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Modeling and Mapping Coyote (*Canis latrans*) Abundance in Northwestern Vermont

An Honors College Thesis

by Lucas Beck

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Abstract

Predators such as, coyotes (*Canis latrans*), have profound effects on ecosystems. Coyotes are recent arrivals in the northeastern United States of America, and in Vermont their ecology remains poorly understood. Even basic population characteristics remain largely unknown. I used a Royle-Nichols Abundance-Induced Heterogeneity Model to estimate coyote site abundance in northwestern Vermont. The model was developed by averaging the outputs of supported candidate models of detection/non-detection data collected from 71 camera traps in 2008, 2011 and 2017. The averaged model included the null model and the following covariates: the proportion of water/wetland, agriculture, coniferous forest, deciduous forest, mixed forest, development, shrub/scrub and the mean bobcat habitat suitability within the radius of an average coyote home range of a site. The candidate model with the strongest empirical support was the null model, followed by the water/wetland model, but all the candidate models assessed had strong empirical support (Δ AIC $\leq$ 2). The covariates water/wetland, agriculture, shrub/scrub and mixed forest had a positive effect on abundance, whereas the other covariates had a negative effect. Abundance ranged from 0.078 coyotes/km^2 to 0.089 coyotes/km^2 and was greatest in the western part of the study area. Using model outputs, I estimated abundance in the state Wildlife Management Units (WMUs) in the study area: B, G, I, F1 and F2. WMU B had the greatest abundance estimate (148 coyotes), while WMU I had the lowest (77 coyotes). Across all WMUs abundance was 457 coyotes. Abundance values predicted from the model were lower than expected based on the state's abundance estimate. One advantage of the model approach is that it incorporated the influence of landscape variables on abundance and resulted in a measure of precision (SE) for each parameter. The model provides managers a means of understanding how coyote abundance varies with features of the environment.

Key words: Abundance, *Canis latrans*, Coyote, Champlain Valley, Density, Occupancy Modeling, Vermont

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Chapter 1: Modeling and Mapping Coyote (*Canis latrans*) Abundance in Northwestern Vermont

Abstract

Predators such as, coyotes (*Canis latrans*), have profound effects on ecosystems. Coyotes are recent arrivals in the northeastern United States of America, and in Vermont their ecology remains poorly understood. Even basic population characteristics remain largely unknown. I used a Royle-Nichols Abundance-Induced Heterogeneity Model to estimate coyote site abundance in northwestern Vermont. The model was developed by averaging the outputs of supported candidate models of detection/non-detection data collected from 71 camera traps in 2008, 2011 and 2017. The averaged model included the null model and the following covariates: the proportion of water/wetland, agriculture, coniferous forest, deciduous forest, mixed forest, development, shrub/scrub and the mean bobcat habitat suitability within the radius of an average coyote home range of a site. The candidate model with the strongest empirical support was the null model, followed by the water/wetland model, but all the candidate models assessed had strong empirical support (Δ AIC ≤ 2). The covariates water/wetland, agriculture, shrub/scrub and mixed forest had a positive effect on abundance, whereas the other covariates had a negative effect. Abundance ranged from 0.078 coyotes/km^2 to 0.089 coyotes/km^2 and was greatest in the western part of the study area. Using model outputs, I estimated abundance in the state Wildlife Management Units (WMUs) in the study area: B, G, I, F1 and F2. WMU B had the greatest abundance estimate (148 coyotes), while WMU I had the lowest (77 coyotes). Across all WMUs abundance was 457 coyotes. Abundance values predicted from the model were lower than expected based on the state's abundance estimate. One advantage of the model approach is that it incorporated the influence of landscape variables on abundance and resulted in a measure of precision (SE) for each parameter. The model provides managers a means of understanding how coyote abundance varies with features of the environment.

Key words: Abundance, *Canis latrans*, Coyote, Champlain Valley, Density, Occupancy Modeling, Vermont

Introduction

Large predators are known to have profound effects on the socio-ecological systems they inhabit (Ritchie et al. 2012). Predators can influence the composition of ecological communities through the initiation of trophic cascades that can affect the abundance, distribution, and composition of species in ecosystem as well as environmental processes (Estes et al. 2011). For example, the avian community in Californian scrub fragments was more diverse in fragments containing coyotes (*Canis latrans*), as coyotes suppress populations of domestic cats (*Felis catus*) which prey extensively on songbirds (Crooks and Soulé 1999). In the Greater Yellowstone Ecosystem, the reintroduction of gray wolves (*C. lupus*) has been linked to the restoration of riparian communities (Ripple et al. 2001, Berger et al. 2001). Wolf predation reduces elk (*Cervus canadensis*) abundance and alters elk foraging behavior, which allows regeneration of riparian vegetation (Ripple et al. 2001). Predators can also have meaningful impacts on human use of the landscape. Coyotes and other predators compete with humans for game, depredate livestock and on very rare occasions can pose a threat to human safety (Treves and Karanth 2003).

In Vermont, wolves and cougars (*Puma concolor*), two once widespread apex predators in the state, were extirpated by 1900 (Gompper 2002). Coyotes, originally from the western plains, were first recorded in Vermont in the 1940s (Vermont Fish and Wildlife Department 2018). The eastward expansion of coyotes is thought to have been facilitated by deforestation and the extirpation of wolves and cougars (Gompper 2002). Some ancestors of Vermont's coyote population hybridized with wolves north of the Great Lakes, as the coyote population expanded east (Gompper 2002, Kays et al. 2010). Hybridization between coyotes and wolves in the Northern Great Lakes region introduced genes to the coyote population that allowed coyotes to partially fill the niche formerly held by wolves in eastern North America (Kays et al. 2010). In reference to their hybrid ancestry and unique ecology, coyotes in eastern North America are often called eastern coyotes (Kays et al. 2010).

While there is a growing body of literature on the ecology of coyotes in the eastern United States, little is known is about the coyote population in Vermont. Coyotes are generally perceived to occupy all major habitats and range throughout the state (Vermont Fish and Wildlife Department 2018). Two notable studies have examined aspects of coyote ecology in Vermont. The first quantified the effects of coyote competition on smaller mesocarnivores such as foxes (*Vulpes vulpes* and *Urocyon cinereoargenteus*) and concluded that coyotes limit fox abundance and distribution in Vermont (Ingle 1990). The second study described coyote home range size and habitat use in the Champlain Valley (Person and Hirth 1991). Average adult home range size was 16.4 km^2 and coyotes utilized agricultural fields, coniferous and deciduous forests, with seasonal shifts in habitat preference (Person and Hirth 1991). No formal evaluation of coyote abundance in Vermont has occurred, yet precise information on abundance is needed to improve management of the species and understand its impacts on other game and non-game species in the state (Vermont Fish and Wildlife Department 2018).

Coyotes, like many other carnivores, typically occur at low densities, and are highly mobile, secretive, often nocturnal and generally wary of people (Bekoff 1977). As a consequence, estimation of population characteristics like abundance can be challenging. Common methods to estimate abundance include capture-mark-recapture surveys, population reconstruction from harvest records, hunter questionnaires, observational surveys, and home range analyses (Gese 2001). Capture-mark-recapture methods rely on identifying individuals from scats and require a large investment in scat surveys and genetic analyses, which are not always practical or cost-effective. Population reconstruction requires sex and age class information from harvested animals and is commonly used to estimate population sizes for game species. However, coyotes are hunted year-round, harvested animals are not always reported, and sex and age information is often absent from known harvest records. Hunter questionnaires provide a relative measure of the number of coyotes in a region. However, these estimates are often fraught with uncertainties. Similarly, observations of individuals (e.g., by camera traps or spotlight surveys) or spoor can yield a relative measure of abundance, but these measures are generally coarse and not suitable as a basis for management. The current estimate of coyotes in Vermont is 6,000 - 9,000 and was based on extrapolating abundance across the state based on average home range size (Vermont Fish and Wildlife 2018, Person and Hirth 1991).

An alternative approach to estimating abundance is the Royle-Nichols Abundance-Induced Heterogeneity Model (Royle and Nichols 2003). This model estimates abundance from detection/non-detection data that can be collected from a variety of methods, including camera trapping (Royle and Nichols 2003). The Royle-Nichols model estimates abundance by accounting for the detectability of the species (Royle and Nichols 2003). The approach requires relatively simple surveys (at least two at each site), is non-invasive, is not prone to errors associated with relative measures of abundance and is generally cost and time efficient (Royle and Nichols 2003, Jones 2011).

The goal of this study was to build a model that predicted coyote abundance in northwestern Vermont. My objectives were to: 1) collect detection/non-detection data from camera traps and build a Royle-Nichols model of site abundance that accounted for the influence of habitat and landscape variables, 2) use the model to map abundance across northwestern Vermont and 3) estimate the number of coyotes in five state management units. The model will allow mangers to estimate and evaluate the coyote population at varying spatial scales.

Methods

Study Area

The study area was located in the northwestern region of Vermont (Fig.1). The area covered 5,558 km^2 and included all or part of 7 counties (Addison, Chittenden, Franklin, Lamoille, Rutland, Washington and Windsor; Fig.1). The area is comprised primarily of forested and agricultural areas (Thompson and Sorenson 2000). Tree species characteristic of the region's low elevation forests include sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), red oak (*Quercus rubra*) and eastern white pine (*Pinus strobus*) (Thompson and Sorenson 2000). High elevation forests were characterized by species such as balsam fir (*Abies balsamea*) and red spruce (*Picea rubens*) (Thompson and Sorenson 2000). The study area was bounded in the west by Lake Champlain and in the east by the spine of the Green Mountains and included an elevation gradient that ranged from 30 to 1,340 m. Agriculture in the study area was mainly composed dairy farms, corn fields and apple orchards. The study area also encompassed several towns and the city of Burlington, which is the largest city in the state.

Surveys

I built the model using detection/non-detection data from three camera trap studies in the study area. The studies were conducted in the fall of 2008 (three surveys of 46 sites) (Williams, 2013), in the fall of 2011(three surveys of 21 sites) (L. Farrell unpublished data), and in the summer-fall of 2017 (2-3 surveys of 4 sites) (L. Beck in 2017). Each survey lasted at least three weeks and involved recording whether a coyote was detected (1) or not detected (0) at the survey site during the survey period. Detections were made by a single passive infrared camera trap (Gamespy D55IR, Moultrie Alabaster, Alabama, USA or Bushnell Advantage Cam, 8 MP Brown, Kansas, USA) at each survey site set approximately 0.6 m from the ground and baited with raw chicken and a scent lure (Craven's Gusto: Minnesota Trapline, Pennock, Minnesota, USA). Survey sites (i.e., camera trap locations) were spaced a minimum of 2.3 km apart; to ensure independence between the detections at each camera location. This distance represents the radius of the mean coyote home range reported by Person and Hirth (1991). Survey sites were located on land owned or managed by the University of Vermont, state and federal agencies, non-profit organizations, municipalities, and private individuals. Detection/non-detection data from all 71 sites was used in the analysis.

Modeling Approach

Coyote abundance was estimated using the Royle-Nichols Abundance-Induced Heterogeneity Model an occupancy model designed to estimate site abundance (Royle and Nichols 2003). The model uses multi-nominal maximum likelihood methods to estimate the probability that a given species occupies a site, using detection/non-detection data, and then estimates abundance for the site. The model accounts for imperfect detection when generating abundance probabilities at a site. Imperfect detection means that a species is present at a site, but not detected by the survey (MacKenzie et al. 2002). The model estimates a parameter for detection (c) and abundance (λ) and allows for the addition of covariates.

The modeling approach followed model selection procedures from Burnham and Anderson (2002). I developed a set of candidate models describing abundance and assessed their level of support using Akaike's Information Criterion (AIC). I considered a model with strong empirical support to have a Δ AIC ≤ 2 (Burnham and Anderson 2002). I developed a set of 9 candidate models that included site covariates I believed *a priori* most likely influenced coyote abundance in Vermont (Table 1). Eight of the models included the effect of a single covariate on the abundance parameter. The remaining model included no covariates and represented a null model. In the case that multiple models had strong empirical support, I model averaged by multiplying the parameter estimate (β or beta) by the weight of that given model. All analyses were performed using the program PRESENCE (V.4.4: J.E. Hines, Patuxent Wildlife Research Center, Laurel, Maryland, USA).

Covariates

Human activities are known to have a dramatic influence on the abundance and distribution of carnivores (Estes et al. 2011). To account for how human presence on the landscape affects coyote abundance, the proportion of developed land was included as a covariate (Table1). Coyotes are more tolerant of development than many other carnivore species and occur in high density in some urban areas such as Chicago, Illinois USA (Ghert et al. 2011). However, within Chicago, coyotes were found to have the lowest densities in the most highly developed areas (Ghert et al. 2011). Urban areas in Vermont do not appear to support large coyote populations (Vermont Fish and Wildlife 2018, Person and Hirth 1991). Vermont's relatively small urban centers may lack the diversity of cover necessary to support a high density of coyotes within the urban matrix. In addition, coyotes in Vermont are hunted year-round, so it seems logical that coyotes in mostly rural Vermont would avoid people and the structures humans heavily use. In the Adirondack region of New York, USA, coyote density was lower in areas of high road density, suggesting coyotes avoid areas of high human use (Kays et al. 2008). After considering the evidence, I predicted that in northwestern Vermont development would have a negative impact on coyote abundance (Table 1).

Given the prevalence of agriculture in northwestern Vermont, it is important to consider the influence of agricultural land cover on coyote abundance. Coyotes evolved in the predominately open environment of the Great Plains of Western North America (Gompper, 2002). It has been hypothesized that eastern coyote abundance would be greater in open areas, like agricultural fields and pasture, than in nearby forested landscapes (Crete et al. 2001). The evidence supporting greater coyote abundance in agricultural lands is not unequivocal. In Quebec, Canada researchers found that coyotes in agricultural areas had better body condition and occurred at greater densities than coyotes in forested environments (Richer et al. 2002). By contrast, another study from Quebec found that open landscapes (like agricultural fields) were not used at greater rates than expected based on their occurrence on the landscape (Crete et al. 2001). In the Adirondack Mountain of New York, USA, coyote abundance was found to be greater in forested landscapes, than in open rural environments (Kays et al. 2008). Person and Hirth (1991) found that in the Champlain Valley of Vermont, open areas, such as agricultural fields and pastures, were preferentially utilized in the summer and fall. Given the season when coyotes were found to preferentially use agricultural fields, it seems possible that coyotes increase their use of agricultural land when ripening crops are available for consumption and crops are possibly attracting prey species or providing cover. I predicted that agricultural land would have a positive effect on coyote abundance (Table 1).

Characteristics of the natural landcover and physical attributes of a landscape also influence the abundance and distribution of wildlife (Kays et al. 2008). Coyote abundance in the Adirondacks was found to be greater in areas that contained edges along waterways and wetlands than in solid forest blocks (Kays et al. 2008). Given the geographic proximity and ecological similarity between northwestern Vermont and the Adirondacks, it seemed likely that the edges created by water bodies and wetlands may also be important to determining how the coyote population is distributed across the Vermont landscape as well. Therefore, water and wetlands were combined as a single covariate for modeling and predicted to have a positive impact on coyote abundance (Table 1).

Forest cover can influence coyote abundance in several ways. In the Adirondacks coyote abundance was greater in areas with forest cover than in areas with other kinds of rural landcover (Kays et al. 2008). However, the same analysis found that abundance was greater in disturbed forest and forests containing natural edges, than it was in unbroken forest (Kays et al. 2008). In Vermont's Champlain Valley coyotes preferentially used forested habitat in the winter and spring, while open habitat was favored in the summer and fall (Person and Hirth 1991). In the Champlain Valley coniferous forest was utilized in proportion to its availability during the breeding season, gestation and the pup-rearing season, but that it was used less than expected during the pup-independence season (Person and Hirth 1991). Deciduous forests were used preferentially during the breeding, gestation and pup-rearing seasons (Person and Hirth 1991). Because both coniferous forest and deciduous forests were utilized by coyotes in Vermont, and that forested environments in Adirondacks were favored over other kinds of rural cover, I predicted that the proportion of coniferous forests, deciduous forests, and mixed forests would have a positive effect on coyote abundance (Table 1).

Because coyotes were historically restricted to mostly open habitat, I also included a model assessing the influence of shrub/scrub habitat on coyote abundance. Shrub/scrub habitat comprises only a small portion of the Vermont landscape, and as such, there is little information about how coyote abundance is impacted by shrub/scrub landcover. Coyotes in the Adirondack region were found to prefer disturbed forest over old growth forest (Kays et al. 2008). This may suggest that coyotes in the East have a preference for early successional habitats, such as disturbed forest and shrub/scrub. Lagomorphs and white-tailed deer (*Odocoileus virginianus*), both prey for coyotes, also frequently use early successional habitats (Fuller and DeStefano, 2003). Based on the available evidence and the coyote's evolutionary history, I predicted that shrub/scrub habitat would have a positive influence on coyote abundance (Table 1).

Another factor that may affect coyote abundance is competition from other carnivores (Levi and Wilmers 2012). The only carnivore in Vermont which seems likely have meaningful niche overlap with the coyote and the potential to displace coyotes is the bobcat (*Lynx rufus*). Both bobcats and coyotes have been found to consume white-tailed deer and snowshoe hare (*Lepus americanus*) in the northeastern United States (Major and Sherburne, 1987). Considering that coyotes and bobcats are probably competing for the same limited prey resources, I predicted that bobcat abundance would have a negative impact on coyote abundance in northwestern Vermont.

I calculated covariate values for each survey site with Geographic Information Systems software (ArcMap 10.5.1, Environmental Systems Research Institute Redlands, California, USA). The landcover and development covariate values were extracted from a dataset using multi-temporal Landsat imagery developed by Gudex-Cross et al. (2017) (Table 1). Bobcat habitat suitability was used a proxy for bobcat abundance, as no spatially explicit estimates of bobcat abundance exist for northwestern Vermont. I built a map (raster) of bobcat habitat suitability, using a model developed by Donovan et al. (2011) (Table 1). All covariate values were estimated at the scale of an average coyote home range in northwestern Vermont: a 2.3 km radius around a site (Person and Hirth 1991).

Estimating and Mapping Abundance

I mapped abundance by applying the final model on a pixel by pixel (size: 30 x 30 m) basis to covariate maps of the study area in ArcGIS. From this map, I calculated average abundance and the number of individuals in 5 state Wildlife Management Units that overlapped the study area (B, G, I, F1 and F2, Table 4).

Results

Coyotes were detected in 45% of occupancy surveys and at 47 of 71 sites, resulting in a naïve occupancy probability of 0.66. All eight models and the null model had strong empirical support based on their Δ-AIC value, so I model averaged (Table 2). The final averaged model included all 8 covariates (Table 3). The covariate with the strongest positive effect was shrub/scrub and the covariate with the strongest negative effect was coniferous forest (Table 3). Detection probability based on the averaged model was 0.42 (Table 3).

Site abundance across the study (when mapped at the pixel level) ranged from 1.28 to 1.46 (Fig. 2). The map indicated a gradient of decreasing abundance moving east from the shore of Lake Champlain toward the spine of the Green Mountains (Fig. 2). However, even in the Green Mountains (where abundance is generally lower) the lowest site abundance still exceeded 1.2 (Table 5). The greatest site abundance, found near the shore of Lake Champlain, exceeded 1.4 coyotes per average home range area. The greatest coyote abundance was in WMU B, while the lowest abundance was in WMU I (Table 4). The model predicted the greatest coyote density occurs in WMU F1 and the lowest density occurred in WMUs G and I (Table 4). The borders of the raster predicting abundance do not correspond perfectly to the borders of the WMUs, therefore the abundance values reported reflect the area covered by the raster not the entirety of each WMU (Fig. 2 and Table 4). The raster covers 90.08% of the area covered by WMUs B, G, I, F1 and F2. The site with the greatest abundance estimate occurred in WMU B, while the site with the lowest abundance estimate occurred in WMU I (Table 5).

Discussion

The null model was the best supported among my candidate models. The null model assumes that coyotes are randomly distributed across the landscape and that detection is solely a product of abundance and inherent detectability. The high level of support for the null model, along with the high values of estimated site abundance across the study area, provides evidence that coyotes in northwestern Vermont are utilizing a wide variety of terrestrial habitat types within the state. Based on the results of my model it appears that the adaptability of the coyote has not only enabled them to make use of a wide variety of habitats at a continental scale (found in every U.S. State except Hawaii), but also at local scales within a single region.

The model predicted that coyote abundance was greatest in the western part of the study area adjacent to Lake Champlain. The high abundance in the western part of the study area reflects the close proximity to water, high proportion of agricultural lands and mixed forest, and the low proportion of highly suitable bobcat habitat. In the east of the study area, the lower abundance estimates reflect the relatively greater proportions of deciduous forest, coniferous forest, and highly suitable bobcat habitat. Though the model predicts a negative impact of development on coyote abundance, a higher proportion of the landscape is developed in the western portion of the study area, where coyote abundance is high. The candidate model for development was the second least supported model in the model set, therefore the negative impact on abundance of the greater development in the west was offset by the higher occurrence of covariates with a positive impact on coyote abundance.

Among the site covariate candidate models, the model for water/wetlands had the greatest amount of empirical support and was found to have a positive impact on coyote abundance. Kays et al. (2008) found that coyotes in the Adirondacks, were present in greater numbers in forest containing natural edges along water bodies than in solid forest blocks. The edges created by water and wetlands may facilitate coyote foraging success, as coyotes have been found to be more efficient at foraging in open than closed environments (Richer et al. 2002).

My model also predicted that agriculture has a positive impact on coyote abundance. Characterizations of the relationship between agricultural land cover and eastern coyote ecology have been ambiguous, with some studies reporting a positive association between coyotes and agriculture and others the opposite. For example, Richer et al. (2002) found that coyotes in Quebec have better body condition and attain greater densities in agricultural environments than in forested environments, because in their study coyotes were found to be more effective predators in the open environment provided by agricultural fields. In contrast, coyotes in the Adirondack Mountains were found in greater densities in forested habitats than in rural open areas (Kays et al. 2008). Several studies found that both agricultural fields and forest cover are suitable habitat. In the Champlain Valley coyote use of forested and open agricultural habitat differed by season, with forested cover being preferred in the winter and spring and open agricultural land in the summer and fall (Person and Hirth 1991). While a second study in Quebec found that coyotes did not preferentially select for agricultural fields or forest habitats, but used both in accordance with their proportion on the landscape (Crete et al. 2001). In North Carolina, USA, both agricultural and forested lands were included in coyote home ranges, but agriculture fields were used at a greater frequency than their availability in the landscape (Hinton et al. 2015). The evidence from the model and the literature suggests that coyotes may utilize both agricultural and some forested habitats to sustain themselves on the landscape. Agricultural fields may provide important food resources to coyotes (as noted in Quebec by Richer et al. 2002), while forested environments provide refuge. Person and Hirth (1991) noted that coyotes made more frequent use of forested habitat during pup-rearing season and more use of open agricultural areas when the pups were independent. The finding may reflect a more general pattern that forested environments are used at times when refuge is prioritized, and agricultural fields when foraging is prioritized. The western proportion of the study area contains a greater proportion of agriculture than the east, but the west also still contains substantial forest cover. However, a greater proportion of the forest in west of the study area than the in east, is the mixed forest cover my model predicts has a positive influence on coyote abundance. Based on the model outputs and previous studies, it seems likely that coyote abundance in northwestern Vermont is greatest in areas with both agricultural fields and a mixed forest cover.

I found that coyote abundance was greater in areas with shrub/scrub habitat. Shrub/scrub habitat is important in the northeastern US for several species on which coyotes prey, especially lagomorphs, but also white-tailed deer and smaller rodents (Fuller and DeStefano, 2003). Shrub/scrub habitat makes up only a small percentage of the landcover in the study area and Vermont in general, therefore it seems unlikely that the availability of shrub/scrub habitat has a major influence coyote abundance at the scale of Wildlife Management Units. However, shrub/scrub habitat may be an important landscape feature for coyotes at the home range scale.

The Vermont Fish and Wildlife Department reported that following the colonization of Vermont by coyotes the bobcat population has declined (2018). The Department attributes the decline in bobcat numbers to coyotes detecting and consuming kills cached by bobcats (2018). Donovan et al. (2011) found that bobcats in Vermont were positively associated with coniferous forest and negatively associated with agriculture. The model results suggest the possibility that coyotes may to some degree suppress bobcats in deciduous forest, mixed forest and agricultural lands. Whether coniferous forest has a negative impact on coyote abundance because coniferous forests are less suitable for coyotes, or because bobcats are the dominant competitor in coniferous forests, is beyond the scope of the analysis conducted here, but an area for further study.

The abundance estimates I generated based on my model are substantially lower, than those estimated by the Vermont Fish and Wildlife Department. I estimated a total of 457 coyotes in my study area. If the density of coyotes were uniform across the state, my estimate yields a total state-wide population of 1,216 coyotes. The Vermont Fish and Wildlife Department estimates the state's coyote population at 6,000 to 9,000 animals (Vermont Fish and Wildlife 2018). The Vermont Fish and Wildlife Department abundance estimate may be greater than mine, as the methods used by the Department seem likely to overestimate coyote abundance. The Vermont Fish and Wildlife Department estimate was primarily informed by extrapolating from the Person and Hirth (1991) study of coyote home ranges and habitat use in Champlain Valley (Vermont Fish and Wildlife Department, 2018). The study reported a mean home range size of 16.4 km^2 for resident adult coyotes using a minimum convex polygon home range estimator, based on VHF radio-telemetry data from 11 coyotes (Person and Hirth 1991). While Person and Hirth (1991) provided the only previously available information on coyote density in Vermont, simply extrapolating from the reported density is unlikely to generate an accurate abundance estimate, as the estimate does not incorporate how abundance or density vary relative to environmental factors across the landscape. The Person and Hirth (1991) study was also limited to the Champlain Valley. My model and other evidence points to the Champlain Valley being the area of Vermont likely to have relatively high coyote abundance (Hinton et al. 2015, Richer et al. 2002). In my model, the WMUs in the Champlain Valley (B, F1 and F2), had the highest mean estimated site abundance, and the highest minimum and maximum estimated site abundance.

Across North America typical coyote home ranges have been reported to vary between 2.5 and 70 km^2 (Hinton et al. 2015). The home range estimate from the Person and Hirth (1991) study is therefore on the small side of the reported range. The small home range size found in the study, aligns with the model's prediction that the Champlain Valley is a relatively high-density area for coyotes.

Prior studies support the likelihood that coyote density would likely be greater and home range size smaller in the more agricultural Champlain Valley than the rest of the state. For example, a North Carolina study reported that coyotes home range size was negatively correlated with agriculture (Hinton et al. 2015) and in Quebec coyotes in an agricultural setting were found to occur at higher densities than in forested areas (Richer 2002). Though the Person and Hirth (1991) study provides the best estimate of coyote home range size in Vermont, it seems likely that the study represents the portion of the state where coyote densities are likely to be greatest. Therefore, estimating the Vermont coyote population by extrapolating from the Person and Hirth (1991) study is likely to overestimate coyote abundance in Vermont. An accurate estimate of abundance will require understanding how abundance varies across the Vermont landscape. The Royle-Nichols Abundance-Induced Heterogeneity model presented here provides a tool for assessing how coyote abundance varies across the northwestern Vermont landscape and accounts for the effect of different habitat conditions. The model also provides a measure of precision (SE) for each parameter, which aids in interpreting predictions.

It is important to acknowledge the limitations of the model. One obvious limitation is that the model only generates abundance predictions for the area covered by the rasters that informed the covariate values. Coyotes are an extremely adaptable species and they may use resources differently across their range (Ellington and Murray 2015). Therefore, using the results of the model presented here to draw conclusions for regions outside the geographic scope of the model must be done with caution. The accuracy of the model is likely limited by the small number of camera traps sites (n=71). Increasing the number of sites would likely increase the precision of the model. Another limitation of the model is that the Royle-Nichols Abundance-Induced Heterogeneity Model is a single season model, but the model presented here was based on three different years of data. I am assuming that between 2008 and 2017 the environmental conditions governing coyote abundance and distribution have not changed significantly. The model was also built using data from occupancy surveys conducted in the summer and fall. Therefore, the model is presumably most accurate at predicting abundance for the summer and fall season. In the Champlain Valley in Vermont, coyote habitat use was found to change seasonally; however, on average the home range of an individual coyote overlapped 85% (± 3.3 SE) between the denning and non-denning season (Person and Hirth 1991). Therefore, the model presented here does not likely differ substantially from a model developed using detection/non-detection data collected across seasons. A limitation inherent to the Royle-Nichols Abundance-Induced Heterogeneity Model, is that it is quite difficult to validate the model without numerous and repeated surveys of coyote abundance.

Despite these limitations, the distribution of coyote abundance in northwestern Vermont projected by the model is ecologically plausible according to current literature regarding habitat use by eastern coyotes. The model presented here provides a starting point for a better understanding of how coyote abundance varies with environmental conditions in northwestern Vermont. This knowledge is essential for making informed management decisions regarding one of Vermont's top predators.

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References

Bekoff, M. 1977. *Canis latrans*. Mammalian Species 79:1-9.

Berger, J., Stacey, P. B., Bellis, L. & Johnson, M.P. 2001. A mammalian predator-prey imbalance: grizzly bear and wolf extinction affect on avian neotropical migrants. Ecological Applications 11:947-960.

Burnham, K., & Anderson, D.R., 2002. Model selection and multimodel inference: A practical information-theoretic approach. Second edition. Springer, New York, USA.

Crete, M., Ouellet, J.-P., Tremblay, J.-P., & Arsenault, R. 2001. Suitability of the forest landscape for coyotes in northeastern North America and its implications for coexistence with other carnivores. Ecoscience 8:311-319.

Crooks, K. R., & Soulé, M. E. 1999. Mesopredator release and avifaunal extinctions in a fragmented system Letters to Nature 400:563-566.

Donovan, T. M., Freeman, M., Abouelezz, H., Royar, K., Howard, A., & Mickey, R. 2011. Quantifying home range habitat requirements for bobcats (*Lynx rufus*) in Vermont, USA. Biological Conservation 144:2799-2809.

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., Carpenter, S. R., Essington, T. E., Holt, R. D., Jackson, J. B. C. , Marquis, R. J., Oksanen, T., Paine, R. T., Pikitch, E.K., Ripple, William J., Sandin, S. A., Scheffer, M.,Schoener, T.W., Shurin, J.B., Sinclair, A. R. E., Soule, M. E., Virtanen, R., & Wardle, D. A. (2011). Trophic downgrading of planet earth. Science 333:301-306.

Ellington, E. H., & Murray, D. L. 2015. Influence of hybridization on animal space use: A case study using coyote range expansion. Oikos 124:535-542.

Fuller, T. K., & DeStefano, S. 2003. Relative importance of early-successional forests and shrubland habitats to mammals in the northeastern United States. Forest Ecology and Management, 185:75-79.

Gehrt, S. D., Brown, J. L., & Anchor, C. 2011. Is the urban coyote a misanthropic synanthrope? The case from Chicago. Cities and the Environment, 4, Article 3.

Gese, E.M. 2001. Carnivore conservation. Chapter 17, Monitoring of terrestrial carnivore populations. 372-396. Cambridge University, Cambridge, England.

Gompper, M. E. 2002. Top carnivore in the suburbs? Ecological and conservation issues raised by colonization north-eastern North America by coyotes: The expansion of the coyote's geographical range may broadly influence community structure, and rising coyote density in the suburbs may alter how the general public views wildlife. Bioscience 52:185-190.

Gudex-Cross, D., Pontius, J. & Adams, A. 2017. Enhanced forest cover mapping using spectral unmixing and object-based classification of multi-temporal Landsat imagery. Remote Sensing of Environment 196:193-204.

Harrison, D. J., & Chapin, T. G. 1998. Extent and connectivity of habitat for wolves in eastern North America Wildlife Society Bulletin 26:767-775.

Hinton, J. W., van Manen, F. T., & Chamberlain, M. J. 2015. Space use and habitat selection by resident and transient coyotes (*Canis latrans*). PLoS ONE 10: e0132203.

Ingle, M.A. 1990. Ecology of red foxes and gray foxes and spatial relationships with coyotes in an agricultural region of Vermont. Master of Science thesis, University of Vermont, Burlington, Vermont, USA.

Jones, J.P.G. 2011. Monitoring species abundance and distribution at the landscape scale. Journal of Applied Ecology 48:9-13

Kays, R., Curtis, A., & Kirchman, J. J. 2010. Rapid adaptive evolution of northeastern coyotes via hybridization with wolves. Biology Letters 6:89-93.

Kays, R. W., Matthew, G. E., & Ray, J. C. 2008. Landscape ecology of coyotes based on large-scale estiamtes of abundance. Ecological Applications 18:1014-1027.

Levi, T., & Wilmers, C. C. 2012. Wolves-coyotes-foxes: a cascade among carnivores. Ecological Society of America 93:921-929.

MacKenzie D. I., Nichols J. D., Lachman G. B., Droege S., Royle J. A. and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83:2248-2255.

Major, J. T., & Sherburne, J. A. 1987. Interspecific relationships of coyotes, bobcats, and red foxes in western Maine. Journal of Wildlife Management 51:606-616.

Person, D. K., & Hirth, D. H. 1991. Home range and habitat use of coyotes in a farm region of Vermont. Journal of Wildlife Management 55:433-441.

Richer, M.-C., Crete, M., & Ouellet, J.P. 2002. The low performance of forest versus rural coyotes in northeastern North America: Inequality between presence and availability of prey. Eco Science 9:44-54.

Ripple, W. J., Larsen, E. J., Renkin, R. A., & Smith, D. W. 2001. Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. Biological Conservation 102:227-234.

Ritchie, E. G., Elmhagen, B., Glen, A. S., Letnic, M., Ludwig, G., & McDonald, R. A. 2012. Ecosystem restoration with teeth: what role for predators? Trends in Ecology and Evolution 27:265-271.

Royle, J. A., & Nichols, J. D. 2003. Estimating abundance from prepared presence-absence data or point counts. Ecology 84:777-790.

Thompson, E. H., & Sorenson, E. R. 2000. Wetland, woodland, wildland: A guide to the natural communities of Vermont. The Nature Conservancy and the Vermont Fish and Wildlife Department. Hanover, New Hampshire, USA.

Treves, A., & Karanth, K. U. 2003. Human-carnivore conflict and perspectives on carnivore management worldwide. Conservation Biology, 17:1491-1499.

Vermont Fish and Wildlife Department. 2018. Vermont Coyote Population Report. Report submitted by Louis Porter to the Vermont Legislature House Committee on Natural Resources, Fish and Wildlife and the Senate Committee on Natural Resources and Energy.

Williams, S.H. 2013. Factors affecting fisher occupancy in forest fragments of an agricultural landscape. Master of Science thesis, University of Vermont, Burlington, Vermont, USA.

Tables

Table 1. Description of covariates used to model coyote (*Canis latrans*) abundance (λ) in northwestern Vermont. Covariate values were measurer either as the proportion of pixels containing a covariate feature, or as the mean value of the pixels within an average coyote home range (area = 16.4 km^2, radius = 2.3 km; from Person and Hirth 1991) of a site.

Covariate Name	Covariate Description	Unit of Measurement	Predicted Effect on λ	Data Source
Water	Water bodies and wetlands	Proportion	Positive	Gudex-Cross et al. (2017)
Deciduous	Forested areas where the canopy is more than 75% deciduous tree species	Proportion	Positive	Gudex-Cross et al. (2017)
Agriculture	Areas of crop cultivation or hay and pasture	Proportion	Positive	Gudex-Cross et al. (2017)
Coniferous	Forested areas where the canopy is more than 75% coniferous tree species	Proportion	Positive	Gudex-Cross et al. (2017)
Bobcat HSI	Habitat Suitability Index for bobcats (*Lynx rufus*) in Vermont	Mean	Negative	Donovan et al. (2011)
Shrub/scrub	Areas dominated by shrubs; with shrub canopy typically greater than 20% of total vegetation.	Proportion	Positive	Gudex-Cross et al. (2017)
Development	Landscapes intensively sculpted for human use (e.g. cities, neighborhoods, parking lots, golf courses, roads)	Proportion	Negative	Gudex-Cross et al. (2017)
Mixed	Forested areas where both deciduous and coniferous trees are present and neither comprises more than 75% of the canopy	Proportion	Positive	Gudex-Cross et al. (2017)

Table 2. Model selection results for coyote (*Canis latrans*) abundance (λ) based on detection/non-detection data from camera trap surveys conducted in 2008, 2011, and 2017 in northwestern Vermont. Each model included the effect of one covariate on λ and no covariates on detection (c).

Model	AIC	Δ-AIC	Weight	K
λ(.),c(.)	268.04	0.00	0.2308	2
λ(Water),c(.)	269.44	1.40	0.1146	3
λ(Deciduous),c(.)	269.50	1.46	0.1112	3
λ(Agriculture),c(.)	269.71	1.67	0.1001	3
λ(Coniferous),c(.)	269.80	1.76	0.0957	3
λ(BobcatHSI),c(.)	269.95	1.91	0.0888	3
λ(Shrub/scrub),c(.)	270.00	1.96	0.0866	3
λ(Development),c(.)	270.01	1.97	0.0862	3
λ(Mixed),c(.)	270.02	1.98	0.0858	3

Table 3. Beta, standard error and weighted beta values for each covariate in the averaged Royle-Nichols Abundance-Induced Heterogeneity Model of coyote (*Canis latrans*) abundance in northwestern Vermont.

Parameter	Covariate Name	Beta	SE	Weighted Beta (Beta*AIC weight)
λ:	Intercept	0.315	0.284	0.073
	Water	0.629	0.775	0.072
	Deciduous	-0.570	0.791	-0.063
	Agriculture	0.563	0.976	0.056
	Coniferous	-0.894	1.854	-0.086
	Bobcat HSI	-0.353	1.217	-0.031
	Shrub/scrub	1.614	8.885	0.140
	Development	-0.196	1.141	-0.017
	Mixed	0.175	1.383	0.015
Detection:	Intercept	-0.311	0.327	

Table 4. Coyote (*Canis latrans*) density and abundance estimates in Vermont Fish and Wildlife Department Wildlife Management Units (WMU) in the study area. Values calculated from the predictions of a Royle-Nichols Abundance-Induced Heterogeneity Model of abundance applied on a pixel by pixel (30 x 30 m) basis in each area. Each pixel value represented the number of coyotes predicted within 1 home range (area = 16.4 km^2, radius = 2.3 km; from Person and Hirth 1991) surrounding each pixel.

WMU	Area (km^2)	Mean Density/km^2 (± SD)	Abundance Estimate
B	1786.81	0.083 (± 0.019)	147.64
FI	964.71	0.085 (± 0.013)	82.26
F2	775.19	0.083 (± 0.013)	64.68
G	1062.54	0.080 (± 0.007)	85.15
I	969.00	0.080 (± 0.007)	77.47
Combined	5558.25	0.082 (± 0.022)	457.19

Table 5. Coyote (*Canis latrans*) site abundance values within each Vermont Fish and Wildlife Department Wildlife Management Unit (WMU) in the study area. Raster area does not correspond perfectly with WMU area. Values calculated from predictions of a Rolye-Nichols Abundance Induced Hetrogeneity Model of abundance within the spatial scale of an average coyote home range (2.3 km radius around the pixel; from Person and Hirth 1991).

WMU	Area (km^2)	Site Min.	Site Max.	Site Mean	SD
B	1786.81	1.29	1.46	1.36	0.03
FI	964.71	1.34	1.46	1.40	0.02
F2	775.19	1.30	1.42	1.37	0.02
G	1062.54	1.29	1.37	1.31	0.02
I	969.00	1.28	1.34	1.31	0.02
Combined	5558.25	1.28	1.46	1.35	0.04

Figures

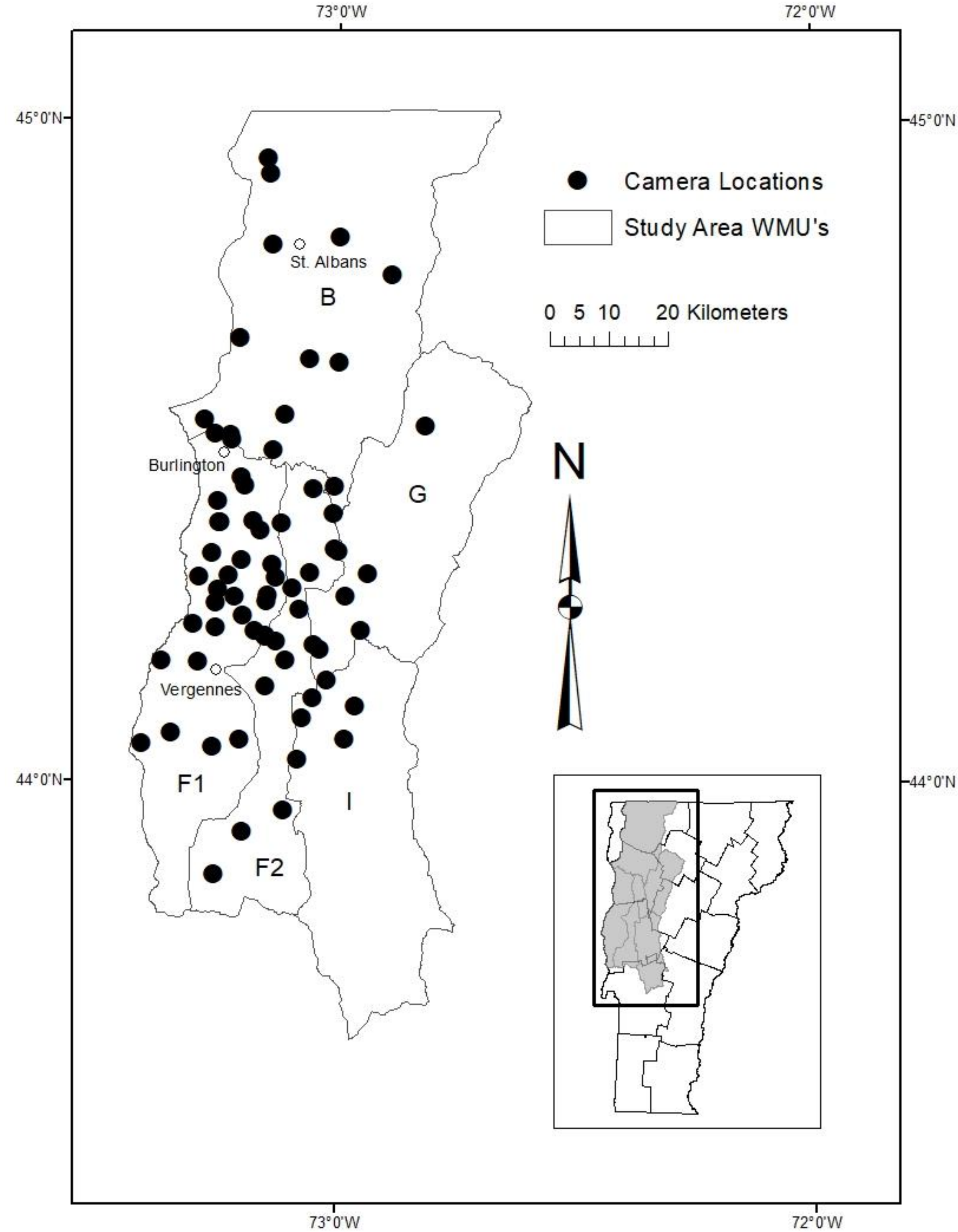


Figure 1. Map of the study area, Wildlife Management Units, and camera trap sites in northwestern Vermont used to survey coyote (*Canis latrans*) abundance. The sites were surveyed in the fall of 2008, and 2011, and summer-fall of 2017.

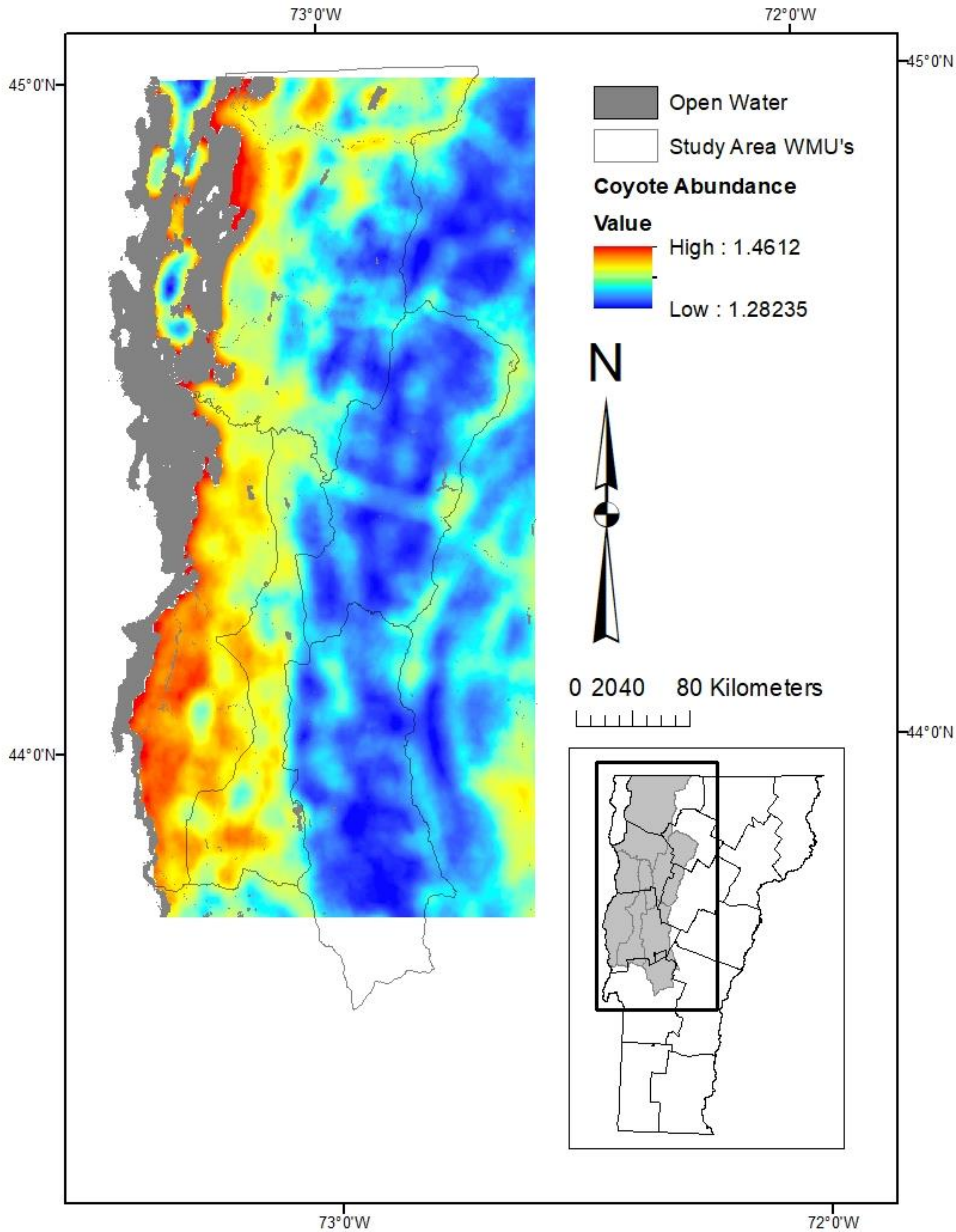
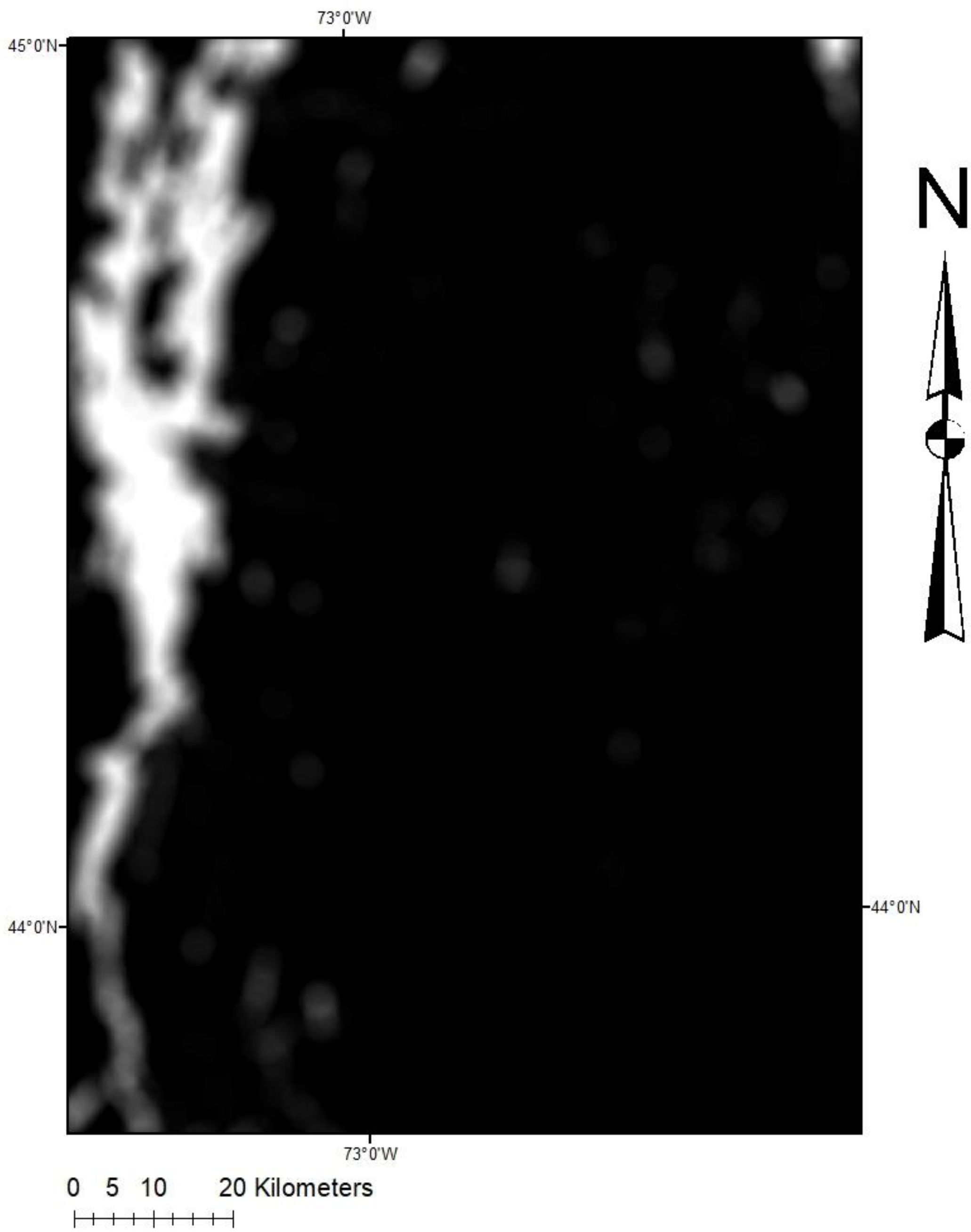


Figure 2. Map of coyote (*Canis latrans*) abundance across the study area in northwestern Vermont. Abundance values estimated from a model averaged Royle-Nichols Abundance-Induced Heterogeneity Model based on detection/non-detection data collected from camera traps in 2008, 2011 and 2017. Values for each pixel represent the number of individuals occurring within an average home range surrounding the pixel (2.3 km radius).

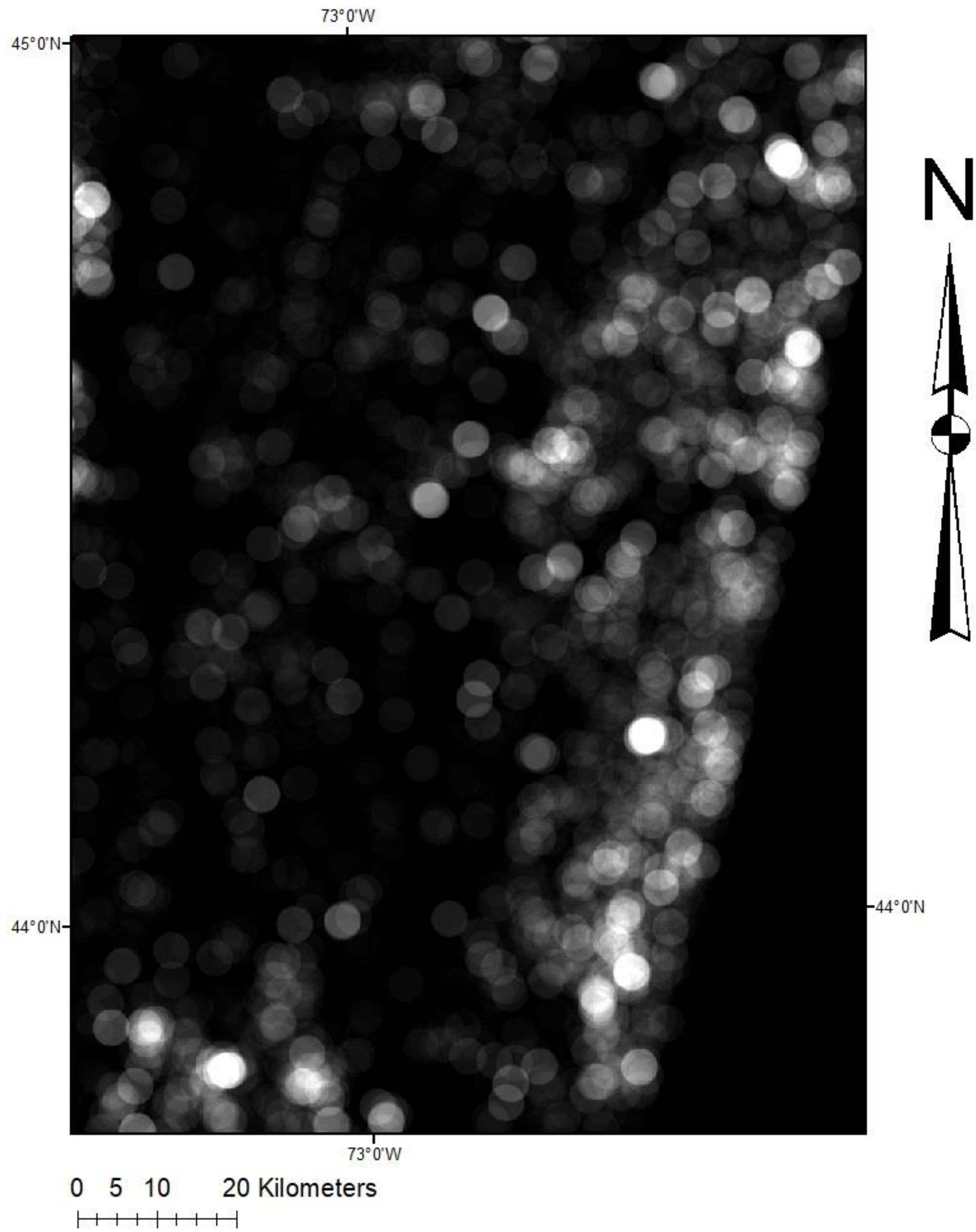
Appendices

Appendix 1. Maps (rasters) of each covariate used to model coyote abundance in northwestern Vermont. Values range from high (white) to low (black). For descriptions of each model covariate see Table 1.

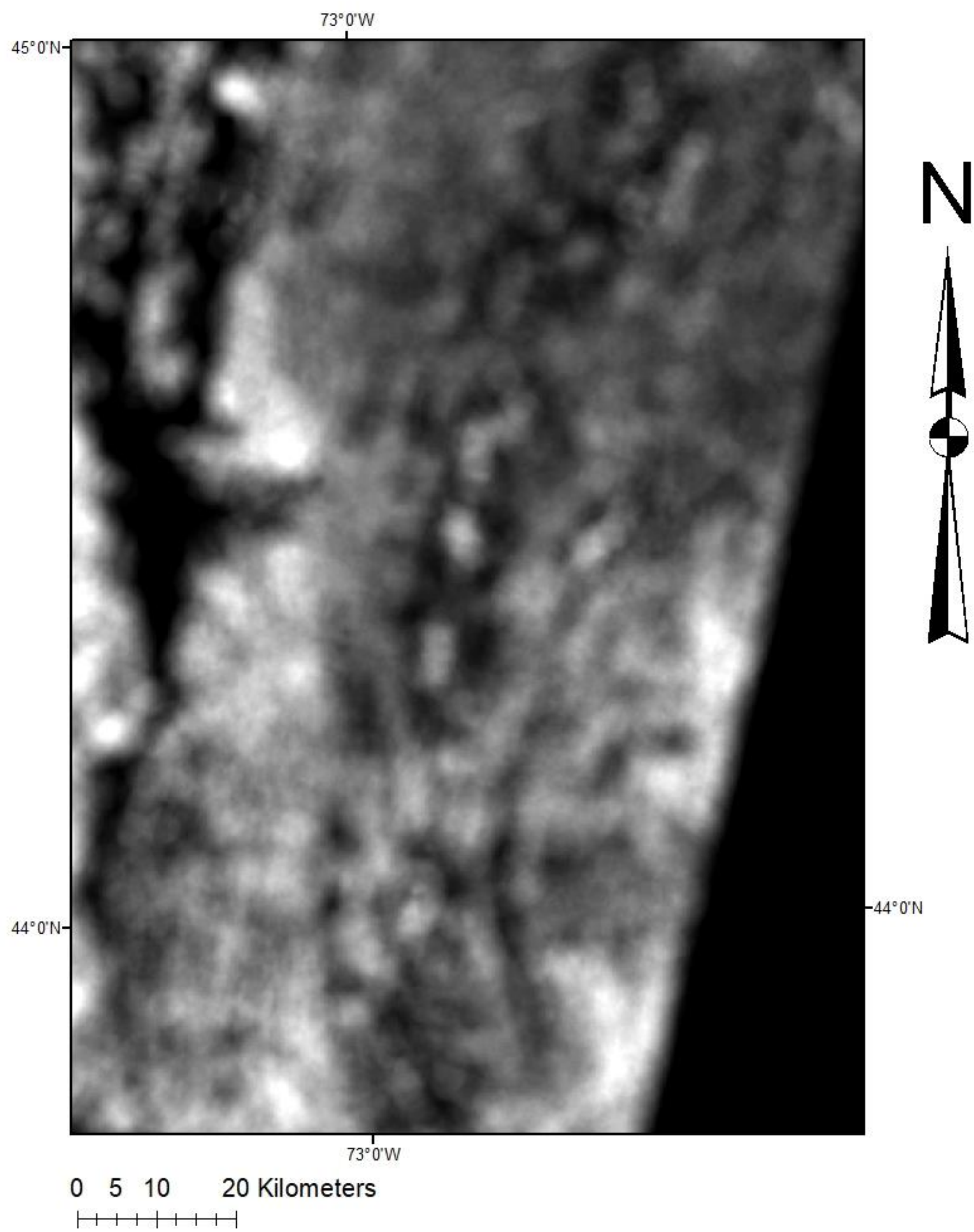
Water Raster



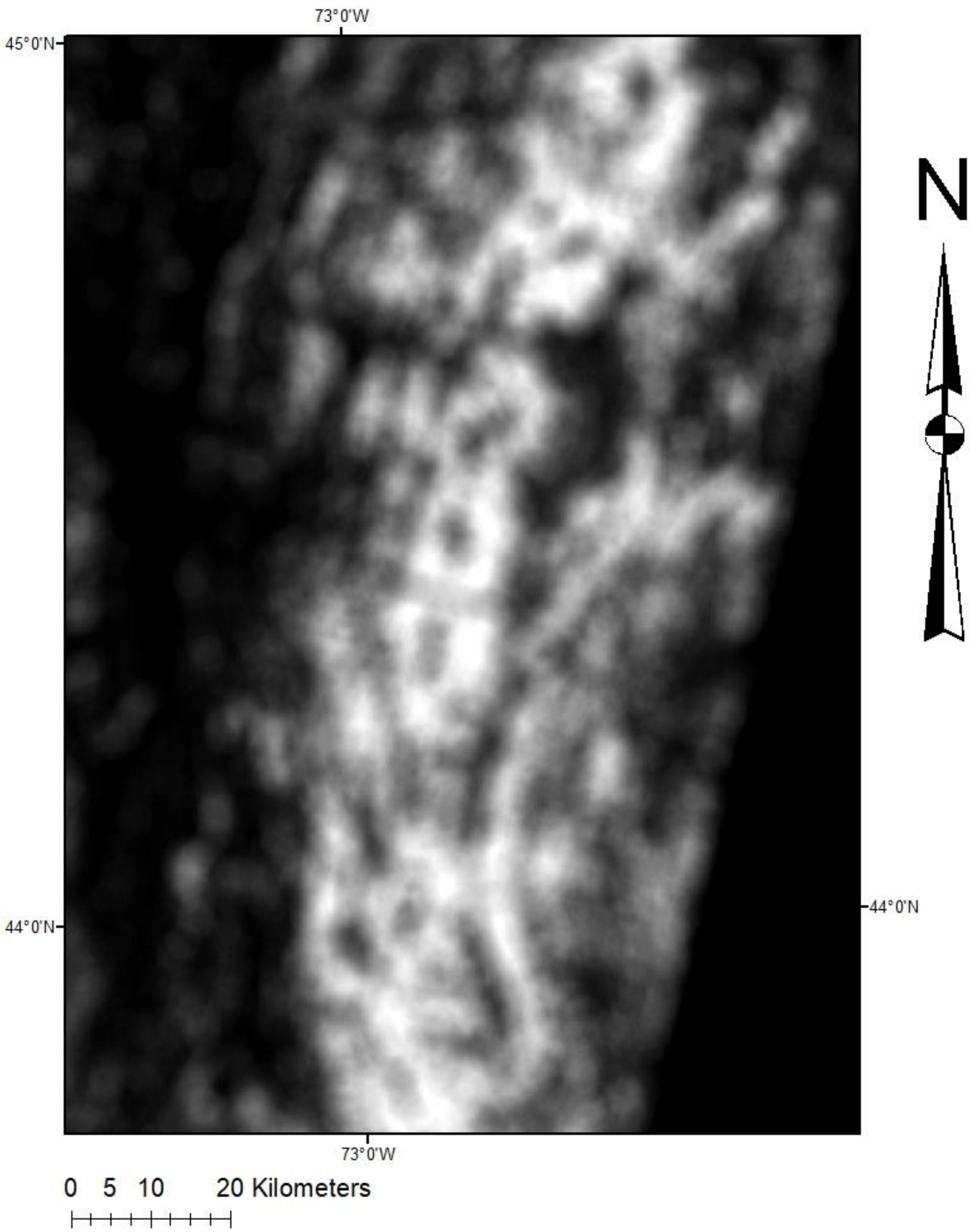
Shrub/scrub Raster



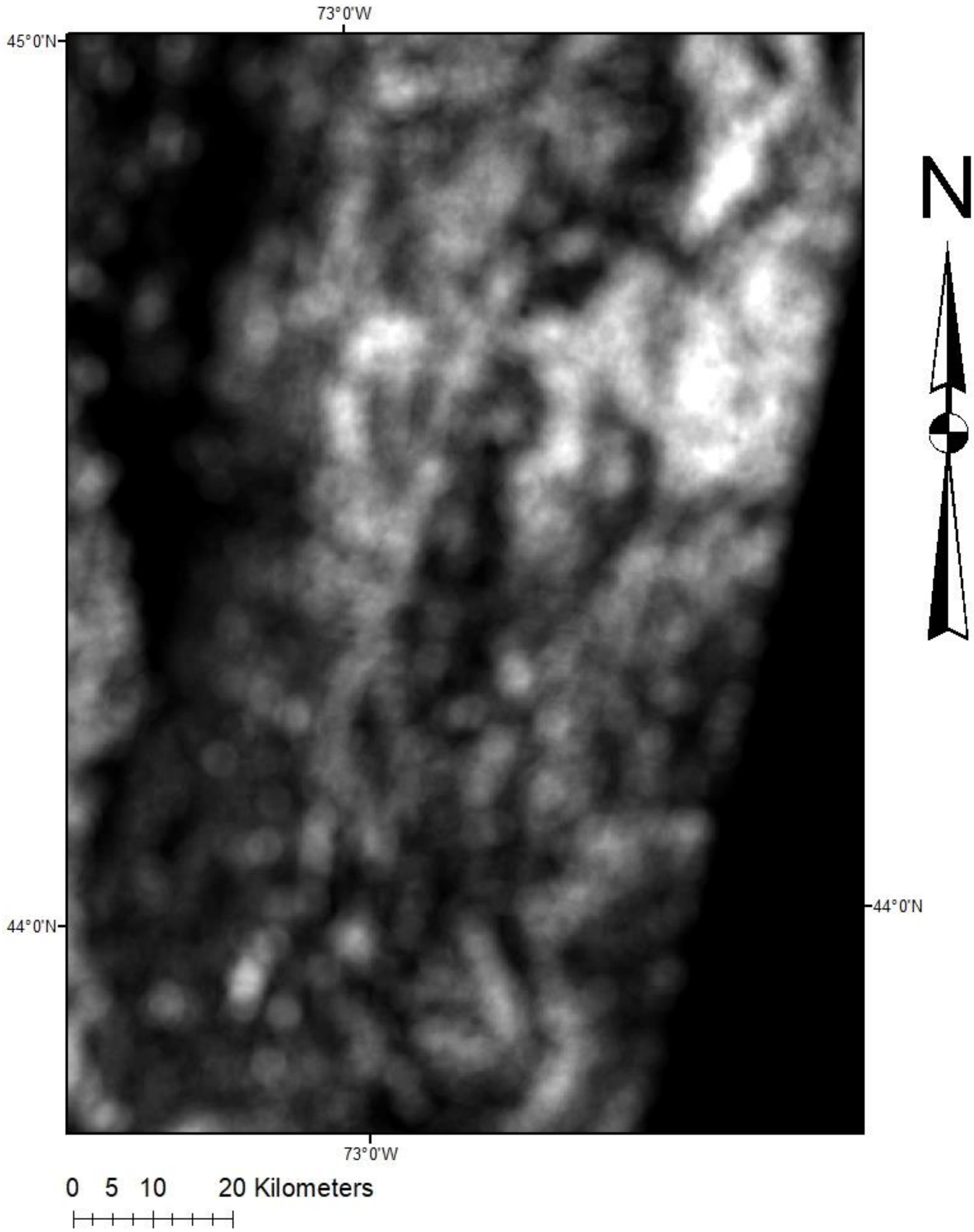
Mixed Raster



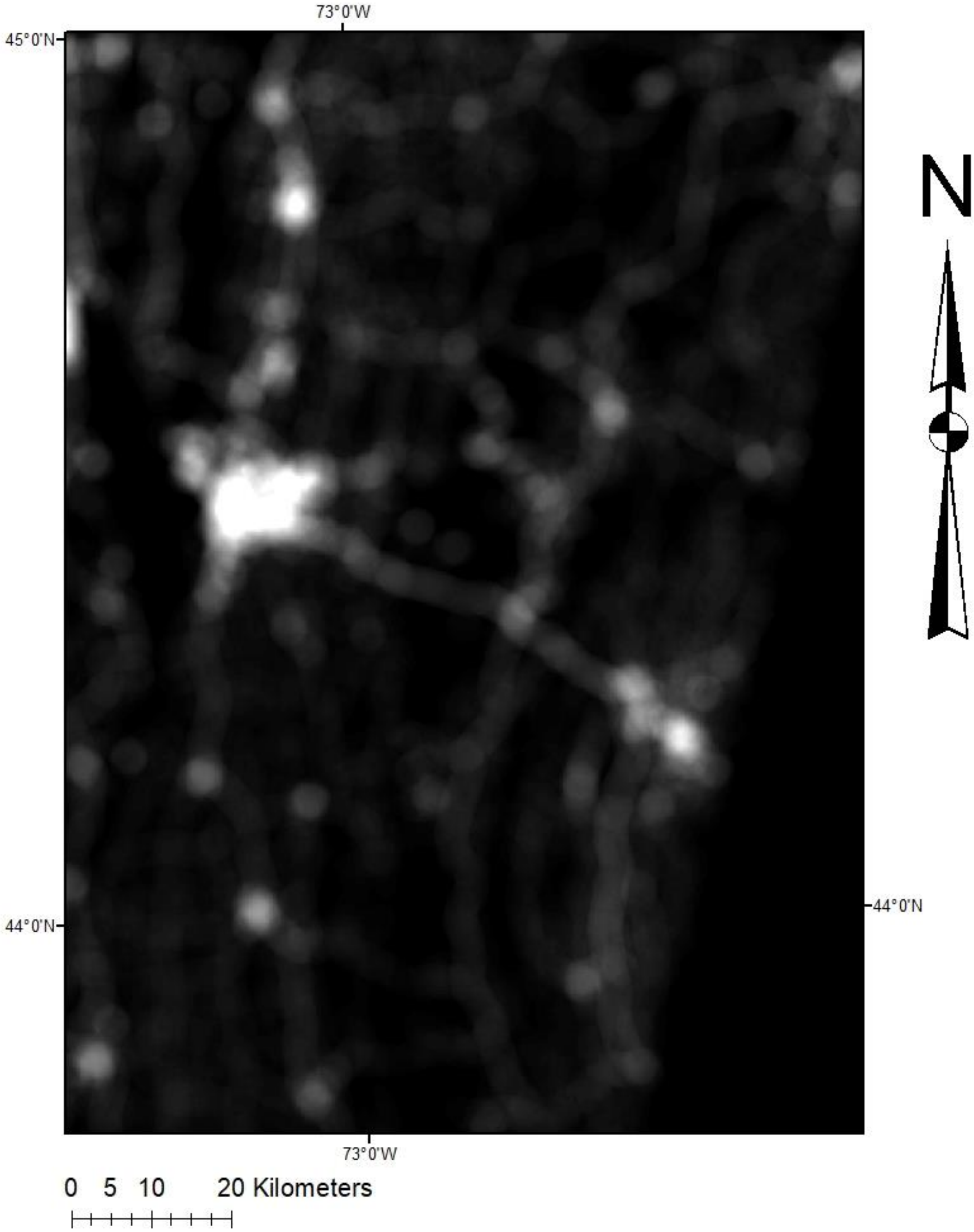
Deciduous Raster



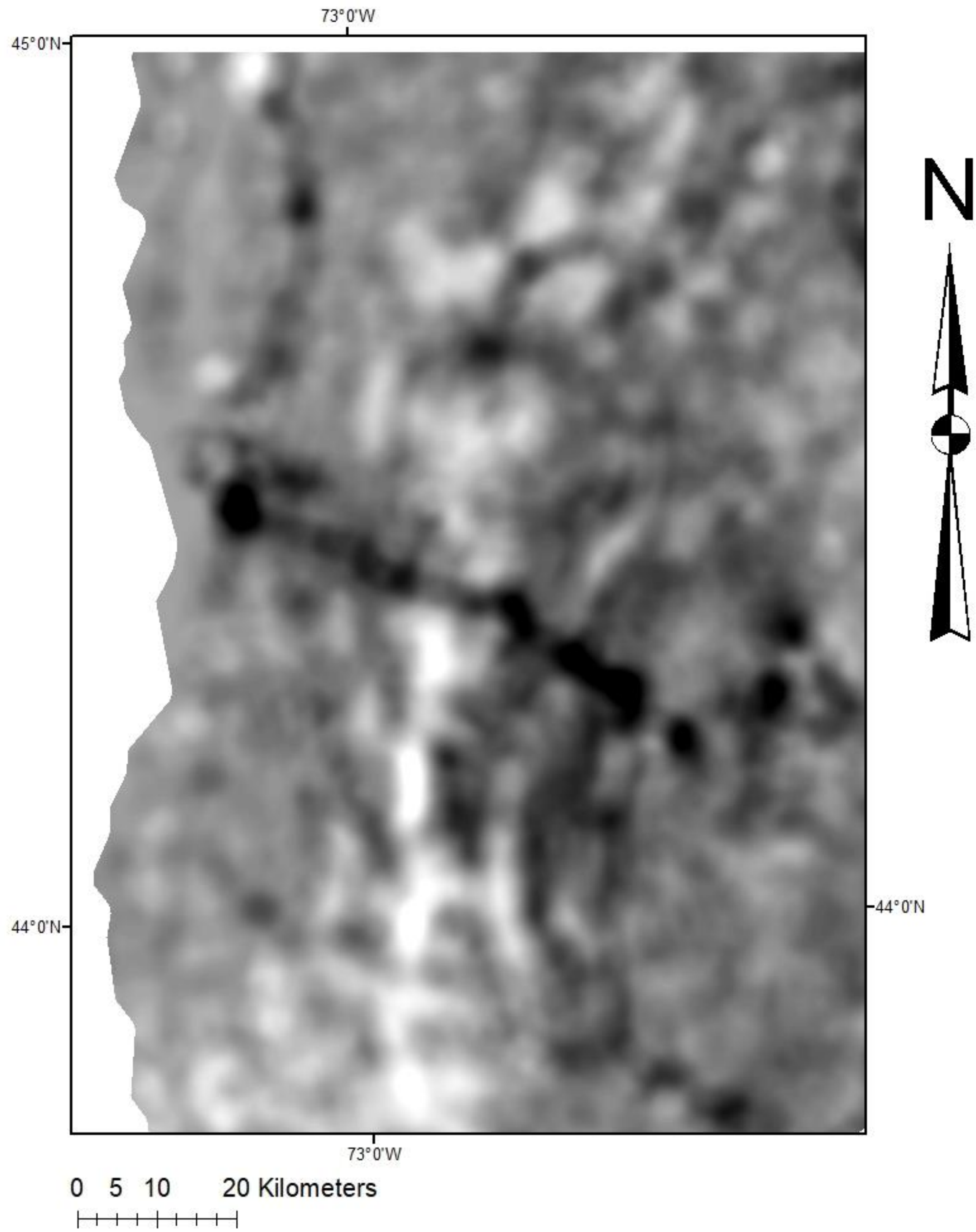
Coniferous Raster



Development Raster



Bobcat Habitat Suitability Raster



Agriculture Raster