

A Habitat Suitability Analysis for Cougar (*Puma concolor*) in Minnesota

A Thesis
SUBMITTED TO THE FACULTY OF
UNIVERSITY OF MINNESOTA
BY

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IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF
MASTER OF SCIENCE
in
Conservation Biology

Stephen Polasky, Ph.D.

November, 2013

Acknowledgements

I would first like to thank my advisor, Dr. Stephen Polasky, for the vast amounts of time, patience and guidance he offered over the years it took to develop and complete this project. I would like to thank Dr. L. David Mech (“Dave”) for his insight into the ecology of large carnivores and ceaseless words of encouragement, and many thanks to Dr. Steven Manson for his willingness to join my committee and for his help with the GIS and MCE portions of this project. I would like to thank J. Seidensticker, K. Murphy, P. Beier, G. Koehler and T. Ruth for sharing their expertise and knowledge at several points along the way, and thanks to J. Erb, M. Grund, J. Abraham and D. Garshelis for providing the data without which the project would not have succeeded.

I am grateful for the support and encouragement of friends and family who never stopped believing in me and my ability to see this project through to the end.

Finally, I cannot begin to truly express my gratitude to my fiancée, Guy, who has been by my side for much of this project, sharing in my frustrations and celebrating the little victories. I am grateful for his support and his endless supply of humor, encouragement, and patience.

Dedication

To Mom: You were right.

Abstract

Cougars are spreading eastward from established source populations in western states such as Montana, Wyoming, and Colorado as well as from more recently established populations in North and South Dakota. Over the last several years, dozens of sightings of individual cougars have been confirmed as far east as Minnesota, Wisconsin, and the Upper Peninsula of Michigan. Cougars employ a land-tenure system in which resident adults establish home ranges in high quality habitat. Sub-adult dispersers utilize marginal and lower quality habitats as they move through an area. Dispersing animals eventually establish home ranges in areas with available mates, a supply of vulnerable prey, and suitable cover for hunting.

I created a habitat suitability model to identify potential cougar habitat in Minnesota. I created and analyzed land cover, road density, and deer density data sets, and combined these to determine the location and amount of suitable cougar habitat available in the state. There are nearly 56,600 km² of ideal habitat in Minnesota, as well as moderate amounts of modified and semi-suitable habitat that could be used as corridors by dispersing individuals.

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Introduction

The cougar (*Puma concolor*) was once found throughout much of North and South America including nearly all terrestrial ecosystems in the United States. After a century and a half of persecution, the cougar appears to be recolonizing many parts of its former range (LaRue & Nielsen 2008, Thompson & Jenks 2010, Knopff 2011, LaRue et al. 2012, Laundré 2012). Verified cougar sightings in many midwestern and southern states including Iowa, Minnesota, Wisconsin, Arkansas and Oklahoma are on the rise. In 2010, the Nebraska Game and Parks Commission (NGPC) confirmed the presence of a newly established breeding population in the Pine Ridge area in the northwest corner of the state (The Cougar Network 2013).

This thesis develops a habitat suitability analysis; a descriptive model created to determine which areas of the state of Minnesota could provide quality habitat for a recolonizing cougar population. A study of road density, deer density and land cover types provide the basis for determining both the amount and location of suitable cougar habitat that exists within the state. This work also provides a platform on which to build more complex analyses in the future.

Large carnivore conservation

Habitat loss, habitat fragmentation, increased human development, and the threat of global climate change are currently threatening many of the world's species. Species whose survival requires large amounts of land for home ranges and a steady supply of prey for which humans may compete are at increased risk.

Conservation initiatives often focus on large carnivores for several reasons. In some cases, the return of a large carnivore to an ecosystem brings about a state that existed pre-human alteration, i.e., the recolonization of cougar and later, the reintroduction of wolves into Yellowstone National Park. In other cases, it is recognized that large carnivores act as an “umbrella”; their need for large tracts of undeveloped land to maintain home ranges and viable populations often provides protection to multiple species of mammals, amphibians, reptiles, plants and insects (Beier 1993, Noss et al. 1996).

In the U.S., conservation, reintroduction and re-colonization of large carnivores has been in the headlines for the better part of the last 25 years. Wolves were successfully reintroduced into Yellowstone National Park in 1995 and there are ongoing efforts to repatriate the Mexican wolf to portions of its native habitat in the southwest. Healthy populations of cougars, wolves (*Canis lupus*), coyotes (*Canis latrans*), lynx (*Lynx Canadensis*), and black and brown bears (*Ursus americanus* and *U. arctos*, respectively) exist in pockets throughout the U.S. and Canada, and work to preserve their habitats and associated ecosystems is ongoing.

Cougar biology

Distribution

Cougars are highly adaptive and are considered habitat generalists. Historically, they have survived in nearly every ecosystem across North and South America (Logan & Sweanor 2000). Given the presence of game and ample cover to stalk prey, the cougar is capable of thriving across a wide range of habitats and climates (Dixon 1982, Hazard 1982, Currier 1983, Lindzey 1987).

Current cougar distribution, however, is greatly reduced from these historic ranges. Endemic large carnivores of North America have been persecuted since the arrival of the first European colonists. Wolves, bears, cougars, bobcats (*Lynx rufus*) and others were hunted, trapped and extirpated from areas of human settlement. Persecution as a nuisance species increased in the 1800's as pioneers moved west and claimed large parcels of land for farming, ranching and mining. Many large carnivores were hunted as a threat to these new livelihoods (Sweitzer et al. 1997). These widespread practices were successful in extirpating cougar populations entirely in the eastern, southern, midwestern and portions of the southwestern United States. Populations maintained a tenuous foothold in the mountains of the west (i.e., the Rockies, the Sierras, etc.) in areas where the land was too remote, too difficult, or too costly to develop and exploit.

Classification of the cougar as a varmint species and subsequent bounty hunting continued well into the middle of the twentieth century. In many western states, including California, Colorado, Idaho and Montana, bounty hunting was still the preferred method for dealing with the species until the mid-to late-1960's (Eaton 1973, Hornocker 1976). It was at that point that the species was reclassified in most areas as a game animal with a designated hunting season or in some cases, given complete protective status (Eaton 1973).

In other parts of the U.S and Canada, cougar numbers are increasing (Logan & Sweanor

2000). Throughout much of the western U.S., cougar populations are thriving in areas removed from human development and activity. Fifteen western states, as well as the Canadian provinces of Alberta, Saskatchewan and British Columbia have viable breeding populations. Confirmed sightings in Arkansas, Oklahoma, Iowa, Minnesota, Wisconsin and the Upper Peninsula of Michigan and the acknowledgement of cougar presence in Manitoba, Quebec, New Brunswick and Ontario indicate that western populations are expanding (The Cougar Fund 2013).

Food Habits

Depending on locale, abundance, availability and seasonality, cougars will eat a wide variety of prey. White-tailed (*Odocoileus virginianus*) and mule deer (*Odocoileus hemionus*) species are the preferred prey of the cougar throughout much of its range (Grinnell et al. 1937, Robinette et al. 1959, Hornocker 1970, Seidensticker et al. 1973, McBride 1976). Other ungulates such as elk (*Cervus Canadensis*), moose (*Alces alces*) and bighorn sheep (*Ovis canadensis*) are taken with regularity in areas with robust populations, particularly in the northwestern U.S. and British Columbia. Wild pigs (*Sus scrofa*) form an important part of the diet of cougars in Florida and California. Raccoon (*Procyon lotor*), porcupine (*Erethizon dorsatum*), skunk (*Mephitis mephitis*), beaver (*Castor canadensis*), opossum (*Didelphis virginiana*) and hares (*Lepus spp.*), as well as any number of small rodent species have all been found to contribute to the cougar diet (Robinette et al. 1959, Anderson 1983, Lindzey 1987, Williams et al. 1995, Sweitzer et al. 1997, Logan & Sweanor 2000, Dickson & Beier 2002, Fecske 2003, Cougar Management Guidelines Working Group 2005, Murphy & Ruth 2010).

Unlike canids who ‘course’ and chase their prey outright (often in a pack), the cougar will trail chosen individuals until they are close enough to mount an ambush-style attack, usually within a leap or two (Gunderson & Beer 1953, Hornocker 1970, Seidensticker et al. 1973, CMGWG 2005, Atwood et al. 2007, Murphy & Ruth 2010).

Habitat Requirements

Cougars utilize a wide variety of habitats, including mountains and high plateaus, deserts, chaparral, northern hardwood and coniferous forests, thick swamps and wetlands. Given plentiful prey and suitable cover, the cougar can survive and even thrive nearly anywhere (Dixon 1982, Currier 1983, Lindzey 1987, Beier et al. 2010).

Cougars are not good long-distance runners, however, and as such, require areas within their range that offer a high level of concealment for stalking and ambush (Hornocker 1970, Seidensticker et al. 1973, Logan & Irwin 1985, Beier et al. 1995, Dickson & Beier 2002, Fecske 2003). Elements of these habitats include steep slopes, dense vegetation, canyonlands, rock outcrops and boulder piles. Areas such as rivers, streams, draws or other types of riparian zones often include thick undergrowth and steep bluffs or banks can provide the right combination of cover elements in an otherwise open landscape (Hornocker 1970, Seidensticker et al. 1973, Logan & Sweanor 2000, Dickson & Beier 2002, Murphy & Ruth 2010). Ideal habitat structure provides sufficient visibility for hunting, but enough cover to allow the cougar to approach undetected, such as edge habitat and open conifer forests (Murphy & Ruth 2010). Cougars may also utilize riparian corridors for hunting and migration purposes, which could act as conduits for eastward range expansion (The Cougar Network 2013, Dickson & Beier 2002, Laundré 2012).

Behavior and Reproduction

Cougars, like most wild felids, are generally shy, secretive and solitary and rarely associate with other cougars (Seidensticker et al. 1973, Hornocker 1976, Lindzey 1987). The exceptions to this rule are mothers traveling together with their young and males and females coming together to mate. Cougars maintain fairly large home ranges and delineate this territory with markings of various kinds (Logan & Sweanor 2000). Not known to be very vocal (they do not possess the necessary anatomical structures for roaring like the 'big' cats), they rely heavily on visual and olfactory cues to maintain their

boundaries. Cougars tend to practice a mutual avoidance defense strategy and while actual physical fighting is not unheard of, it is not typical in stable populations (Hornocker 1970, Seidensticker et al. 1973, McBride 1976).

Females reach sexual maturity around two years of age, males at three. Females can mate and give birth at any time of year, and litters are typically comprised of two or three altricial kittens (Grinnell et al. 1937, Logan et al. 1996, Logan & Sweanor 2000). The natal den is rarely an organized nest but is often little more than a tangle of branches or shrubs (Grinnell et al. 1937, Lindzey 1987). Hunting, stalking and ambush behavior in cougars is innate but practice is required, achieved by the mother teaching her young by example. Kittens too young to accompany the female on hunts are brought live prey on which to practice their hunting skills (Wade 1929). Later, they will be called to a carcass once a kill is made (Wade 1929), and eventually they will be brought along on the hunt itself. By the second winter of their lives, the kittens are always present at a kill with their mother (Seidensticker et al. 1973), having learned by this time many of the necessary skills to hunt successfully on their own. At independence, juveniles disperse to find and establish a home range elsewhere. Age at time of dispersal can be as young as 12 months (Hornocker 1970), but more typically, juvenile cougars are 16-24 months old when they leave the natal territory (Hemker et al. 1984, Lindzey et al. 1994, Beier 1995, Logan et al. 1996).

Dispersal

Dispersal serves several important purposes in the biology and ecology of the cougar. It is a crucial component of gene flow between distant populations, providing much-needed diversity in otherwise isolated conditions. Beier (1993) showed that even extremely low immigration rates into a population increases the probability of survival.

In addition, it is believed that dispersal (specifically, the greater dispersal of males) acts as a barrier to inbreeding as males move away from their mother's (and possibly

siblings') territory (Logan & Sweanor 2000). Virtually all males disperse away from their natal range regardless of population densities (Beier et al. 2010). Males sometimes travel extreme distances in their quest for their own home ranges and potential mates. Females typically do not travel as far as males; instead, they sometimes display philopatric behavior and establish a home range near their natal range (Logan & Sweanor 2000, Sweanor et al. 2000).

Newly independent animals typically do not restrict their movements, reuse sites or show any affinity for a particular area (Seidensticker et al. 1973). Instead, dispersers will continue to move through suitable corridors and habitats until coming upon other cougars with which they can breed. This behavior likely accounts for the wide-ranging cougar sightings across the Midwest and other portions of historic cougar range.

The History of Cougars in Minnesota

Prior to large-scale settlement by Europeans in the mid 1800's (and statehood in 1858), the northern part of Minnesota was dominated by old-growth pine and spruce forests. The southeast portion was predominantly hardwood deciduous forest, and native prairie spread north to south along the western half of the state. White-tailed deer inhabited the southern forests and mule deer survived on the prairies in what was at that time the eastern edge of their range (Roberts 1932). Laundré (2012) suggests that ample cougar habitat was present pre-European settlement, and that the riparian areas that bisected the prairie and the prairie/forest boundary matrix likely supported a small but stable cougar population.

European settlers altered the natural landscape as they moved west. The southern hardwood forests were harvested for timber, nearly extirpating the white-tailed deer from that portion of the state. The deer moved north to the coniferous forests, surviving in what would be considered marginal habitat for the species. Mule deer disappeared as the western prairie was drained, plowed and converted to agricultural use (Roberts 1932).

Eventually, timber harvests expanded to include the northern conifer forests, and the second-growth hardwood that replaced it allowed white-tailed deer to flourish and extend their range farther north. Increased management and protection of the species for sport hunting helped boost deer numbers to their current status as one of the most common cervids in the Midwest. They are found nearly everywhere in Minnesota, from the second-growth forest in the north, the agricultural and pasturelands in the west and south and even in most urban areas.

It's doubtful that large numbers of cougars were ever found in Minnesota (Roberts 1932, Swanson 1945, Nowak 1976), but they likely utilized most habitats with the exception of the northern portion which was lacking in quality deer habitat (Gunderson & Beer 1953). Recorded occurrences are few, limited to reports of sightings and kills from early

explorers, trappers and surveyors such as Sibley, Carver and Faribault.

Reports of cougar sightings in Minnesota continued throughout the rest of the 20th century, possibly a mix of released or escaped captive animals and dispersing individuals moving through the area from other established populations in the west (Nowak 1976, Nero 1977, Buchwald 1978, Hazard 1982, Erb pers. comm.). Cougars recolonized the Black Hills of South Dakota in the 1990's and are now recognized as a breeding population of approximately 150-200 individuals with documented dispersal (Fecske 2003, LaRue & Nielsen 2008, South Dakota Department of Game, Fish and Parks 2010), including one radio-collared individual who traveled through North Dakota into northeastern Minnesota in 2004 (The Cougar Network 2013, Erb pers. comm.).

The Cougar Network is a nonprofit research organization exploring the expansion of cougar populations into their former range. A portion of the project is involved in mapping confirmed cougar sightings across the country. In Minnesota, five sightings were confirmed prior to 2007, but since 2009, the MN DNR and the Cougar Network have acknowledged over a dozen confirmations from at least seven individuals thought to be wild dispersers. As of late 2013, seventeen confirmed cougar sightings have been recorded (see Figure 1; The Cougar Network 2013, MN DNR 2013).

A cougar killed by a vehicle in Bemidji, MN in 2009 proved to be a male disperser from the Badlands population in North Dakota, while genetic testing of another individual spotted in Champlin, MN in December 2009 identified him as related to the Black Hills population. This cougar was tracked through the northern suburbs of the Twin Cities metro area over several days. He continued east into Wisconsin and was identified several more times on his passage into New York state and eventually to Connecticut, where he was struck and killed by a car in 2011.

As habitats west of Minnesota become increasingly crowded, juvenile males will disperse in search of other cougars and unoccupied habitat suitable for establishing a home range.

In doing so, they will cross marginal or unsuitable habitat, including areas of little cover. (Sweaner et al 2000, Thompson et al. 2009).

By some accounts, there may be more cougars in the western United States than ever, including prior to European settlement, and there is solid evidence that current cougar range is expanding into the Midwest (LaRue & Nielsen 2008 & 2011, Beier et al. 2010, LaRue et al. 2012). In 2003, wildlife biologist and carnivore expert Maurice Hornocker stated, “Lions will hit the Mississippi in the next decade. The East and Midwest is beautiful cat country - full of deer and cover”.

Interspecific competition between wolves, bears and cougars

The availability of suitable habitat and abundant prey are not the only factors determining a species' successful (re)colonization of an area. The presence or absence of other species belonging to a similar guild (i.e., species that utilize their environment in similar ways) or niche may determine the degree to which a species is able to persist in a new environment. Several other species of carnivores occur in the regions of Minnesota that this model has identified as having ideal cougar habitat. Black bears, wolves, coyotes, bobcats and lynx are all considered established resident carnivores in the state and utilize similar prey and habitats. This spatial and dietary overlap can lead to interference competition among guild members, characterized by hostile, direct, competitive actions that can lead to the exclusion of individuals from a resource (Ruth 2004a, Ruth & Murphy 2010).

Competition is often considered asymmetric due to differences in morphology and behavior among various guild members (Murphy 1998, Palomares & Caro 1999, Ruth 2004a). The definitive categorization of dominant and subordinate predators within a guild or trophic system is sometimes a simple one: a much larger species is clearly dominant to a smaller species. A cougar can chase off or kill coyotes, smaller felids or even a lone wolf, but they are subordinate to bears (due to the vast size difference) and to wolves in packs (Murphy et al. 1998, Ruth 2004b, Ruth & Murphy 2010). In the case of wolves and cougars that outwardly are more evenly matched, the differences between social behavior (pack life vs. solitary), hunting behavior (courser vs. ambush predator) and feeding behavior (consumption vs. caching) are the drivers of the dominant/subordinate paradigm (Murphy 1998). There is a "positive significant relationship" between body sizes of species involved in aggressive confrontations, and species working in groups or packs can kill larger individuals than those acting alone (Palomares & Caro 1999). Wolves, therefore, have a greater competitive advantage over cougars due to the fact that they live and hunt in packs, making them the dominant predator in their interactions with cougars (Akenson et al. 2005, Ruth & Murphy 2010).

For the better part of the last century, wolves and cougars have not coexisted throughout most of their historic range (Ruth 2004a). As both species continue to expand their ranges, they are likely to be found recolonizing similar habitats. Where they occur together, particularly in areas with a great deal of spatial and dietary overlap or where they occur at high densities, the potential for interference competition is very high (Murphy et al. 1998, Ruth 2004a, Akenson et al. 2005, Donadio & Buskirk 2006, Kortello et al. 2007). The degree to which they compete (directly or indirectly) is related to the extent of overlap they face in a particular area (Kitchen et al. 1999).

The subordinate predator is affected by interference competition in three ways: 1) the subordinate predator is killed outright in direct interactions with a dominant predator; 2) the dominant predator usurps food, often in the form of a carcass, from the subordinate predator (kleptoparasitism or usurpation); or 3) the subordinate predator may alter their spatial and temporal use of the habitat as an avoidance measure (Creel et al. 2001). However, the closer individuals are to the same size, the frequency of interactions leading to death decrease (Donadio & Buskirk 2006).

Kleptoparasitism is one way cougars come into contact with competitors in the same habitat. Given that cougars hunt and kill disproportionately large prey relative to their size and that they are solitary hunters and feeders, an individual will typically spend several days feeding on a single carcass (Hornocker 1970, Seidensticker et al. 1973, Ruth & Murphy 2010). Cougar kills act as a lure for other carnivores; the presence of a partly eaten carcass is a draw for scavengers as well as other predators. To conceal a carcass, a cougar may cache it under brush, grass, tree limbs or snow (Hornocker 1970, Seidensticker et al. 1973, Beier et al. 1995, Ruth & Murphy 2010). In habitats with heavy cover, this is fairly easily achieved, particularly with smaller prey such as deer. Larger prey (e.g., elk) is killed more easily in open areas, but is difficult to conceal due their size and the lack useful litter. This may lead to higher rates of discovery and usurpation by large competitors such as wolves or bears (Seidensticker pers. comm., Ruth & Murphy 2010). Black bears may compete directly with wolves and cougars on a seasonal basis,

primarily through kleptoparasitism. Open areas also increase visibility, which may increase the number of competitive interactions between carnivores (Creel et al. 2001, Ruth 2004a, Ruth & Murphy 2010), potentially exposing a cougar to a direct encounter with dominant predators. A habitat that offers more cover (horizontal and/or vertical) may allow a cougar with a carcass to avoid detection in the first place (Ruth 2004a). In the case of a direct confrontation with a dominant predator, cougars also utilize complex cover (i.e., hiding in rocky outcroppings or climbing tall trees) to escape an attack (Ruth 2004a).

Competitive interactions are extremely influential and can change hunting and feeding behavior, increase mortality, and alter spatial distributions and habitat-selection behavior of the subordinate competitor (Koehler & Hornocker 1991, Ruth 2004a). More specifically, the implications of kleptoparasitism are potentially significant. While the impact of kleptoparasitism specifically on cougar populations is not yet well understood and the effects on reproduction and survival are not yet clear, some studies point to repeated interactions with, and loss of carcasses to, bears and wolves leading to increased stress, decreased body condition and possibly to low annual survival rates (Ruth 2004b, Kortello et al. 2007). On an individual level, the usurpation of a carcass likely requires a cougar to hunt more frequently than it would otherwise; it must make up for the energetic costs of the lost kill. The risks inherent in pursuing large prey (e.g., the possibility of injury or death during pursuit) also increase with the frequency of hunting (Murphy 1998, Logan & Sweanor 2000, Murphy & Ruth 2010).

While seasonal overlap, similar diet and similar habitats are likely to increase the rate of direct interactions (Koehler & Hornocker 1991, Donadio & Buskirk 2006), subordinate species can avoid interference competition by shifting their spatial and temporal patterns of habitat use (Creel et al. 2001). In fact, certain spatial distribution patterns can be the *result* of continued, aggressive interactions (Linnell & Strand 2000). The strategies of utilizing areas safe distances from dominant competitors and being active at alternate times of day, along with differences in hunting behavior and prey selection, can reduce

the frequency with which subordinate and dominant competitors come into contact with one another. This partitioning of habitat and resource use can decrease both direct and indirect competitive interactions.

Continued direct interactions between wolves and cougars could be detrimental to a cougar population over the long term (Ruth 2004a, Akenson et al. 2005). High rates of interaction and competition have the potential to impact a species' population dynamics; changes in reproductive output and timing of births, lower dispersal success, and lower recruitment of adults have all been observed to lead to overall changes in cougar behavior due to increased contact with wolves (Ruth 2004b, Akenson et al. 2005). However, differences in hunting ability (e.g., pack hunters who chase prey vs. solitary ambush hunters), and behavior changes such as variations in spatial use (including active avoidance of areas recently utilized by wolves) and preferred prey species may encourage resource partitioning, allowing these species to occupy different niches within the same habitat (Kunkel et al. 1999, Ruth 2004a, Ruth 2004b, Akenson et al. 2005, Kortello et al. 2007, Bartnick 2010). These behaviors can also affect overall cougar survival, predation rates and success in rearing offspring (Buotte et al. 2008).

Competition among wolves, bears, and cougars in Minnesota

Wolves, and to a lesser degree, black bears on a seasonal basis would be the primary competitors of a colonizing cougar population in Minnesota (see Figures 2 and 3). Wolves prey primarily on white-tailed deer and utilize both forest and open habitats throughout northwestern Minnesota (Erb 2008). Black bears are also found throughout northwestern Minnesota in a variety of habitats, and are known to scavenge cougar carcasses (Murphy 1998). Such a high degree of spatial and dietary overlap may lead to direct, aggressive interactions between these species and cougars, resulting in the death of the subordinate cougar. The overlap will also likely lead to a great deal of competition for prey and other resources. As the dominant predators, wolves and bears could act as a barrier to cougar colonization, making it difficult for cougars to gain a foothold even in

ideal habitat.

Research examining the competitive interactions of wolves and cougars has been undertaken in two distinct arenas: 1) areas where wolves and cougars occur together in the same habitat; and 2) areas where wolves have been reintroduced into historic ranges where cougar had become the dominant predator after the extirpation of the original wolf population. The results of this research can be extrapolated to construct some general conclusions regarding interactions that could occur in Minnesota and the ramifications these might have for a colonizing cougar population in the state.

Where wolves and cougars have been sharing the same habitat continuously, research has borne out general trends of avoidance and negative spatial relationships between wolves and cougars (Kunkel et al. 1999, Ruth 2004a, Alexander et al. 2006, Kortello et al. 2007). Overall, cougars avoided wolves both temporally (avoiding areas recently utilized by wolves) and spatially (Koehler & Hornocker 1991, Ruth 2004a, Alexander et al. 2006, Kortello et al. 2007). Resource partitioning was evident in most cases. Alexander et al. (2006) found “a general trend of avoidance” between wolves and cougars in the eastern front ranges of the Canadian Rockies. Early in winter, cougar and wolves partitioned space differently, first by elevation, then by slope. Later in the season, when both species were restricted to lower elevations, they showed opposing preferences for both topography (cougars preferred more rugged terrain while wolves utilized the valley floor) and land cover. Logan and Sweanor (2000) found evidence of both bears and wolves killing cougars outright in direct interactions driven by the spatial proximity of the species to one another.

Where wolves had recently recolonized (or been reintroduced to) historic ranges where cougars had long been the dominant predator, cougar populations suffered considerable instability due at least in part to competition with wolves (Seidensticker pers. comm.). Prior to any kind of explicit resource partitioning, Atwood et al. (2007) found that prey species - primarily elk - tended to seek refuge in more complex habitats as an avoidance

behavior toward a species they were not familiar with. Wolves favored hunting in the open spaces of the preferred grassland grazing areas of elk, and the response to this new predator was to seek safety in more complex habitat, thereby increasing prey availability in the short term for cougars. However, Atwood et al. (2007) found “...complexities...quickly accrue” when a predator recolonizes an area, and differences in hunting style, home range size, adaptability to changes in the environment and new methods of predator avoidance by prey lead to volatility in the newly-subordinate species’ population.

Research in Yellowstone National Park (YNP) showed definitively that cougars were physically displaced from their kills by wolves in 8 out of 10 documented visits. Wolves and bears also scavenged cougar-killed prey after the cougar had attempted to cache it, including 6.9% of carcasses scavenged by wolves and 12.5% by bears (Ruth 2004b).

Akenson et al. (2005) found evidence that cougars moved out of an area following wolf recolonization and that the cougar population suffered low recruitment, decreased numbers of adults and disrupted hierarchical structure due to increased competition from wolves. Over time, however, species may be able to minimize the negative effects of competition by learning to partition resources such as food, habitat and space, leading to long-term coexistence (Akenson et al. 2005, Kortello et al. 2007).

In addition to research investigating interference competition between wolves and cougars, a very limited amount of work has examined the interactions between bears (grizzly and black) and cougars. Murphy (1998) found that interactions between bears (grizzlies and unknown) and cougars in Glacier National Park (GNP) and YNP were highly competitive. In Glacier, bears visited 15% of 55 studied cougar kills, scavenged 1 in 7 cougar-killed ungulates, and displaced cougars from 1 in 14 carcasses, whereas in Yellowstone, bears (grizzly, black and unknown) visited 33% of 58 cougar kills, 1 in 3 carcasses were scavenged, and cougars were displaced from 1 in 8 kills. Murphy (1998) hypothesized that in the face of high rates of interference, cougars may alter behavior

patterns and habitat usage such that the dominant species would cease to benefit from direct competition.

In Minnesota, it is reasonable to expect that some resource partitioning will likely occur along the lines of hunting style and land cover type. Cover type may play a determining factor in prey selection. Coursing predators such as wolves prefer to hunt in more-open, less-complex habitats, chasing down more-disadvantaged prey, selecting a greater proportion of young, old and malnourished individuals (Husseman et al. 2003, Stark 2009, Ruth & Murphy 2010). While a pack is less limited in terms of the size of prey it can subdue, in open habitats, infirm prey are easier to tire out and run down, requiring less energy expenditure on the part of the pack. As solitary ambush predators, cougars are limited in the size of prey they can physically subdue; prey choice is based more on size than condition. Prey size may primarily be constrained by the risk of injury to the cougar (Murphy & Ruth 2010). Heavier cover and more-complex habitats offer an advantage, allowing cougars to stalk and surprise larger prey (Williams et al. 1995, Husseman et al. 2003, Ruth & Murphy 2010). This type of spatial partitioning may serve to reduce interactions between wolves and cougars.

It is worth noting however, that where white-tailed deer are abundant or where the habitat is not suitable for coursing there may not be large differences in prey selection between the two predators. More-complex cover or dense undergrowth may influence wolf hunting behavior. In the case of Ruth's research in northwestern Montana (2004a), wolves and cougars selected the same prey (white-tailed deer) and killed individuals of the same sex, condition and age classes. There did not appear to be differential selection of prey due to hunting methods, possibly due to the dense vegetation present much of the year. Ruth (2004a) and Kunkel et al. (1999) hypothesized that wolves in these conditions hunt by stalking close and then chasing prey over fairly short distances.

Prey behavior may also influence the degree to which wolves and cougars compete. Depending on the amount of predation pressure cougars put on the white-tailed deer population in an area, deer may begin avoiding forested habitats and utilize more open

areas. As discussed in Atwood et al. (2007), formerly naïve prey may begin to seek refuge in areas less hunted by the new predator; in this case, cougars. This shift in behavior may temporarily increase the amount of prey available to wolves and may drive cougars into more open/less complex habitats. This, in turn, may increase competition, as open areas increase visibility, which Ruth & Murphy (2010) and Husseman et al. (2003) discuss as a possible driver of competitive interactions.

The primary prey of cougars in Minnesota would be white-tailed deer, leading to direct competition with wolves for their primary food source (DelGiudice 1998). In other parts of their range, cougar prey on lagomorphs, raccoons, porcupines, skunks, beavers and opossums, as well as any number of small rodent species, all of which are present in the areas identified by this model as prime cougar habitat (Fecske 2003, CMGWG 2005). This ability to shift to other food sources may help decrease competition, particularly if deer are not abundant or wolves restrict cougar access to deer.

In montane areas wolves use lower elevations and valleys in summer for denning and rearing young (Alexander et al. 2006), while cougars follow prey herds to higher elevations (Bartnick 2010, Ruth & Murphy 2010). However, wolves in Minnesota appear to utilize similar habitats year-round; there does not appear to be a distinction between summer and winter home ranges (Mech 1973, Fritts & Mech 1981, Fuller 1989, DelGiudice 1998). This lack of temporal partitioning may mean that competition and competitive interactions remain steady throughout the year. There is a seasonal component to competition with bears due to black bear hibernation over much of the winter. Murphy (1998) hypothesized that bear detection of cougar-killed prey in GNP and YNP increased in areas where there was a high degree of spatial overlap and the three species occurred at high densities. The presence of a nutritious food source such as cougar-killed deer carcasses could prove beneficial for bears, possibly influencing their behavior and survival (Ruth & Murphy 2010).

Given the amount of spatial and dietary overlap that would exist among cougars, wolves

and bears in Minnesota, the colonization of cougars in that state is not a forgone conclusion. Whereas ideal habitat is present and prey abundant, competition for resources might exert pressure on cougars with varying effects. However, the mechanisms that may drive these species to partition their habitat may lead to coexistence, and the adaptability of the cougar may allow it to continue to expand its range even in the face of strong intraguild competition.

Cougar population status and mapping efforts in North and South Dakota

Cougars have established permanent breeding populations in historic ranges in the Black Hills of South Dakota and the Badlands of North Dakota within the last 15 years. In 2010, Nebraska acknowledged the presence of a small breeding population in the Pine Ridge area (The Cougar Network 2013, Nebraska Game and Parks Commission 2013), and confirmed cougar sightings are on the rise in Wisconsin and Michigan (The Cougar Network 2013, Wisconsin Department of Natural Resources 2013).

South Dakota

The cougar was quite widespread in South Dakota in the 1800s and “considered numerous” in the Black Hills (South Dakota Department of Game, Fish and Parks 2005). Unregulated hunting and a bounty that was in place from 1889-1966 reduced the population to nearly zero by the early twentieth century.

It is believed that the re-colonization of the Black Hills in South Dakota was the result of dispersers leaving natal home ranges in established populations of cougars throughout Montana, Wyoming and Colorado (Berg et al. 1983, Fecske & Jenks 2003, The Cougar Network 2013). After being declared a state-threatened species in 1978, the species made a steady recovery. Besides the Black Hills, there are occasional reports of cougar sightings in other parts of the state including the Badlands, the Missouri River breaks in central South Dakota and as far east as the James and Big Sioux rivers (Fecske & Jenks 2001).

In 1985, the South Dakota Department of Game, Fish and Parks (SDGF&P) began to document cougar sightings throughout the state. There was a marked increase in the number of sightings between 1995 and 1999 (Fecske & Jenks 2003, SDGF&P 2005) and this, combined with the potential for increased cougar/human and cougar/livestock interactions, drove SDGF&P to begin developing a management plan for the species in 2003. Some of the long- and short-term objectives of the plan were to create population goals for the cougar in various parts of the state, as well as identify research and

monitoring requirements for maintaining healthy populations. In 1998, the SDGF&P enlisted the help of South Dakota State University's Department of Fisheries and Wildlife Sciences in creating a research project designed to monitor trends in the cougar population, determine current population size and verify the distribution of the species in the state.

Researchers at South Dakota State University created a habitat-relation model that ranked habitat types based on their suitability for cougars in the Black Hills. The model included elements such as habitat that would increase the success of kills (slopes greater than 50%), white-tailed and mule deer distribution, concealment habitat (drainages and dense vegetation), and human development components (i.e., proximity to roads and development) that research has shown to have an effect on cougar habitat use. These elements were ranked according to their suitability for cougar habitat as discerned from an in-depth literature review of cougar preferences (for slope, cover and hunting areas) and tolerances (of anthropogenic features). Utilization of available digital databases combined with the results from the literature allowed for the identification of high quality prey habitat, ranking of slopes, creation of distance-to-water variables and identification of unsuitable, human-altered habitat. A final map was created by summing the ranked layers of prey, slopes and riparian areas, and multiplying this by the human development layer. Results of this analysis identified 6,702.9 km² of high quality habitat in the Black Hills.

In order to test the habitat-relation model, as well as to estimate the size of the cougar population in the Black Hills, 12 cougars were radio collared and monitored weekly during the winters of 1998-2001. Estimates from this fieldwork put total numbers of cougars in the Black Hills in 2003 at 127-149 individuals (Fecske 2003). Mean annual home ranges for adult males were found to be larger than those in other cougar populations (see Table 1), possibly driving an overall population density lower than those in other areas in the west. Fecske (2003) speculated that these results meant either habitat quality in the Black Hills wasn't as high as in other parts of the cougars' range, or that the

Black Hills population had not yet reached capacity.

The information collected from the detailed documentation of sightings and the data from the more intensive research project supported the creation of a sport-hunting program in 2005. The hunt has continued with a yearly increase in quotas. The 2013 hunting season closed March 31 with 61 cougars taken, short of the quota of 100 individuals or 70 females. The SDGF&P has stated that their current cougar management goal is to reduce cougar numbers in the Black Hills, but some feel SDGF&P's cougar census data is flawed, leading to unsustainable quotas and possible population decimation (Woster 2013).

North Dakota

Like South Dakota, cougars were thought to have been extirpated from North Dakota in the early 1900's. However, when sightings of the animals began increasing in the 1990's, the North Dakota Game & Fish Department (NDG&F) began keeping track of those reports considered confirmed and credible, creating a database to track the information. In 2004, the NDG&F instituted a more formal method to record and verify cougar sightings in the state. Department staff gathered as much data as possible from individuals reporting a sighting, including location information and specific details such as the behavior of the animal at the time of the observation. Efforts were made to recover any physical evidence of the animal such as scat, tracks, video or photos, or a documented site of a kill (of wild prey or livestock). Following an investigation, the sighting was categorized as unfounded, improbable/unverified, probable/unverified, or verified. From 2001-2005, there were 41 verified reports of cougars in North Dakota, including 32 animals in the vicinity of or within the Badlands (NDG&F 2006).

In 2005, the NDG&F was directed by the state legislature to determine the status of cougars in the state. The NDG&F were seeking to answer the following questions:

- 1) Are cougars found throughout North Dakota, or are they concentrated in certain areas?

- 2) Are there breeding females in the state?
- 3) Is there an established breeding population in the state?
- 4) What habitats are important to cougars in the state?
- 5) Can the state support a population of cougars or does it serve as a dispersal habitat for young cougars?

To answer these questions, the NDG&F reviewed the sighting data compiled between 2001 and 2005, and surveyed resident hunters for additional relevant information. In 2005, the department also held an experimental cougar hunt (limit 5 cougars) with the stated objective of it being a cost-effective way of gathering more data regarding the presence of the animal in the state. In addition, the NDG&F created a habitat suitability map to identify those areas of the state that might contain the appropriate habitat for a breeding population of cougars.

To create the habitat suitability map, the department identified and ranked four different landscape characteristics critical to cougars: concealment and stalking cover (vegetation such as trees and shrubs), concealment and stalking topography (slope), habitat suited to travel (drainages) and unsuitable habitat (urban, residential, developed, open water). Within each one of these classes, values were assigned to categories based on their suitability to the species (see Table 2). The final map was created by summing the three ranked categories (cover, topography and travel habitat) and multiplying by the unsuitable habitat quality layer. Ideal cougar habitat was that which had at least 50% cover per square mile, occurred in habitat with slopes greater than 50%, and was within a square mile of a permanent water source. Given these parameters, it was found that 94% of the land area in the state was considered unsuitable. The 6% that was deemed either moderate-high or high quality was found in the Badlands, the Northern Missouri River Breaks, the Turtle Mountains, Pembina Gorge and parts of the Knife River, and was indicative of riparian areas (NDG&F 2006). Of these, only the Badlands and the Northern Missouri River Breaks were large enough to be able to sustain even a small population of cougars, using Beier's (1993) calculation of 1000-2200 km² needed to support a population for 100 years in the absence of immigration. The mapping project also

revealed potential travel corridors throughout the state, based on an area's proximity to permanent streams.

Creating a habitat suitability analysis: a framework from the literature

Building the model

Varying methodologies can be employed to create a habitat suitability model. Inductive, statistical techniques such as multivariate regression functions are common, and typically use empirical data to link environmental characteristics to suitability. These approaches require data regarding species abundance or presence/absence within the study area (Ahmadi-Nedushan et al. 2006), however, and were not suitable for this project. Other methods, such as Habitat Suitability Indices (HSIs) and GIS-based models utilize expert opinions and literature reviews to understand the relationships between species and critical habitat factors (Jones-Farrand et al. 2011).

Multicriteria evaluation (MCE) is one of three main GIS-based methodologies used to create suitability models (Malczewski 2004). MCE allows for the evaluation of alternative options that involve impacts on multiple dimensions by combining scores across these different dimensions with weights on these scores supplied by stakeholders or the analyst. In GIS specifically, several criteria maps are combined using map algebraic operations and cartographic modeling practices to create suitability maps. The modeler's preferences are included in the analysis by way of user-specified weights assigned to the criteria based on their importance (Collins 2001, Store 2003).

The criterion necessary to create a habitat suitability model (e.g., the landscape preferences for a particular species) must be identified first in order to create attribute maps for use in a GIS. This information is commonly derived from empirical data gathered from animal space-use studies. In the absence of empirical research (as is the case for cougars throughout much of the Midwest), models can instead be constructed with expert knowledge (Store 2003, Store 2001).

Habitat features can be identified either as 'constraints' or 'factors'. Constraints serve to

define certain areas as wholly unsuitable for the decision at hand (Eastman 1999). Malczewski (2000) suggests these maps be made early in the modeling process to identify the feasible alternatives on which the rest of the model is built. Further analysis should not take place until those areas identified by the constraint maps as unsuitable are essentially removed from consideration.

Factors are scaled data sets that convey varying degrees of suitability (Eastman 1999). In this case, the data must be standardized and weighted in order to be used in any further analysis. One way to accomplish this is to calculate the relative importance of the factors using pairwise comparisons. A common methodology for calculating these relative weights is the Analytical Hierarchy Process (AHP; Saaty 1994). The process requires experts to evaluate and compare all possible factor pairings and enter ratings for the pairs based on a pre-determined continuous scale. This technique transforms raw data into standardized, comparable scores based on expert opinion, while other methodologies use linear scale transformations or simple Boolean overlays (Eastman 1999, Malczewski 2000, Store 2001).

Landscape preferences

Mladenoff et al. (1995) found that land cover, land ownership, and human population and road densities influenced recolonizing wolves in Wisconsin. Similarly, studies of cougar habitat over the last few decades have shown there are several landscape characteristics that are critical to cougar habitat utilization. These include availability of vulnerable prey, suitable vegetation and cover types, presence and density of improved primary roads, and, to some degree, anthropogenic disturbance.

It has long been believed that cougars required isolation and large tracts of wilderness with low human population densities and low rates of development (Seidensticker et al. 1973, Van Dyke 1983, Van Dyke et al. 1986a). Van Dyke et al. (1986a) found, for example, that cougars chose areas with no recent timber harvesting and “few or no sites

of human residence”, and Sweanor et al. (2000) discovered that lower human population densities resulted in fewer barriers to young cougar dispersal. However, it is likely cougars were found in these more out-of-the-way places because they offered refuge from over a century of persecution and bounty hunting; the assumption that cougars require remote or pristine habitat followed logically. More recent work has weakened that assumption, recognizing cougar use of suburban, exurban and rural development (Beier 1995, Beier et al. 2010, Burdett et al. 2010, Knopff 2011, Kertson et al. 2013, Laundré 2013). Use of these areas is primarily attributed to dispersing subadults, although adult residents have been found to utilize suburban and wildland/urban interfaces as well (Beier 1995, Beier et al. 2010, Kertson et al. 2013), while simultaneously attempting to minimize their exposure to human activities (Dickson et al. 2005, Beier et al. 2010, Kertson et al. 2011a, Kertson et al. 2011b). However, Knopff (2011) found a decrease in negative cougar responses to human development as anthropogenic features increased in an area, indicating an ability to adapt to changing landscapes.

Road density plays a role in cougar habitat use and home range establishment. Cougars choose home ranges with overall lower road densities (Van Dyke et al. 1986b, Dickson & Beier 2002). Van Dyke et al. (1986b) found average road densities of .26 km/km² on the Spider Cross U ranch in central Arizona, .43 km/km² on the Kaibab Plateau in northern Arizona, and .25 km/km² near Escalante in south central Utah. Van Dyke et al. (1986a) found road densities in an active timber sale zone were slightly higher (0.6 km of road/km²) than on the overall Kaibab Plateau Study Area (0.4 km of road/km²), and noted that cougars may have avoided sale areas in part due to the increased road densities.

Dickson and Beier (2002) found a general avoidance of roads by cougars in the Santa Ana Mountains in southern California. Density of roads (both low-speed and total paved roads) in cougar home ranges was much lower than the overall road density in the study area. Compared to average study area densities of .4km/km and .46km/km of low-speed and total paved roads, respectively, female cougar home ranges had densities of 0.11 km/km² of low-speed roads, and .18 km/km² of total paved roads. Male home ranges had

densities of .22km/km² of low-speed roads and 29km/km² of total paved roads.

In addition, road type appears to also be a factor; cougars utilize unimproved roads (such as small dirt roads and trails) with greater frequency than improved and hard-surface roads (Van Dyke 1983, Van Dyke et al. 1986b, Beier 1995, Kertson et al. 2001b).

Road types and densities can also be indicators of the level of anthropogenic development of an area, particularly when combined with land cover data (Beier pers. comm., Mech pers. comm., Murphy pers. comm.).

While cougars are habitat generalists and demonstrate a tolerance for many different vegetation and habitat types, they show a strong preference for areas that provide plenty of stalking cover, primarily forest with significant canopy or overstory (Seidensticker et al. 1973, Logan & Irwin 1985, Williams et al. 1995, Dickson & Beier 2002). They appear to avoid areas of fragmentation (Taverna et al. 1999), and seem to prefer areas that are influenced by topography, such as mountain passes, corridors and riparian zones that allow easy travel (Seidensticker et al. 1973, Dickson & Beier 2002).

Cougars are typically associated with ungulate-sized prey, such as elk, mule deer and white-tailed deer. These species are the primary food source for the cougar throughout its range (Grinnell et al. 1937, Eaton 1973, Hornocker 1976, Anderson et al. 1992).

Methods

To create the maps necessary for analysis, I used ESRI ArcGIS for Desktop 9.2 & 10.1: ArcMap, Spatial Analyst, and Microsoft Excel 2011.

Utilizing the basic methodological framework of MCE, I created three spatial datasets for use in identifying suitable cougar habitat in Minnesota. Road density, deer density and land cover/land use are parameters that have been shown to be critical in cougar habitat utilization (Van Dyke et al. 1986a, Dickson & Beier 2002, Beck et al. 2005). These data sets were created, reclassified, and combined to create a single map identifying high quality cougar habitat.

Datasets

I concluded that county-level data was too coarse a filter for the purposes of this project. A more accurate analysis could be achieved instead using geographically smaller townships as the basis of determining densities and compiling data. The 2010 Minor Civil Divisions (mcd2010) dataset from the Legislative Coordinating Commission's GIS office (LCC-GIS) provided the polygon data layer for townships and cities throughout the state.

I obtained road information from the Minnesota Department of Natural Resources (MN DNR) Data Deli website. The "DOT Basemap Roads - All Types" dataset is a line data layer that includes all roads found on USGS 1:24000 maps, tiled by county. It is the primary source of spatial road data for the state of Minnesota. This layer includes all interstate highways, trunk highways, township roads, city streets, and other improved roads that were current through the end of the 2000 construction season. Road length as an attribute is included in this dataset, allowing for the calculation of road density.

I downloaded land cover/land use data from the Data Deli, in the form of a single raster dataset for the entire state. The layer was created using the 2001 National Land Cover

Database (NLCD) from the federal agency collaborative land cover data program referred to as the Multi-Resolution Land Characteristics Consortium (MRLC). The data set consists of three elements: land cover, impervious surface and canopy density. For the purposes of this project, I selected only the land cover data for download and utilization. Land cover data is broken up into 16 different classes (see Table 3).

Minnesota has a wide variety of vegetation and land use types. Forest cover (coniferous, deciduous and mixed forests) is found primarily in the northern and northeastern parts of the state. The entire western portion, ranging from the Canadian border in the north to the Iowa border in the south, as well as most of the southern part of the state from South Dakota to Wisconsin, is agricultural and pastureland. Wetlands are interspersed throughout the state, with the largest concentration found across a great deal the northern portion.

Calculating densities

I calculated road density by first using the Analysis/Intersect tool to combine the roads and the mcd2010 datasets. Using the Calculate Geometry function, I recalculated road length to provide the total miles of road found within each township, and exported the data such that it could be opened in Excel. I combined all the individual files into one large file and created a pivot table to sort the records and prevent duplication. Using the township area data included in the mcd2010 attributes; I calculated road density in miles of road per square mile and then converted this to kilometers of road per square kilometer (km/km^2). I imported this file into ArcMap10.1 and, using the join function, linked it to the mcd2010 layer and exported it as a shapefile.

Road densities in Minnesota range from 0.002 – 18.52 km/km^2 . The highest densities are found in the cities of Minneapolis and St. Paul. Moderate densities exist in the surrounding suburbs that make up the Twin Cities metro area, as well as in the small cities and large towns found in outstate Minnesota. Much of the state has road densities

below 1.87 km/km² (see Figure 4).

Deer density data was provided by Marrett Grund and Jason Abraham at the MNDNR. Pre-fawn deer densities from multiple years were simulated from population modeling “that subtracts losses, adds gains, and keeps a running total of the number of animals alive in various sex-age classes during successive periods of the annual cycle” (Grund & Walberg 2012). This model was run for each deer permit area (DPA) in Minnesota from 2007-2012 with the exception of three DPAs (224, 235 and 238) due to errors associated with their small population size, and DPA 602 located in the Twin Cities metro area, due to limited hunting opportunities in an urban setting. The data was provided in deer/mi² and was converted to the number of deer/km². I downloaded the DPA shapefile from the Data Deli, and edited the attribute table to include pre-fawn deer density data from 2011 (the most recent complete data set) for each DPA. I then intersected this layer with the mcd2010 layer. I summarized the table based on township name, and included statistics for the sum of DPA and mcd area and average deer densities. I imported this summary table into ArcMap 10.1, joined it to the mcd2010 layer and exported it as a shapefile.

Deer densities range from 0.00 – 76.00 deer/km². Deer numbers are highest in the north, while much lower densities are seen along the western edge and in the southern portions of the state (see Figure 5).

As the land cover data exists only in raster format, I converted the road and deer density shapefiles from vector to raster format to facilitate further analysis.

Reclassification and Weighting

I determined through discussions with cougar and carnivore experts that presence vs. absence of deer was more important than specific deer densities (Beier pers. comm., Mech pers. comm., Murphy pers. comm.). Therefore, the deer density layer was reclassified using Boolean variables 0 (deer density of 0; unsuitable) and 1 (deer density

≥ 1 deer/km²; suitable) (see Table 4 and Figure 6).

High road densities indicate high levels of anthropogenic development and these areas are not considered to contain high quality habitat for cougars (Beier pers. comm.). For this reason, road densities were also reclassified using a Boolean operator. Densities of ≥ 3.05 km/km² were assigned a 0 (unsuitable), and areas with densities of ≤ 3.05 km/km² were assigned a 1 (suitable) (see Table 4 and Figure 7). This density cutoff value was determined by overlaying the land cover and road density maps. Areas where urban road densities and “developed” land cover categories overlapped (i.e., road density of ≥ 3.05 km/km²) were identified as unsuitable for cougar habitat use.

I consolidated the original 16 land cover categories (see Table 3 and Figure 8) into five new classes (Barren/Developed, Agriculture, Grassland/Wetland, Shrub/Scrub and Forest), ranking them based on the weightings from LaRue’s (2007) expert-opinion AHP methodology (Mech pers. comm.). According to the results of the AHP, forest cover types such as mixed, deciduous, and evergreen forest are considered the most suitable cover for cougar habitat, resulting in a score of 1.0 or 100%. Barren and developed lands are considered to be 10% as suitable as forest cover, resulting in a score of .10. I used the Map Algebra tool in ArcMap 10.1 to assign weights to the variables using values ranging from 0.10 – 1.0 (see Table 5 and Figure 9).

The road and deer density maps are considered constraint maps and were used to identify areas that would be wholly unsuitable for cougar habitat (areas with high road densities and absent of deer). The land cover map is a factor map that utilizes the AHP performed by LaRue (2007) as the basis for standardization and weighting. No further weighting of or across variables was necessary.

Using the Boolean And tool in the Spatial Analyst toolbox in ArcMap 10.1, I multiplied the two constraint maps to produce a map identifying the feasible alternatives. Areas receiving a score of 0 were considered unsuitable due to a lack of deer and/or high rates

of anthropogenic development as identified by road density. The areas receiving a score of 1 were considered suitable, and would be included in the next step of analysis.

I then multiplied this feasible alternatives map with the land cover factor map using the Times tool in Spatial Analyst. This final composite map identifies potentially suitable habitat for cougars in the state by assigning scores to different habitat types. I calculated the total area for each habitat type by multiplying cell size by the total number of cells in each category.

Sensitivity Analysis

To test the sensitivity of the model to the various inputs, I altered the cutoff values for both the deer density and the road density factor maps to see how they affected the model outcomes.

Originally, areas with deer densities of 0 deer/km² were considered unsuitable, while areas with deer densities of ≥ 1 deer/km² were considered suitable. Deer density cutoff values were altered as follows:

- Deer densities of ≤ 5 deer/km² were considered unsuitable and given a Boolean value of 0, while deer densities of ≥ 6 deer/km² were considered suitable and given a value of 1;
- Deer densities of ≤ 10 deer/km² were considered unsuitable, while higher deer densities were considered suitable.

Road densities were also altered in 2 ways. Originally, road densities of ≤ 3.05 km of road/km² were considered suitable (and assigned a value of 1), while higher road densities were considered unsuitable and assigned a value of 0. Road density cutoff values were changed as follows:

- Road densities of ≤ 2 km of road/km² were considered suitable and assigned a value of 1, while higher densities were considered unsuitable and assigned a value of 0.

- Road densities of ≤ 6.10 km of road/km² were considered suitable, while higher road densities were considered unsuitable.

Results

Road density, deer density, and land cover were combined by multiplying the layers together (see Figure 10). Areas with a final score of 1.0 are considered very high quality habitat, providing ample cover, low anthropogenic development and deer densities greater than 0 deer/km². Cover is primarily forest, consisting of evergreen, deciduous, and mixed forest types. These areas provide approximately 56,598.58 km² of potential cougar habitat.

Areas associated with scrub/shrub cover are considered moderate habitat and are assigned a score of .58 (i.e., it is considered to be 58% as important as forest cover). Wetland and Grassland cover types scored lower, at .35, but these areas have the potential to provide higher quality cover on a seasonal basis, as do some Agricultural regions (those areas receiving a score of .15). Areas displaying a score of 0 are considered unsuitable for cougar because of a lack of deer, high rates of development, lack of suitable cover and/or high road densities. See Table 6 for total area calculations for each cover type.

Sensitivity Analysis

To test the sensitivity of the model to the various inputs, deer and road density cutoff values were altered. Changes made to the road density cutoff value did not cause major changes in results for habitat area. Only slight changes were seen in the amount of habitat considered wholly unsuitable (areas with a score of 0) when the road density cutoff was reduced to ≤ 2 km of roads/km²; the total area of unsuitable habitat increased from 8508.15 km² to 10,429.92 km². This additional 1921.77 km² of unsuitable habitat occurs in small amounts near the Twin Cities, near the Iron Range cities of Grand Rapids, Hibbing, Virginia, and in the Brainerd area. Some of these areas (namely those near the Iron Range) included some ideal habitat in the original analysis (see Figure 10), however, under this scenario, a relatively small amount of ideal habitat (532.95 km²) is lost (see Figure 11).

Increasing the amount of road density considered suitable also did not produce any significant changes in the total amount of ideal habitat available. Doubling the road density cutoff value to $\leq 6.10 \text{ km}^2$ resulted in a gain of only 56.54 km^2 of ideal habitat. Other minor changes included an increase of 131.62 km^2 of developed area (scores of .10) and a reduction of 444.90 km^2 of wholly unsuitable habitat (scores of 0), mostly from urban areas in the southern part of the state (see Figure 12).

Changes made to deer density cutoffs produced much larger changes in habitat area. Increasing the suitable deer density cutoff to $\geq 6 \text{ deer/km}^2$ greatly increased the amount of habitat considered wholly unsuitable for cougars by $12,809.30 \text{ km}^2$, from 8508.15 to $21,303.45 \text{ km}^2$. Most of this increase came at the expense of marginal habitat. Ideal habitat decreased by only 273.26 km^2 . These changes occurred primarily in agricultural areas in the northwestern and southwestern portions of the state (see Figure 13).

Further increasing the suitable deer density to $\geq 11 \text{ deer/km}^2$ produced even larger changes in the amount of unsuitable and marginal habitat. This change in what would be considered suitable deer density led to an increase of $51,201.64 \text{ km}^2$ of wholly unsuitable habitat. These changes were found primarily along the western edge of the state, and are mirrored by a reduction of $39,004.55 \text{ km}^2$ of agricultural land in that area. Additionally, changes were seen in the northeastern portion of the state, most notably, a loss of 4901.73 km^2 of ideal habitat and a loss of 4337.79 km^2 of land consisting of grasslands and wetlands (see Figure 14).

This model appears to be fairly sensitive to deer densities, while road densities do not affect model outcomes in any significant way.

Discussion

Rather than choosing an arbitrary point to define the “highest suitable” habitat, LaRue (2007) utilized a cut-off percentage, chosen from her analysis of Fecske’s (2003) work in South Dakota. LaRue determined that the average habitat percentage of all cells in the Black Hills habitat was 75%. Using this cutoff in my analysis, the model identifies 56,598.58 km² of nearly contiguous land as suitable cougar habitat in Minnesota, located primarily in the north central and northeastern portion of the state. This area is characterized by a mixed forest canopy consisting of pine, tamarack, spruce and fir, as well as aspen, birch and other second-growth species. Deer densities throughout much of the region are high, and both road densities and quantity of high-speed paved roads are lower than in many other portions of the state. Large mining operations along the Iron Range result in some lower score ‘pockets’ in the area, but overall, this region offers a good deal of high quality cougar habitat. The area in the in this part of the state that is considered entirely unsuitable (received a score of 0) has been identified as being barren of wintering white-tail deer by Nelson & Mech (2006). Deer utilize this area seasonally, but given that they are not present year-round, this area was excluded from further analysis. It is highly suitable habitat in other respects; the area has very low road densities and is characterized by ideal mixed forest cover, and could offer suitable cougar habitat on a seasonal basis.

Other areas received lower scores but may still offer marginal or modified habitat useable by newly established young cougars or dispersers. These areas may have higher road densities/quantities of improved surface or high-speed roads or higher rates of human disturbance and development, but given the presence of vulnerable prey and cover, they may be marginally suitable for cougar survival. Agricultural and grassland areas in the central and western portions of the state could offer appropriate amounts of cover on a seasonal basis. Laundré (2012) suggests the edge habitat found between what was historically the prairie grassland and deciduous forest biomes from the Canadian border to the Twin Cities could provide a useful combination of forest and open space for cougar

utilization. Riparian areas throughout the state would also provide at least seasonal cover and hunting habitat (Dickson & Beier 2002, Dickson et al. 2005, Laundré 2012).

The area identified as highly suitable for cougar habitat is also the primary range for wolves and black bears (see Figures 2 and 3), both of which are considered dominant predators to the subordinate cougar in the areas where the species overlap. The presence of either of these competitors could act as a barrier to (or substantially curtail) cougar recolonization if habitat and prey cannot be successfully partitioned. While bear and wolf densities were not modeled for this project, it should be noted that their presence will have an impact on the ability of cougars to colonize the northern and northeastern portions of the state.

In addition to road density, road type may have an impact on a cougar's identification of suitable habitat (Seidensticker pers. comm.). High-speed and improved roads can play a significant role in cougar mortality (Beier 1995, Logan & Sweanor 2000, Dickson & Beier 2002, Beier et al. 2010). Similar to the cougar response to human development, the existence of paved and/or high-speed multi-lane roads may not automatically make an area unsuitable, but a cougar may avoid these road types within their own home ranges (Van Dyke et al. 1986b). Beier (1995) found dispersing cougars were hesitant to cross newly-encountered freeways in their travels; they would stop and rest near the freeway and would wait until the following night to either cross or turn around and return the way they originally came. Overall, cougars avoided high-speed and improved roads (Dickson et al. 2005, Beier et al. 2010), but appear to utilize unpaved, low-traffic roads and trails to facilitate movement and hunting (Beier 1993, Beier 1995, Dickson et al. 2005, Kertson et al. 2011b).

Recent studies have shown that cougars do not require pristine wilderness and remote habitats far from anthropogenic disturbance in order to survive (Beier et al. 2010, Kertson et al. 2011b & 2013, Laundré 2013). In many cases, cougars will avoid developed areas within their home ranges (Van Dyke et al. 1986a, Burdett et al. 2010), but that does not

prevent them from establishing the home range and utilizing more ideal portions of the area and habitat. Burdett et al. (2010) and Kertson et al. (2011a & 2013) found that the areas between wildlands and urban, suburban, and exurban development offer habitat cougars may perceive as not ideal, but not wholly unsuitable.

Beier et al. (2010) stated that cougars are “habitat generalists that seem to require only three things: 1) freedom from excessive human interference, 2) adequate numbers of large ungulate prey, and 3) stalking or ambush cover.” These conditions can be met at the boundaries of the wildland-urban interface and pockets of habitat within suburban areas. These areas often provide edge habitat that some have suggested is ideal; sufficient visibility for hunting and enough cover for stalking, resting and traveling undetected (Beier et al. 2010, Murphy & Ruth 2010, Laundré 2012, Kertson et al. 2013). Dispersers are most likely to come into contact with human infrastructure and development (Van Dyke et al. 1986a, Kertson et al. 2013; they are bolder in their use of habitats and take more risks than adults (Beier 1995, Logan & Sweanor 2000, Beier et al. 2010). Beier (1993) found the majority of dispersers in his study (7/9) ventured into urban environments using habitat peninsulas, traveling at night to avoid human activity, and Kertson et al. (2013) found subadult dispersers utilized developed areas at a much higher rate than adult residents. This was likely due to the disperser’s exploration of all potential suitable habitat in an area with already-established adult home ranges.

Newly independent and dispersing cougars are often forced to establish home ranges in less-than ideal conditions due to their rank in the land tenure system employed by the species (Pierce et al. 2000). A disperser must either find a vacant home range within an established population or displace an older resident. If population density in an area is high enough such that a vacancy does not exist, the disperser must move on (Hansen 1992). In a recolonization scenario, founding cougars would likely choose home ranges in the most ideal habitats. Less ideal habitats would be filled over time, until those areas with marginal suitability (i.e., near human development/activity) are left. In addition, cougar response to human development is likely to be individualistic; there may not be a

broad pattern of acceptance of human activity across an entire population. Kertson et al. (2011a & 2011b) emphasized that the variation seen in spatial use patterns may be due to individual cougar approaches to utilizing habitat near human-dominated landscapes.

It is unlikely that an adult cougar would establish a home range in proximity to highly developed, urban areas, but it is possible that cougars might choose to settle near other smaller suburban and exurban areas on the edge of wildlands, particularly those in areas of high deer densities.

For recolonization to occur, both male and female dispersers must be present in an area of suitable habitat. Males are understood to be the primary dispersers, and are rarely, if ever, philopatric (Logan & Sweanor 2000, Logan & Sweanor 2010), while females demonstrate a fairly high degree of philopatry, establishing home ranges adjacent to or overlapping their natal range. Lindzey et al. (1994) found female cougars in southern Utah exhibited philopatry 70% of the time, while Logan and Sweanor (2000, 2010) have consistently found rates of at least 50%. In addition, average male dispersal distances are 2-4x that of females (Logan & Sweanor 2010). It appears that female dispersal may be at least in part density dependent; competition with other females for resources drives sub-adults from their natal ranges (Logan & Sweanor 2010, Thompson & Jenks 2010), while male dispersal is thought to be independent of local male densities (Logan & Sweanor 2010).

Unless the Black Hills or Badlands populations reach a density threshold that prompts female dispersal, and given that females do not typically disperse as often or as far as males, the likelihood of cougars (re)colonizing Minnesota from the Black Hills or the Badlands may have a low probability. Recent research however, has found that females may be capable of longer dispersal distances than once thought. Stoner et al. (2007) were able to retrace the steps of a GPS-collared, dispersing sub-adult female 357 km from her natal range in Utah to her eventual harvest in Colorado nearly a year later. In between, the female crossed four major rivers, an interstate highway, and moved through portions

of Utah, Wyoming and Colorado.

In addition, Thompson and Jenks (2010) found a 60% dispersal rate among females in the Black Hills, and 5 females dispersed farther than 50 km. While they found that males dispersed more often (100% of the time) and farther than females, they determined both males and females traveled farther on average than previously documented in the literature. At the time, there appeared to be a high degree of competition between females for resources in the study area, leading to higher rates of female dispersal. These individuals either left the Black Hills entirely, or set up home ranges in the remotest forest habitat available within the study area. Males also moved first to these remote areas, but then continued out into less suitable prairie and agriculture cover types. The authors noted that these particular habitats, though considered less than ideal for cougar use, did not act as a barrier to dispersal from the Black Hills.

Thompson and Jenks (2010) state that the dispersal of females, particularly from a population found on the edge of the species range, is indicative of true range expansion. While individual females may not disperse as often or as far as males, Swenor et al. (2000) suggested that they may disperse to “closer, stepping-stone populations and subsequently produce young that disperse to more distant patches.” This stepping stone idea, in combination with the higher rates of some female dispersal as noted by Thompson and Jenks (2010), as well as the ability of females to travel perhaps farther than previously understood, may mean that the breeding populations in North Dakota, South Dakota and Nebraska might produce enough dispersers of both sexes to (re)colonize portions of Minnesota.

Conclusion

Growing source populations of cougars in the west (i.e., North and South Dakota, Montana and Wyoming) are producing increasing numbers of dispersers that have been identified in Nebraska, Missouri, Iowa, Minnesota, Wisconsin and the Upper Peninsula of Michigan (The Cougar Network 2013). Dispersing individuals are known for traveling great distances to find mates and suitable home ranges.

This habitat suitability analysis for Minnesota has shown where cougars would likely settle in the event that these dispersers were to establish a breeding population in the state. Areas of low anthropogenic development, significant forest cover and the predictable presence of deer would provide the best habitat for incoming cougars. Most of this area is concentrated in the north and north-central parts of the state. This information could be used to assist in the development of empirical studies of dispersers and later, resident cougars; knowledge of the location of suitable habitat could be utilized to determine the location of track surveys, aerial surveys, rub pads for collecting hair, or camera traps.

In addition, this analysis should be seen as a base for further work. Including empirical data on deer densities and the densities of potential competitors such as bear and wolves would help to further refine habitat suitability. Adding more detailed criterion such as suburban and exurban boundaries and other landscape attributes would increase the complexity of the model and allow for more specific analysis of issues such as anthropogenic development. Further GIS modeling on corridors, barriers to dispersal, estimates of contiguous habitat, and possible migration routes of cougars could assist in predicting numbers of individuals who might be moving into or through Minnesota.

Once it is determined that a breeding population of cougars exists in the state, this expanded model could be utilized in the development of a species management strategy. The ability to assess the status of the population, track changes in cougar habitat through

time, identify and track individual cougars, and catalog reports of human-cougar conflict such as depredation of livestock would prove valuable to the agency tasked with management of this species.

Table 1: Mean annual home range size of adult male cougars

Population	Author
Black Hills 680 km ² [<i>n</i> = 9]	Fecske 2003
Alberta, 334 km ² [<i>n</i> = 6]	Ross & Jalkotzy 1992
Arizona, 196 km ² [<i>n</i> = 5]	Cunningham et al. 1995
Colorado, 256 km ² [<i>n</i> = 12]	Anderson et al. 1992
Florida, 432 km ² [<i>n</i> = 12]	Maehr 1997
Montana, 462 km ² [<i>n</i> = 2]	Murphy 1983
New Mexico, 188 km ² [<i>n</i> = 72]	Logan and Swenor 2001
Wyoming 320 km ² [<i>n</i> = 2]	Logan 1983

Source: Fecske, D.M. 2003

Table 2: Landscape characteristics used to create a habitat suitability map for cougars in the Badlands, North Dakota

Landscape characteristics	Category	Value
Concealment/stalking cover (trees and shrubs)	0 % cover per 2.6 km ²	1
	1-25% cover per 2.6 km ²	2
	26-50% cover per 2.6 km ²	3
	>50% cover per 2.6 km ²	4
Concealment\stalking topography (slopes)	0% slope	1
	1-20% slope	2
	21-50% slope	3
	>50% slope	4
Travel habitat (drainages)	No streams present within 2.6 km ² area	1
	Intermittent streams present within 2.6 km ² area	2
	Perennial streams or shoreline present within 2.6 km ² area	3
Unsuitable habitat	Residential/urban areas; open water	0

Source: North Dakota Game and Fish Department, 2006

Table 3: NLCD Classification Schemes

11 Open Water
21 Developed, Open Space
22 Developed, Low Intensity
23 Developed, Medium Intensity
24 Developed, High Intensity
31 Barren Land (i.e., exposed bedrock, mines and gravel pits)
41 Deciduous Forest
42 Evergreen Forest
43 Mixed Forest
52 Scrub/Shrub
71 Grassland/Herbaceous
81 Pasture/Hay
82 Cultivated Crops
90 Woody Wetlands
95 Emergent Herbaceous Wetland

Source: MRLC, 2001

(<http://www.epa.gov/mrlc/nlcd-2001.html>)

Table 4: Reclassified deer density and road density values

Data Set	Original Value	Reclassified Value
Deer Density	≥ 1.0 deer/km ²	0
	0.0 deer/km ²	1
Road Density	≥ 3.05 km/km ²	0
	≤ 3.05 km/km ²	1

Table 5: Reclassified land use values

Land Use Category	New Value
Barren & Developed Areas (Classifications 21, 22, 23, 24 & 31)	0.10 (10%)
Agriculture (Classifications 81 & 82)	0.15 (15%)
Grasslands & Wetlands (Classifications 71, 90 & 95)	0.35 (35%)
Shrub/Scrub (Classification 52)	0.58 (58%)
Deciduous, Evergreen, & Mixed Forest (Classifications 41, 42 & 43)	1.0 (100%)

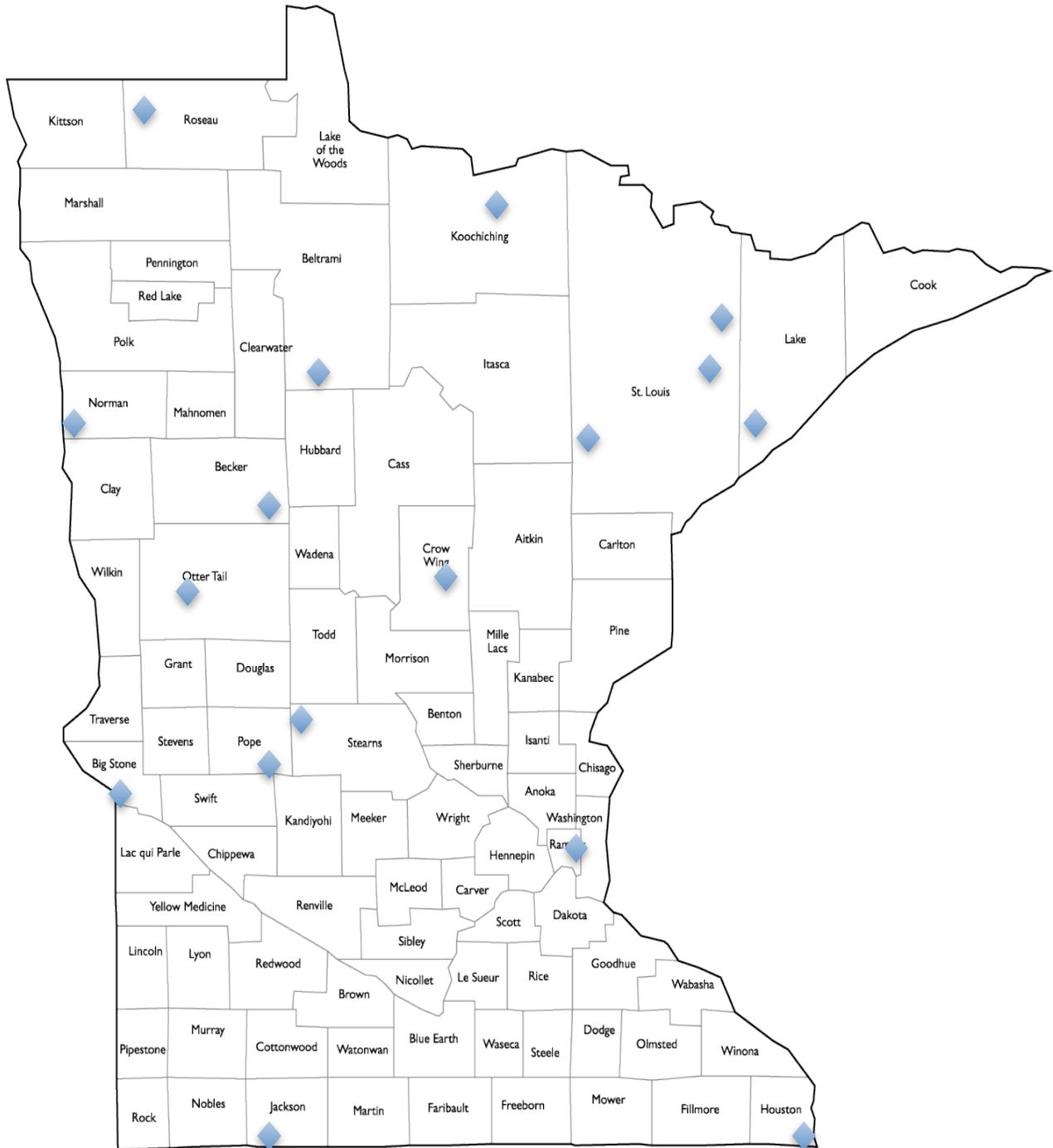
New values are based on LaRue's AHP ranking of land cover variables. Forest cover is considered the most suitable cover for cougar habitat, resulting in a score of 1.0 or 100%. Barren and developed lands are considered to be 10% as suitable as forest cover, resulting in a score of .10

Table 6: Total area of habitat types

Calculations of area for final composite map (see Figure 10).

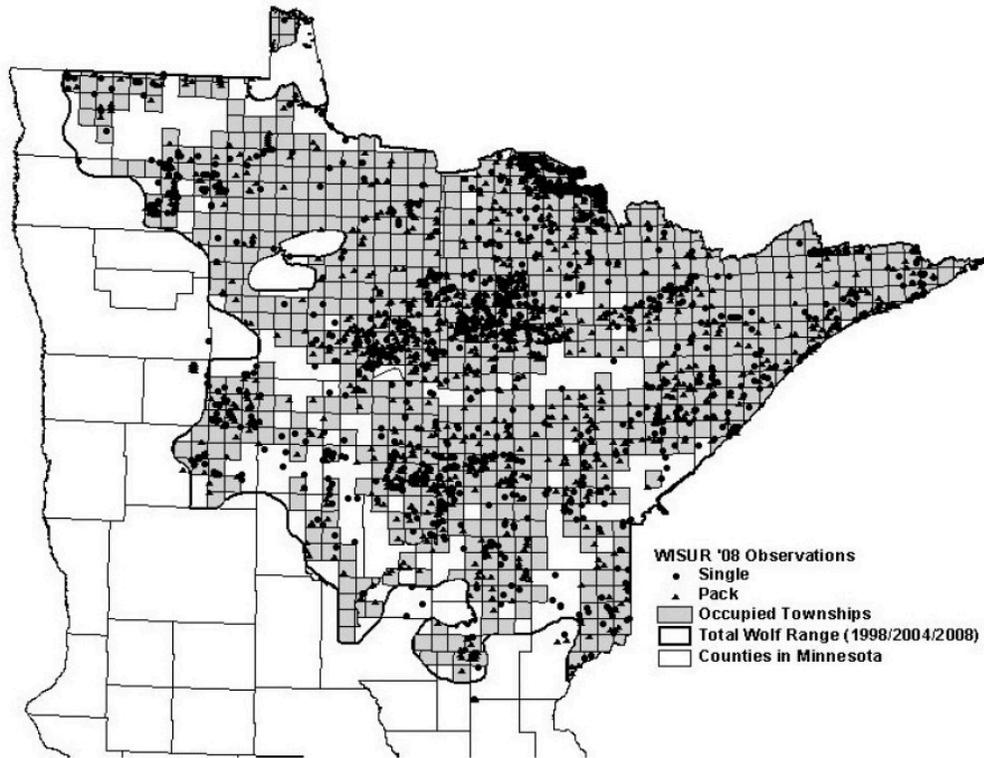
Cover Type Classification	Total Area (km ²)
Forest Cover (1.0)	56598.58
Shrub/Scrub (.58)	2788.62
Grasslands & Wetlands (.35)	32031.52
Agricultural lands (.15)	96627.81
Barren & Developed (.10)	8105.67
Wholly Unsuitable (0)	8508.15

Figure 1: Confirmed cougar sightings in Minnesota, 2004-2013



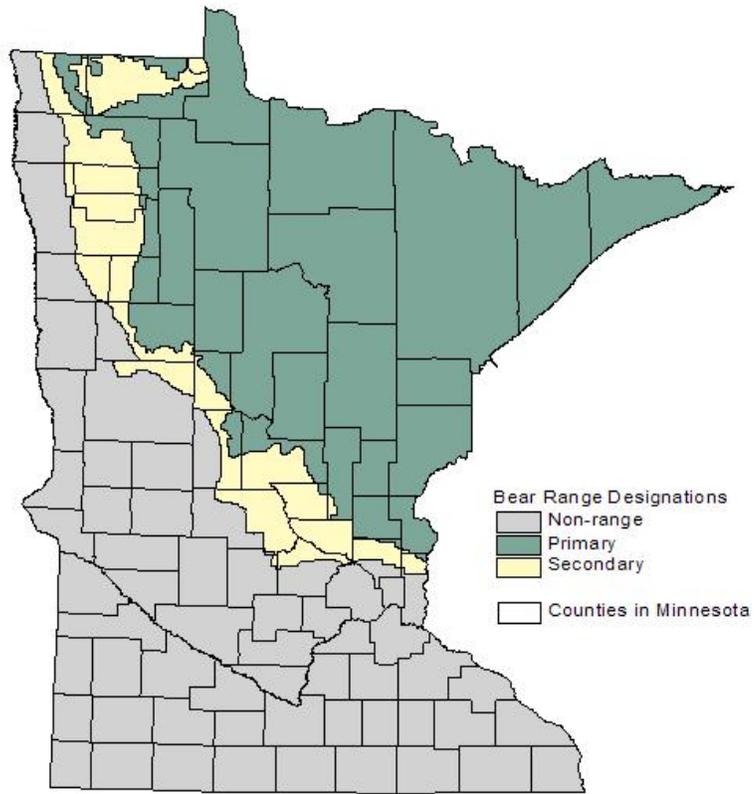
Confirmed sightings must be verifiable by a qualified professional, and may be based on physical evidence (e.g., the body of a dead cougar, DNA, scat, hair, tracks), radio telemetry, photos and/or video. Sources: The Cougar Network 2013, worldatlas.com 2013

Figure 2: Wolf-occupied townships in Minnesota, winter survey 2008



Source: Erb, J. 2008

Figure 3: Bear range by section in Minnesota, 2000



Source: Garshelis, D.L. 2008

Figure 4: Road density in Minnesota (km of roads/km²)

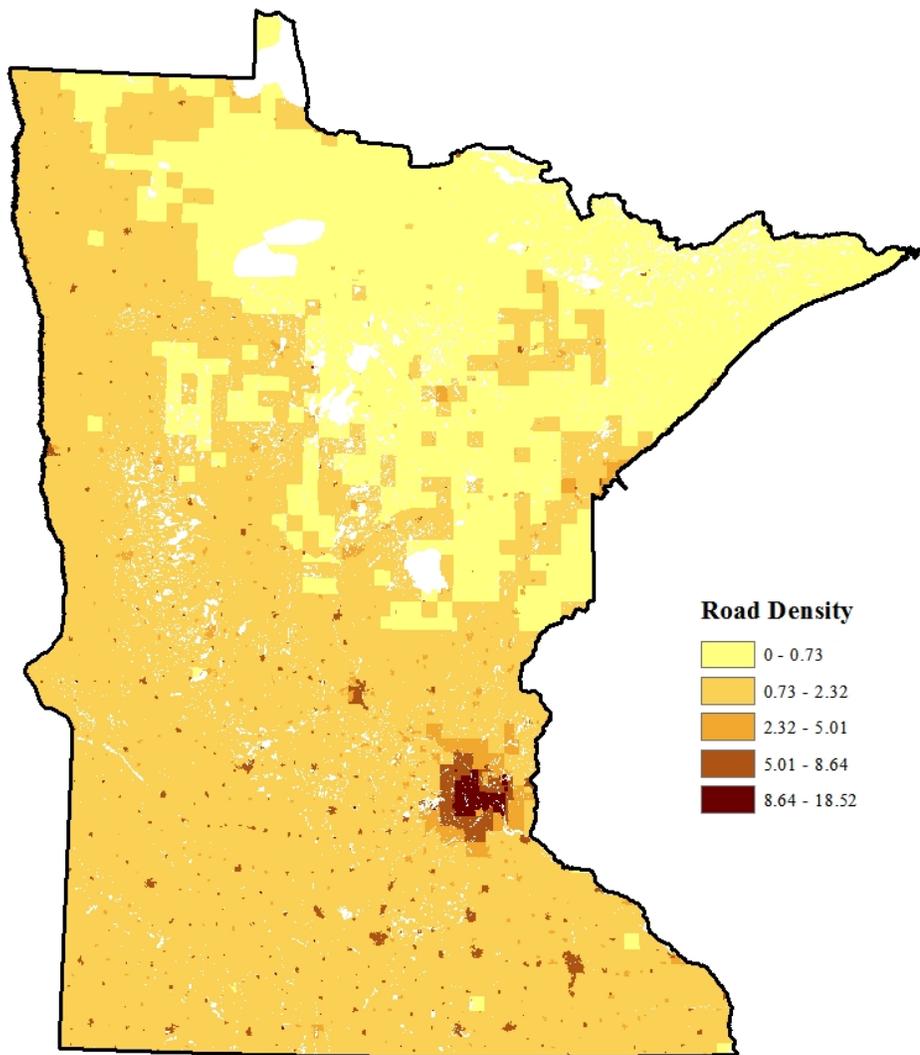


Figure 5: Deer density in Minnesota (deer/km²)

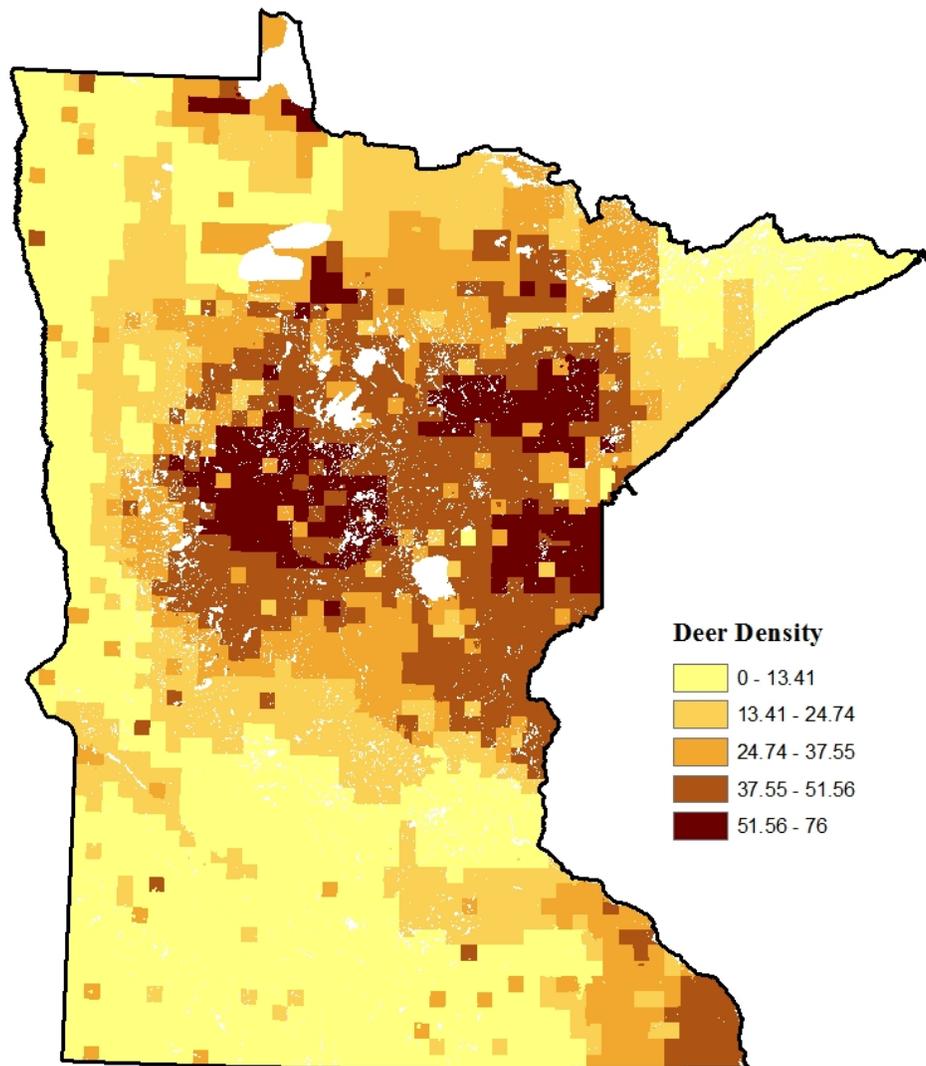
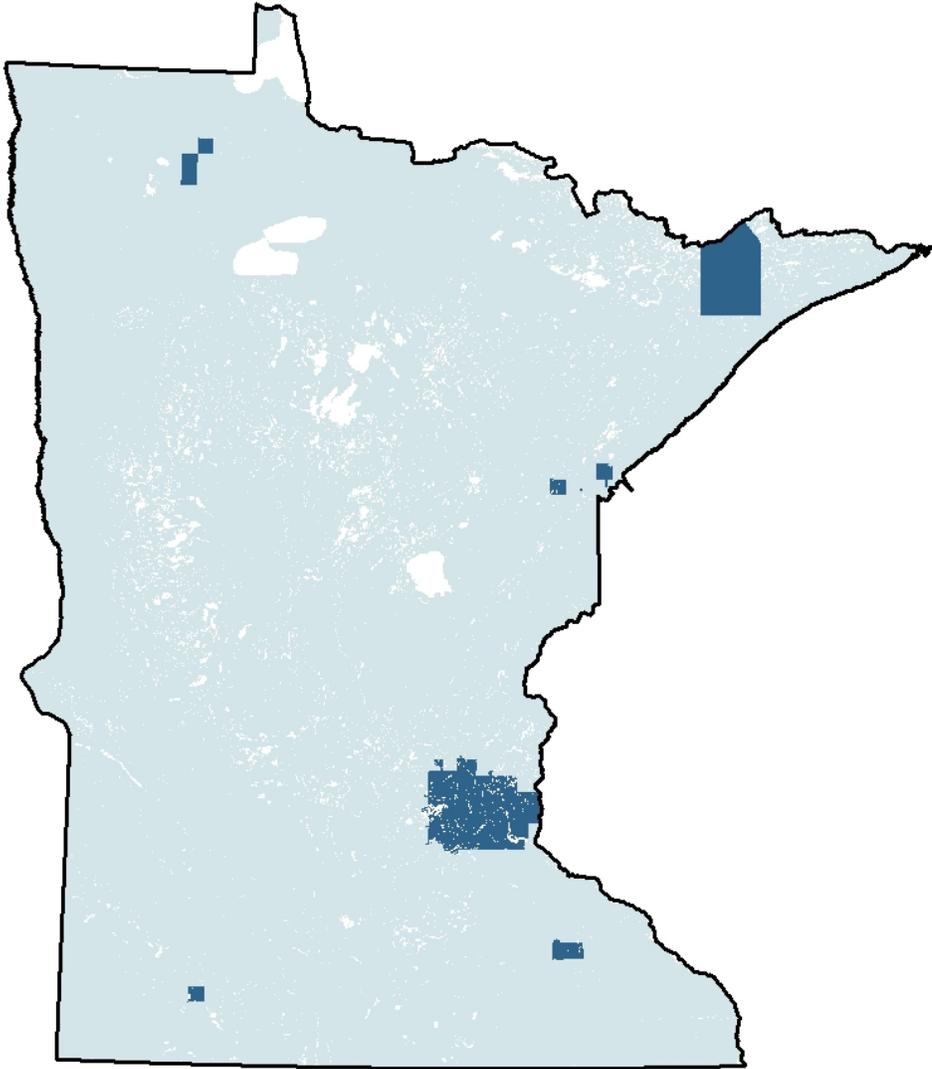
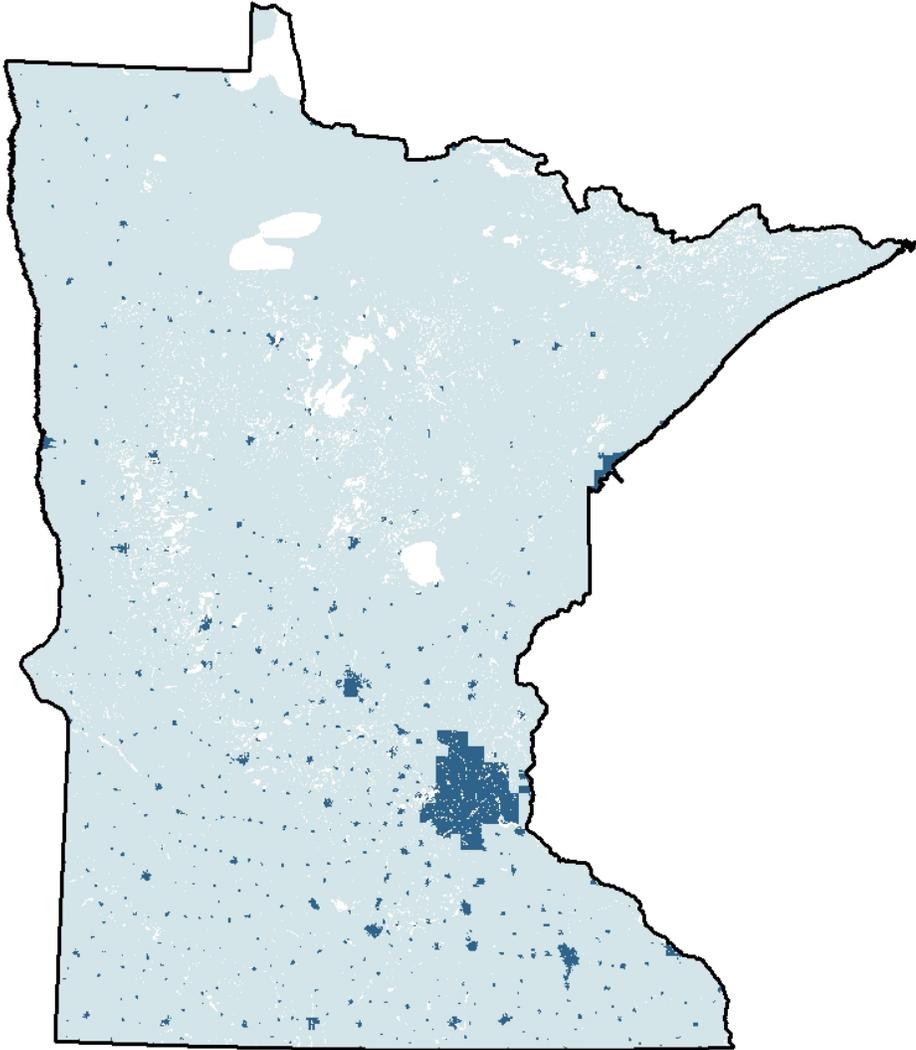


Figure 6: Factor map - Deer



Dark shaded areas indicate deer densities of ≤ 0 deer/km².

Figure 7: Factor map - Roads



Dark shaded areas indicate road densities of ≥ 3.05 km/km².

Figure 8: Land cover in Minnesota

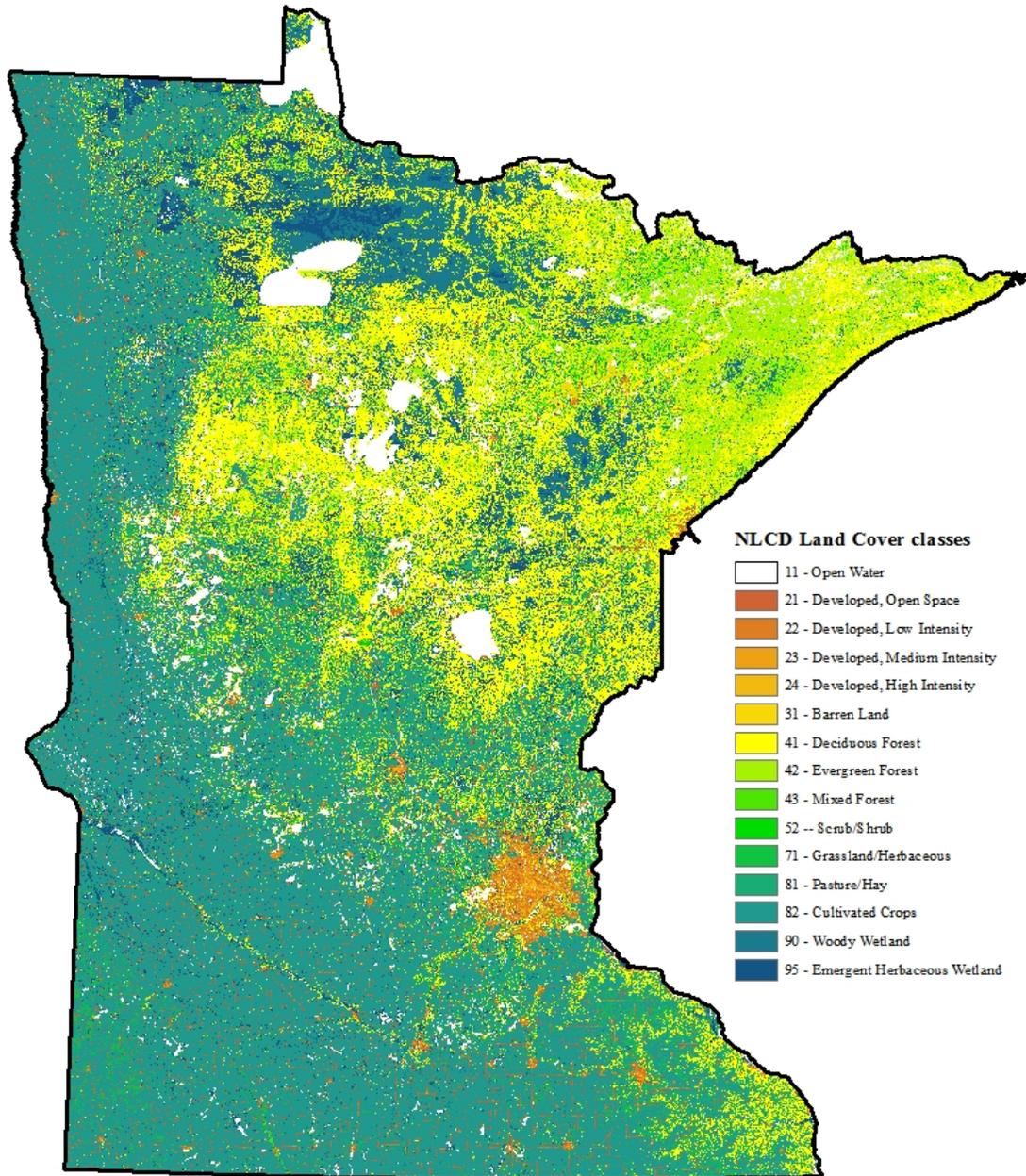


Figure 9: Reclassified land cover map utilizing weights from LaRue's (2007) AHP

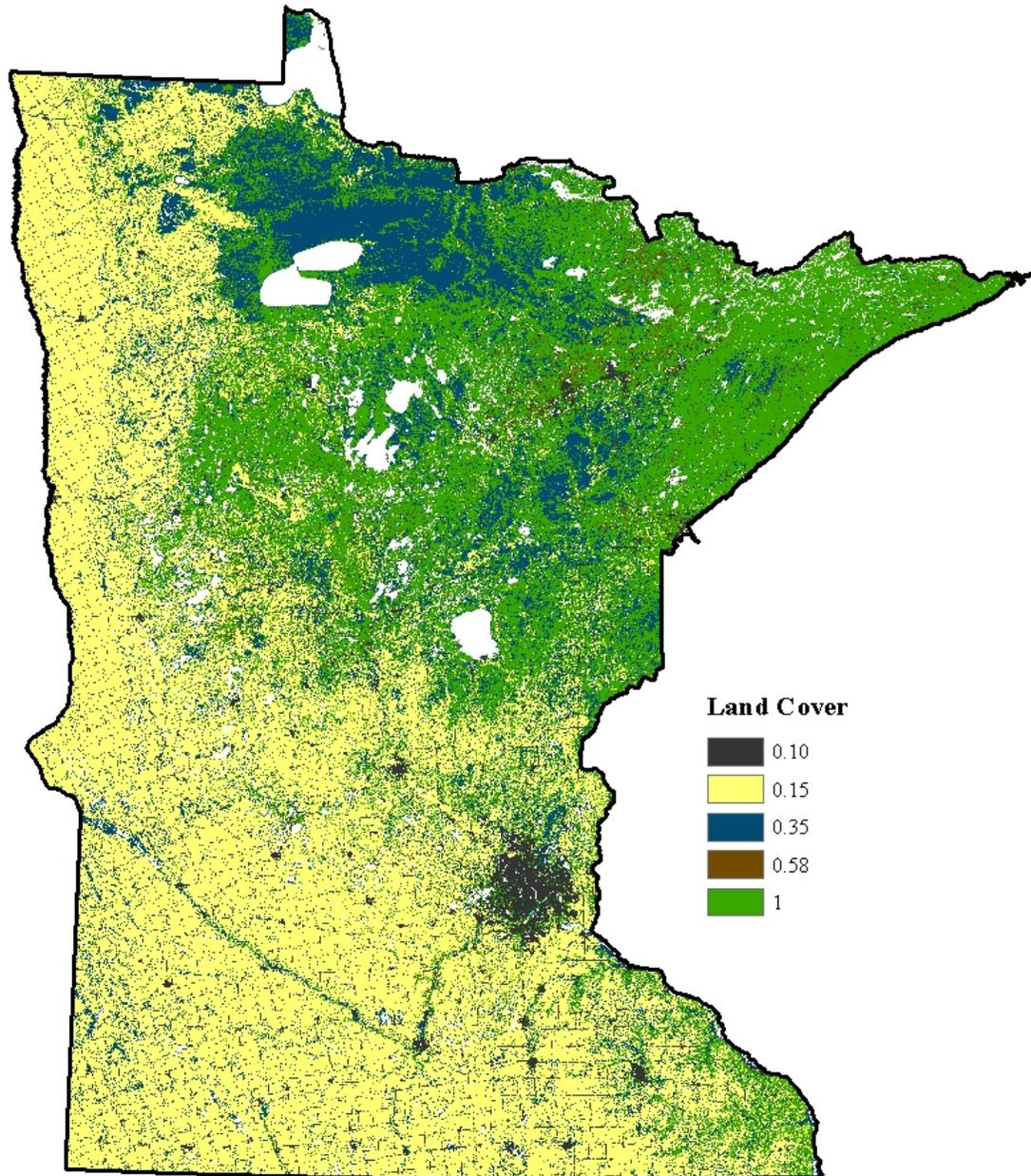


Figure 10: Final composite map of suitable cougar habitat in Minnesota

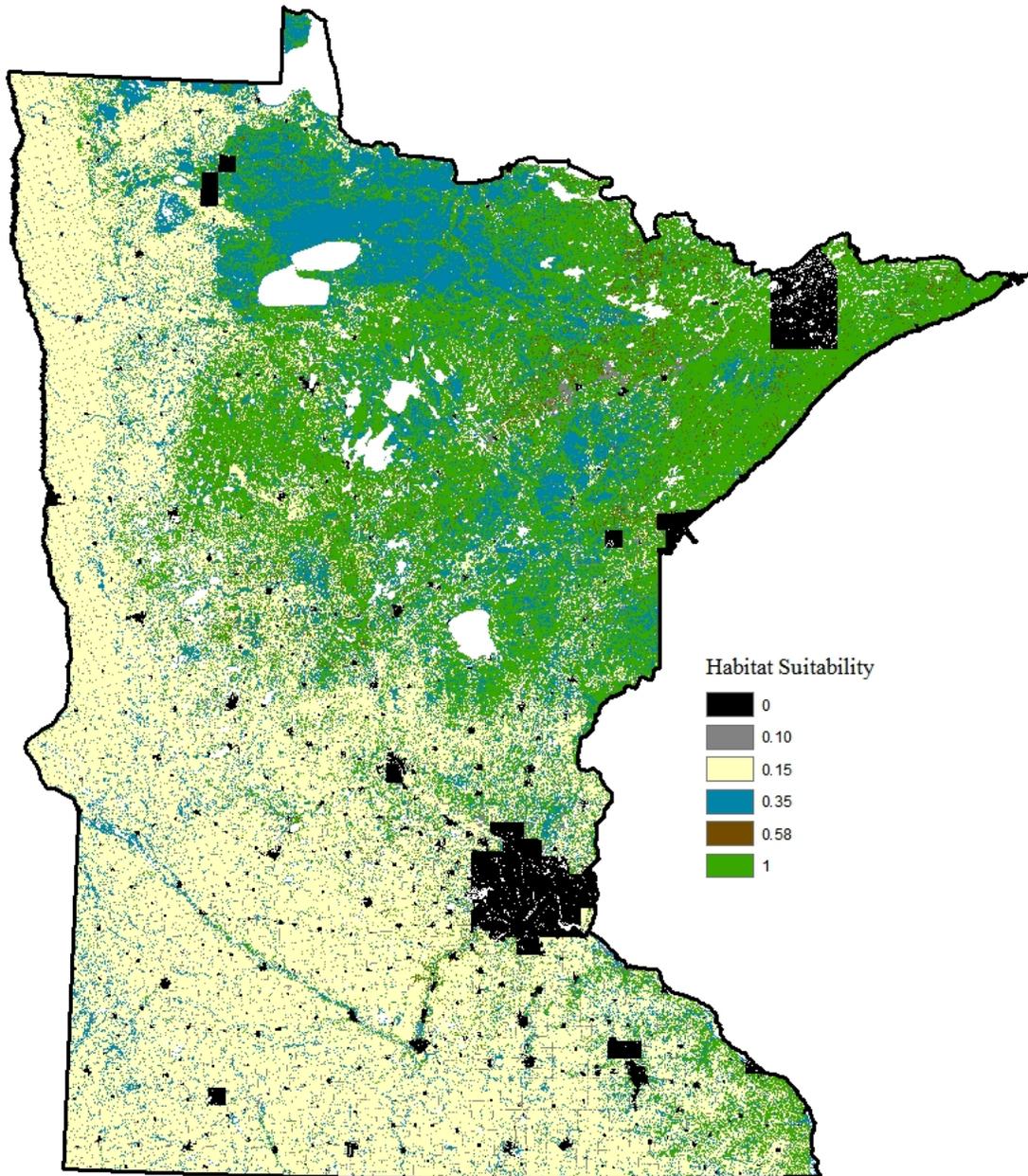
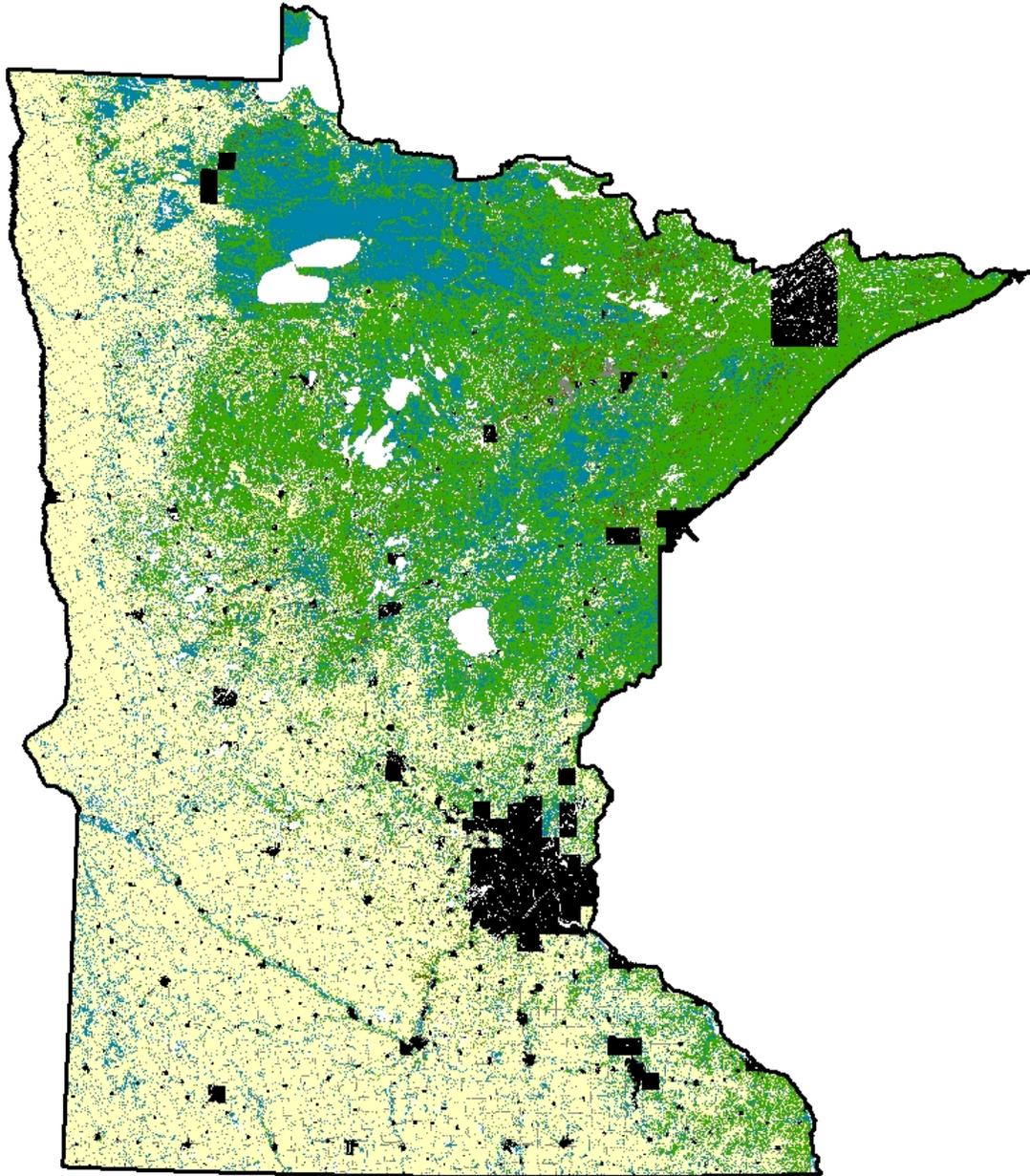
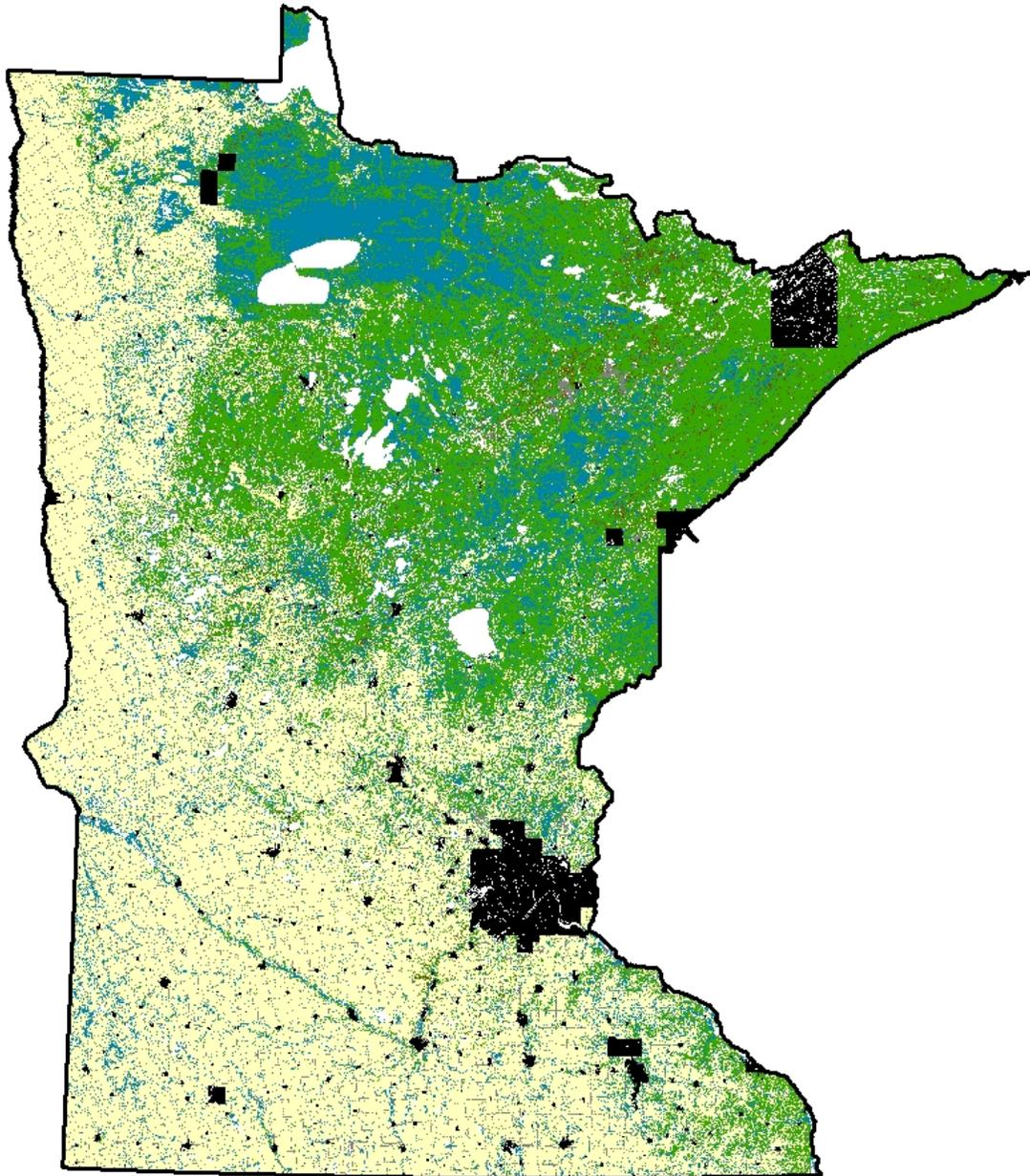


Figure 11: Sensitivity analysis: road density decreased to ≤ 2 km of roads/km²



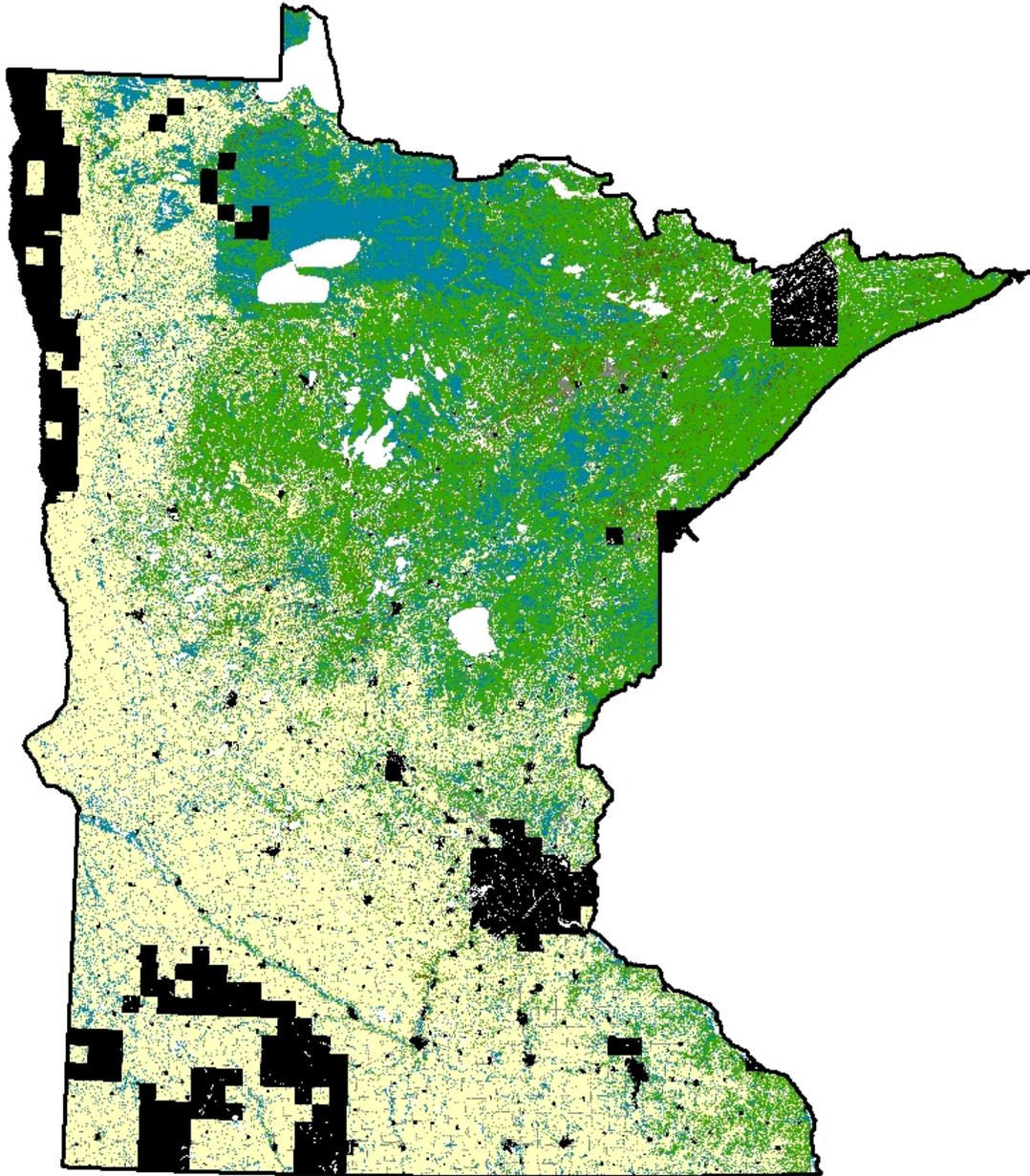
Road density cutoff value changed to ≤ 2 km of roads/km². All other model inputs remain the same.

Figure 12: Sensitivity analysis: road density increased to ≤ 6.10 km of roads/km²



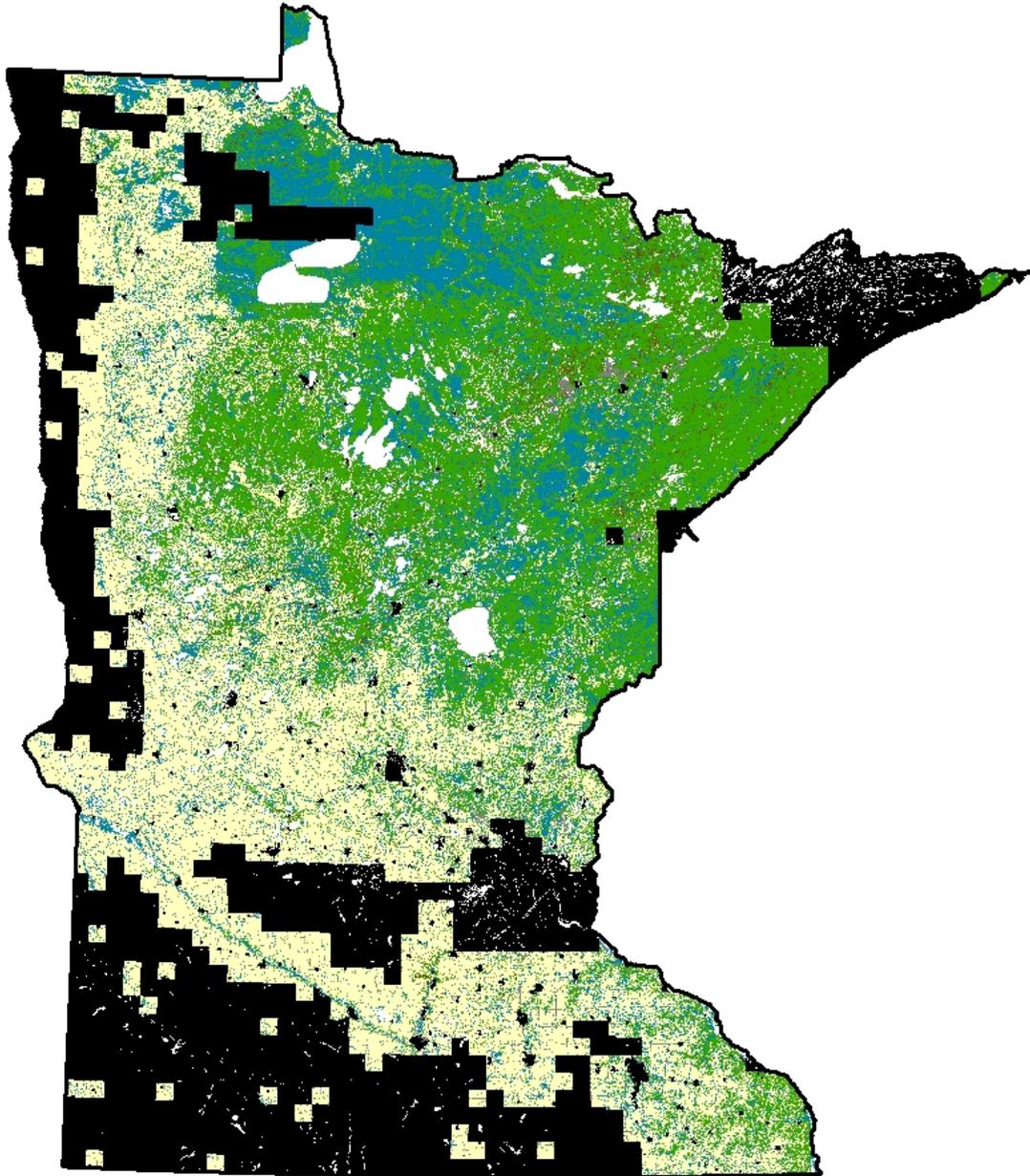
Road density cutoff value changed to ≤ 2 km of roads/km². All other model inputs remain the same.

Figure 13: Sensitivity analysis: deer density increased to ≥ 6 deer/km²



Deer density cutoff value changed to ≥ 6 deer/km². All other model inputs remain the same.

Figure 14: Sensitivity analysis: deer density increased to ≥ 11 deer/km²



Deer density cutoff value changed to ≥ 11 deer/km². All other model inputs remain the same.

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