 2014). In a heavily hunted area, males may wander farther in search of females, thus creating larger home ranges. The Ideal Free Distribution hypothesis (Fretwell and Lucas 1969) theorizes that as intraspecific competition decreases, animals move to higher quality habitat and thus, would require smaller home ranges (Mitchell and Powell 2012). Since females are primarily resource driven, this suggests that in an area of high harvest, female mountain lion home ranges may decrease in size despite a lower population density.

Mountain lions are solitary, moderately territorial, obligate carnivores. Ultimately, the density of mountain lions on the landscape is set by the number of available home ranges, which in turn is dependent on the size of an average home range, which itself is set by the available resources. I wished to test this relationship to determine if, or how accurately, mountain lion density could be predicted in novel areas using their known resource selection behavior. Here, I first tested the relationship between habitat quality and mountain lion density as represented by home range size. I then used compiled density estimates to test how well resource availability can predict density. Finally, I
tested competing hypotheses to determine the best predictor of mountain lion density; bottom-up resource availability or a combination of bottom up and top-down forces.

The “resource availability hypothesis” predicts that the main driver of mountain lion abundance is primary productivity and other landscape traits as derived from an RSF. I will find support for this hypothesis if the most parsimonious model of mountain lion density contains only one covariate, RSF score (i.e. the sum of RSF values). The “hunting hypothesis,” predicts that hunting will have the strongest effect on mountain lion abundance. This hypothesis will be supported if the top model includes both the RSF and a variable representing areas of hunting. The “interspecific competition hypothesis” will be supported if the top model includes covariates for the RSF and for wolf or bear presence. Finally, the “additive effects hypothesis” predicts that additive effects of hunting in areas with active wolf packs will negatively affect mountain lion abundance and will be supported if the top model includes covariates for the RSF, wolf presence and hunting.

**STUDY AREA**

I collected published reference densities across USA and Canada (table 1). These sites span the desert southwest, montane, and alpine zones of the Rocky Mountains, and the temperate rain forests of the Pacific Northwest, thus the study area is best represented as current North American mountain lion range (figure 1, Hornocker and Negri 2010, Nielsen et al. 2015). Elevations in the study area range from sea level to over 14,000’, precipitation from <5” in southern California to >200” in the Pacific Northwest, and land-use varies from highly urban areas to isolated wilderness.
METHODS

I wished to test the efficacy of two resource-based population estimate methods; home range prediction and reference density. To do so I used a previously published mountain lion RSF as the basis of my analysis (Chapter 1). Before either abundance estimation method was executed, I validated the concept of using these methods by examining the relationship of home range size and resource availability as represented by the RSF. Because the RSF included all habitat including very poor habitat, I first needed to screen out non-habitat (i.e. areas that cannot support a mountain lion) to create a map of mountain lion range in North America. To do this, I set a threshold for viable mountain lion habitat (i.e. the minimum resources a single animal would need to establish a home range) and screened out all areas that fell below this threshold. I then used the resulting map to predict mountain lion abundance in two ways. The first method was based on mountain lion home range and resource availability. I determined the average RSF requirements needed for an individual mountain lion, as measured by summing the RSF value within a number of sample mountain lion home ranges. I then divided total available resources by the number needed for each animal. For the second method, I regressed the RSF against reference densities and used the model to predict mountain lion abundance in USA and Canada. Finally, I tested four hypotheses; resource availability, hunting, interspecific competition, and additive effects to determine what best predicted mountain lion densities across North America.

Collar data

Early mountain lion studies used triangulation or aerial homing to estimate locations of animals fitted with very high frequency (VHF) collars. Since the early 2000’s,
researchers have adopted GPS collars which provide more accurate locations and span the diel period with multiples fixes per animal per day. I obtained mountain lion collar data from state agencies and non-government organizations across USA and Canada. I restricted the data to GPS collar locations from independent adults. Most data did not include position dilution of precision or other measure of precision therefore I did not filter points based on this metric. I removed locations that were clearly erroneous with single point data errors > 100 miles from the previous point in < 4 hours.

**Home range estimation**

I used the ctmm package (Fleming and Calabrese 2021) in R to create 95% autocorrelated kernel density home ranges from independent mountain lions exhibiting resident behavior. I applied a filter to only retain data showing high confidence that a home range was established (degree of freedom > 4; Fleming and Calabrese 2021). Because mountain lions tend to shift home ranges over time, the length of time that the data spans greatly affects the size of the home range. For this reason, I limited the data span to 1 year per animal.

**Relation of resources and home range size**

Home range size and corresponding densities is thought to expand and contract with resource availability (Mitchell and Powell 2012). If RSF score predicts habitat quality, and thus density, and if home range sizes expand and contract based on habitat quality (Mitchell and Powell 2004, Mitchell and Powell 2007, Mitchell and Powell 2012), then the RSF score should show a negative relationship to home range size. Because home range sizes were not normally distributed and showed higher variation as size increased, I
log transformed the areas (km²). I then regressed the log transformed areas against the summed RSF values within each home range.

**Mountain lion range**

My RSF was derived from 900m² pixel (30m x 30m) covariate layers. As most mountain lion home ranges are ~100km² (Hornocker and Negri 2010), it is therefore possible to have small areas of high-quality habitat that could still not be enough to support a single animal. To define a minimum threshold which could theoretically support a mountain lion, I summed RSF probabilities within each home range and divided by the home range size for each animal. This produced a distribution of the mean RSF value per home range per unit area (i.e. a habitat index score). I then used the lowest quantile of this distribution as the minimum habitat quality needed to support a mountain lion. I then determined the smallest area that could support a mountain lion based on the distribution of home range sizes; again, selecting the lowest quantile. I used these values, the lowest habitat quality needed and the smallest area needed, in a moving window using the terra package in R (Hijmans 2022, R core team 2021) to remove areas that fell below this threshold. The resulting layer should represent a liberal estimate of areas of contiguous habitat that could support a single mountain lion home range.

**Density prediction**

Home range size-based estimation

To predict mountain lion density using an estimate of home range availability, I first summed the RSF values within each individual mountain lion home range. I used this distribution of within-home range sums to determine low (5th percentile), median, and
high values (95\textsuperscript{th} percentile). These values represent the potential amount of resources needed by a single mountain lion to establish a home range. I then summed the RSF values for current mountain lion range in USA and Canada. Finally, I divided the later sum by the 5\%, median and 95\% values, for males and females separately, to determine the number of mountain lions the USA and Canada could support. By dividing total resources available by the number of resources needed per animal an estimate for mountain lion abundance is achieved. To estimate potential populations if historic range was also occupied, I repeated the same procedure for their historic habitat in eastern USA and Canada.

Reference density-based estimation

The second method of population prediction based on resource availability uses reference densities. As stated above, several methods have been proposed to produce mountain lion population and density estimates including genetic spatial-capture-recapture, intensive monitoring, statistical population reconstruction (Howard et al 2020), and combined techniques (Murphy et al. 2019). I collected published density estimates from studies using these methods by searching the literature using Web of Science and Google Scholar. As most studies did not provide an accurate study area polygon, I used a large area around the study area centroid. First, I created a 1000\textsuperscript{km\textsuperscript{2}} buffer around the centroid from each published density estimate. Then, I summed the RSF values within this area using the raster package in R (Hijmans 2022, R core team 2021). Since all “study areas” were 1000 \text{km}\textsuperscript{2} this provided a standard resource selection “score”. When publications contained multiple estimates from the same site (e.g. repeated years), I used the same measure of RSF paired against the different population estimates.
To predict mountain lion populations, I first regressed the reference densities against the RSF scores. I then summed the RSF values for the current range of mountain lions in USA and Canada and used this sum in the model to predict the total number of mountain lions. Again, I repeated this procedure for their historic range in eastern North America.

**Model fitting**

I wished to test the relationship of resources, wolves, bears, and hunting to mountain lion density. I accessed species distributions maps from International Union for Conservation of Nature (IUCN 2022). I used these maps to create a binary variable (0 or 1) to represent presence of resident wolf packs and bears. I included another binary variable (0 or 1) to represent areas of hunting which includes all western states excluding California and national parks. As mentioned above, my estimates of mountain lion density were obtained through published literature and my RSF scores were created by sampling from a centroid of each study site. Next, I regressed the compiled density estimates against my set of candidate models (table 1). I used Bayesian Information Criterion (Sakamoto et al. 1986) to identify the most parsimonious model.

**RESULTS**

**Home ranges**

After filtering animals for high confidence in residency, I calculated 336 annual home ranges from 336 different animals. While home ranges varied between sites, male home ranges were consistently larger than female. Mean home range size was 826 km² for males and 306 km² for females (table 2). For both sexes, home range size showed a
significant negative relationship with habitat quality as represented by the habitat index score (figure 4; $r^2 = 0.2642$, $f(1, 334) = 121.3$, $p < 0.00$). The fitted regression model was: $7.8551 – 2766.8181*(\text{Habitat quality index})$.

**Screening non-habitat/mountain lion range**

The lowest quantile of home range sizes was 25km$^2$. The lowest quantile of habitat quality as represented by the RSF was 2,000. Using this threshold for the moving window process, I found that there was 3,862,848 km$^2$ of potential mountain lion habitat in USA and Canada, only 2,218,154 km$^2$ (57%) of which is currently occupied (figure 3).

**Hypothesis testing**

I found equal support for 2 top models; the simplest model containing only RSF value and the model which included presence of wolves (table 3). Contrary to my predicted responses, I found that presence of wolves had a positive effect on mountain lion density. Although insignificant, presence of bears and hunting also showed positive effects on density.

**Population estimates**

Using the median within-home range RSF sum, I calculated 9,962 females and 4,130 males for a total of 14,092 independent, resident adults (table 4). In the eastern United States, using the same method, I calculated potential abundances of 34,394 females and 14,260 males for a total of 48,654 independent, resident adults. I found 142 reference densities that met the criteria for this analysis which I then used to build the reference-density model. Using the reference-density model, I calculated 16,600 total independent
mountain lions in their current range and 57,320 potential independent mountain lions in their historic range (table 4).

DISCUSSION

I found support for my “resource availability” hypothesis that habitat quality was the main driver of mountain lion density. I did not find support for my hypotheses that presence of hunting, wolves, or bears negatively impacted mountain lion densities. Surprisingly, the presence of wolves showed a significant effect in the opposite direction. Higher mountain lion densities were correlated with wolf presence. This may be explained by the extirpation of wolves from most of North America and where the species has been reintroduced/and or recovered, coincides with higher quality habitat in northern latitudes. At a local scale, wolves may reduce mountain lion populations through direct competition (Elbroch et al. 2015, Elbroch et al. 2020), however at a landscape the effect of wolves on mountain lion populations is unknown. Historically wolves and mountain lions likely exhibited niche differentiation to minimize conflict in co-occupied areas (Elbroch et al. 2015).

For either method of resource-based population estimation to be viable there must be a significant relationship between home range size and resource availability. I found that home range size was strongly negatively correlated with resources (figure 4). In addition, reference densities showed a significant relationship to the RSF. Although these relationships were significant, only 3% of the variation in published densities was explained by habitat quality.
Previous work has touched on the connection between mountain lion home range size and habitat productivity (Stoner et al. 2018), however, there has not been a robust analysis of this relationship over widespread geographic areas. Despite a range of bioregions, hunting schemes, and competition with other carnivores, mountain lion home ranges for both sexes were consistently smaller in higher quality habitat. This suggests that habitat quality, which was mainly driven by primary productivity as represented by NDVI, is the leading factor influencing mountain lion home range size, and likely, density. This was also supported by my finding that RSF was equally supported in terms of the best model to explain variation in published density estimates. Similar relationships have been found in previous carnivore home range studies (Duncan et al. 2015) including recently by Snider et al. (2021) in which the authors found a strong relationship between the home range sizes of leopards (Panthera pardus) and landscape productivity as indexed by NDVI.

One challenge of this analysis was determining viable mountain lion habitat and choosing the scale and method by which to screen out non-habitat and establish a putative range layer. This step is crucial for the RSF/home range-based method and can greatly affect population estimates and densities. My approach was to base viable habitat on the minimum area and amount of resources that could support a single mountain lion (2,000 RSF within a 25km² area). Instead, viable habitat could be set by defining the minimum area and amount of resources that could support an entire mountain lion population with connectivity and dispersal taken into account (2,200km²; Beier 1993). At the other end of the spectrum, habitat can be defined at the smallest scale; the resolution of the RSF map. This is the method Dellinger et al. (2020) used to estimate mountain lion habitat in
California. Any pixel in the RSF map that fell below a specified threshold (0.08 probability; Dellinger et al. 2020) was removed as non-habitat. Interestingly, despite the different methodologies used, my analysis found a similar amount of viable mountain lion habitat in California as Dellinger et al. (2020) with 164,788km² compared to their estimate of 165,350–170,085 km² depending on the season. There are valid justifications for using each of these methods and more research is needed to determine which is optimal.

A notable weakness of the RSF/home range-based estimation method is the assumption of zero home range overlap. This is especially problematic for females that can share significant portions of their range with other females (~26% overlap; Guzman 1998). If nearly a quarter of every female home range was shared with another female, total abundance estimated would increase by approximately 1.26. In this analysis, I calculated autocorrelated kernel density home ranges using the ctmm package in R (Fleming and Calabrese 2021). This method has been shown to predict animal space use with greater accuracy than traditional kernel density estimation (Fleming et al. 2015), however, the home ranges that I calculated were larger than previous estimates for mountain lions (e.g. ~100 km² vs 306 km² and 816 km² for females and males respectively). This would suggest that home range overlap is also greater than previous estimates and a correction factor higher than 1.26 is needed. More research is required regarding the complex topic of home range overlap to determine an appropriate adjustment factor to improve this method of population estimation. In addition, future research may wish to investigate whether home range overlap changes with habitat quality, potentially increasing as habitat quality increases.
Another challenge of the RSF/home range-based method is determining how many RSF “points” (i.e. the within-home range sum) a mountain lion needs to survive and reproduce. For 336 mountain lions, the within-home range sum ranged from 13,204 - 1,578,368 for females and 61,658 – 3,280,897 for males (figure 2). The corresponding abundance estimate can vary widely depending on this range of values. However, regardless of the high variation in with-in home range RSF sums, this methodology is useful for comparing potential abundances across regions. The eastern U.S. appears to offer a large amount of high-quality habitat and should mountain lions eventually repopulate their historic range, they could do so in high numbers (~3.5x the western mountain lion population).

Despite a significant relationship between habitat quality and published density estimates, the model left much of the variance unexplained ($r^2 = 0.03$). This is likely due, in part, to the high variation in different methods of population estimation (Beausoleil et al. 2021, Murphy 2022) as discussed earlier. Further, in a large review of 1,772 mammalian carnivore population estimates, Smallwood and Schonewald (1998) found that 78% of variation in densities was explained by the method of delineating spatial extent of study areas rather than biological factors. This is especially pertinent to a species such as mountain lions that have large home ranges which often overlap borders of the study area. If the study area boundary intersects the home range of an animal, but the density estimate fails to account for the proportion of occupancy, then the estimate is inaccurate (e.g. if 50% of the animal’s home range is within the study area, the animal should be counted as 0.5 occupancy rather than full occupancy). In addition, study sites are often clustered around populations of study animals which will inflate density
estimates if the estimate is extrapolated to a larger area (Smallwood and Schonewald 1998).

Due to the limited scope of this project, my ‘top-down’ variables such as hunting were binary (e.g. hunted or not hunted). A more refined variable that indicates level of hunting pressure might have explained more variance. For example, all of the reference densities acquired from Texas, where unlimited harvest occurs outside of protected areas, fell below the predicted level. Although several of these estimates came from the protected Big Bend National Park, the amount of hunting in surrounding areas may limit immigration, further influencing the model. A model that incorporated levels of hunting pressure based on harvest reports and management schemes could greatly improve the fit of the model. Along the same lines, my variables for presence of wolves and bears were also binary. More precise estimates of wolf and bear density may further improve the model or if not, may provide clearer insights into the ability for these top carnivores to coexist without lowering mountain lion densities.

A final piece regarding the high variance left unexplained in the reference-density model is that I did not include variables representing prey density. Ungulate management varies widely, and ungulate densities have the potential to affect mountain lion abundance (Carbone and Gittleman 2002; Karanth et al. 2004). The link from habitat to prey abundance to predator abundance is obfuscated by the levels of hunting pressure on prey along with other influences that may limit prey populations. Certain areas may have high NDVI values and are otherwise high-quality mountain lion habitat, but intensive hunting of ungulate populations might limit mountain lion populations and cause discrepancies in the habitat-based model.
Habitat quality is the main driver in determining home range sizes and corresponding abundances of carnivores and as such, remains a valuable focus for conservation efforts. Habitat quality is an important predictor of abundance and even though top carnivores have a number of complex factors affecting their abundance including competition, territoriality, and human influences, habitat-based model may be valuable in estimating their populations. Although a precise estimate of mountain lion populations is difficult to achieve using these methods, these habitat-based models may be used as a foundation for a more accurate integrated population model (Proffitt et al. 2015; Montana Department of Fish, Wildlife, and Parks 2018).

FIGURES AND TABLES

Figure 1. Study area extent, defined as the current and historic ranges of mountain lions in USA and Canada. In yellow are locations of 142 reference density estimates from published literature from 1979 to 2021.
Figure 2. RSF sums for 336 mountain lion annual home ranges from 2002-2021.
Figure 3. Resource selection function probability map for mountain lions in North America created from 476 mountain lions from 20 study sites from years 2002-2021.

Figure 4. Mountain lion home range size compared to a habitat quality index (RSF sum/area) for 336 mountain lions from years 2002-2021.
Figure 5. 142 published density estimates from years 1979-2021 regressed against a habitat quality index derived from the resource selection function developed in Chapter 1.
Table 1. Candidate models regressing bottom-up and top-down forces against mountain lion density estimates.

<table>
<thead>
<tr>
<th>Model Description</th>
<th>p-value</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Density ~ RSF score</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Density ~ RSF score + wolf presence</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Density ~ RSF score + hunting</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Density ~ RSF score + presence of bears</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Density ~ RSF score + wolf presence + hunting</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Density ~ RSF score + wolf presence + bear presence</td>
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<td></td>
</tr>
</tbody>
</table>
Table 2. Male and female mountain lion home range size summary statistics from 20 study sites in North America for years 2002-2020.

<table>
<thead>
<tr>
<th>Sex</th>
<th>N annual home ranges</th>
<th>Min (km²)</th>
<th>Max (km²)</th>
<th>Mean (km²)</th>
<th>Median (km²)</th>
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</thead>
<tbody>
<tr>
<td>Male</td>
<td>146</td>
<td>76</td>
<td>7,180</td>
<td>826</td>
<td>562</td>
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<tr>
<td>Female</td>
<td>190</td>
<td>12</td>
<td>4,262</td>
<td>306</td>
<td>179</td>
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Table 3. BIC scores, beta estimates, p values and r² for tested models.

<table>
<thead>
<tr>
<th>Model</th>
<th>BIC score</th>
<th>Beta estimates (p value)</th>
<th>r²</th>
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<tr>
<td></td>
<td>RSF</td>
<td>Wolf</td>
<td>Bear</td>
</tr>
<tr>
<td>Density ~ RSF + wolf presence</td>
<td>420.13</td>
<td>4.076e-07 (0.504)</td>
<td>2.009e-01 (0.0172)</td>
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<tr>
<td>Density ~ RSF</td>
<td>420.98</td>
<td>1.170e-06 (0.0285)</td>
<td>-</td>
</tr>
<tr>
<td>Density ~ RSF + presence of bears</td>
<td>423.67</td>
<td>1.278e-06 (0.0174)</td>
<td>-</td>
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</table>
Table 4. State estimates and densities for independent, resident mountain lions based on the 5%, median and 95% within-home range RSF sums and the reference density model. Densities (independent mountain lions/100km²) are provided in parentheses.

<table>
<thead>
<tr>
<th>State</th>
<th>Habitat area (km²)</th>
<th>5%</th>
<th>Median</th>
<th>95%</th>
<th>Reference density-based population estimates</th>
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<tr>
<td>Arizona</td>
<td>92887</td>
<td>1886 (2.03)</td>
<td>559 (0.60)</td>
<td>137 (0.15)</td>
<td>690 (0.74)</td>
</tr>
<tr>
<td>California</td>
<td>164788</td>
<td>4050 (2.46)</td>
<td>1200 (0.73)</td>
<td>295 (0.18)</td>
<td>1472 (0.89)</td>
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<tr>
<td>Colorado</td>
<td>94108</td>
<td>1716 (1.82)</td>
<td>508 (0.54)</td>
<td>125 (0.13)</td>
<td>629 (0.67)</td>
</tr>
<tr>
<td>Florida</td>
<td>12568</td>
<td>260 (2.07)</td>
<td>77 (0.61)</td>
<td>19 (0.15)</td>
<td>103 (0.82)</td>
</tr>
<tr>
<td>Idaho</td>
<td>130013</td>
<td>2695 (2.07)</td>
<td>798 (0.61)</td>
<td>196 (0.15)</td>
<td>983 (0.76)</td>
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<tr>
<td>Montana</td>
<td>127213</td>
<td>2915 (2.29)</td>
<td>863 (0.68)</td>
<td>212 (0.17)</td>
<td>1062 (0.83)</td>
</tr>
<tr>
<td>State</td>
<td>Code</td>
<td>Pop.</td>
<td>Year</td>
<td>Mort.</td>
<td>H.</td>
</tr>
<tr>
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<td>------</td>
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</tr>
<tr>
<td>Nevada</td>
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<td>556</td>
<td>137</td>
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<tr>
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<td>237</td>
<td>70</td>
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<tr>
<td>Oregon</td>
<td>140224</td>
<td>3214</td>
<td>952</td>
<td>234</td>
<td>1170</td>
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<tr>
<td>South Dakota</td>
<td>5079</td>
<td>134</td>
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<tr>
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<td>53718</td>
<td>1107</td>
<td>328</td>
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<td>409</td>
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<td>Utah</td>
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<td>497</td>
<td>122</td>
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<td>Wyoming</td>
<td>82435</td>
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<td>441</td>
<td>108</td>
<td>546</td>
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Appendix A. 142 published density estimates for mountain lions for the years 1979-2021.

<table>
<thead>
<tr>
<th>Publication</th>
<th>Adults per 100km²</th>
<th>Hunted</th>
<th>Wolves</th>
<th>Bears</th>
<th>Location</th>
<th>Data timespan</th>
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<td>Anderson Jr, C.R., 2006. Cougar Management Guidelines.</td>
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<td>Texas</td>
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<tr>
<td>Authors</td>
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<td>Journal</td>
<td>Year</td>
<td>Density</td>
<td>Study Area</td>
<td>Data Collection Year</td>
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<td>---------</td>
<td>------</td>
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<td>Author(s)</td>
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<td>Year</td>
<td>Location</td>
<td>Pages</td>
<td>Academic Institution</td>
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<td>----------</td>
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<td>Dennison, C.C., 2013.</td>
<td>Use of camera traps to determine mountain lion density and prey availability in the Davis Mountains, Texas.</td>
<td>0.66</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>Texas</td>
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<td>Dennison, C.C., 2013.</td>
<td>Use of camera traps to determine mountain lion density and prey availability in the Davis Mountains, Texas.</td>
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<td>Dennison, C.C., 2013.</td>
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<td>Texas</td>
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<td>Elbroch, L.M., Ferguson, J.M., Quigley, H., Craighead, D., Thompson, D.J. and Wittmer, H.U., 2020.</td>
<td>Reintroduced wolves and hunting limit the abundance of a subordinate apex predator in a multi-use landscape.</td>
<td>0.64</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>Wyoming</td>
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<tr>
<td>Reference</td>
<td>Abundance</td>
<td>mule deer</td>
<td>elk</td>
<td>Location</td>
<td>Year</td>
<td></td>
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<td>Author</td>
<td>Title</td>
<td>Location</td>
<td>Population Characteristics</td>
<td>Year</td>
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<td>Johnson, R.D., Jenkins, J.A., Tucker, S.A. and Wilckens, D.T.</td>
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<td>North Dakota</td>
<td>2005</td>
<td>0.49</td>
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<td>Mountain lion (Puma concolor) population characteristics in the Little Missouri Badlands of North Dakota.</td>
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<td>2008</td>
<td>0.83</td>
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<td>Johnson, R.D., Jenkins, J.A., Tucker, S.A. and Wilckens, D.T.</td>
<td>Mountain lion (Puma concolor) population characteristics in the Little Missouri Badlands of North Dakota.</td>
<td>North Dakota</td>
<td>2010</td>
<td>1.46</td>
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<td>Johnson, R.D., Jenkins, J.A., Tucker, S.A. and Wilckens, D.T.</td>
<td>Mountain lion (Puma concolor) population characteristics in the Little Missouri Badlands of North Dakota.</td>
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<td>2012</td>
<td>1.2</td>
<td>1</td>
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<td>Mountain lion (Puma concolor) population characteristics in the Little Missouri Badlands of North Dakota.</td>
<td>North Dakota</td>
<td>2013</td>
<td>1.33</td>
<td>1</td>
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Robinson, H. and DeSimone, R., 2011. The Garnet Range mountain lion study: characteristics of a hunted population in west-central Montana. Montana Department of Fish, Wildlife & Parks. 1.31 1 1 1 Montana 1999

Robinson, H. and DeSimone, R., 2011. The Garnet Range mountain lion study: characteristics of a hunted population in west-central Montana. Montana Department of Fish, Wildlife & Parks. 1.2 1 1 1 Montana 2000


1.53 1 1 1 Montana 2003


1.64 1 1 1 Montana 2004


1.56 1 1 1 Montana 2005


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66


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1.3 1 0 1 Utah 2001


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2.9 1 0 1 Utah 1997


2.75 1 0 1 Utah 1999


2.9 1 0 1 Utah 2000


2.9 1 0 1 Utah 2001