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Home Range And Habitat Selection Of Gray Wolves (canis Lupus) On Red Lake Indian Reservation And Surrounding Areas

June Levin

HOME RANGE AND HABITAT SELECTION OF GRAY WOLVES (*CANIS LUPUS*) ON RED LAKE INDIAN RESERVATION AND SURROUNDING AREAS

by

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TABLE OF CONTENTS

LIST OF FIGURES vii

LIST OF TABLES x

ACKNOWLEDGMENTS xiii

ABSTRACT xv

CHAPTER

I. GRAY WOLVES (*CANIS LUPUS*) ON A HUMAN DOMINATED LANDSCAPE 1

Introduction 1

Research Questions and Objectives 14

Data Collection 15

Methodological Considerations 15

Literature Cited 18

II. HOME RANGE OF RED LAKE GRAY WOLVES (*CANIS LUPUS*) 28

Abstract 28

Introduction 29

Objectives 35

Methods 37

Results 48

Discussion 88

Literature Cited 96

Appendix A 102

Appendix B 105

III. HABITAT USE AND SELECTION OF RED LAKE GRAY WOLVES (*CANIS LUPUS*).. 122

Abstract 122

Introduction 123

Objectives.. 127

Methods.. 128

Results.. 135

Discussion 161

Literature Cited 167

Appendix A 173

Appendix B 175

Appendix C 193

Appendix D 212

Appendix E.. 217

LIST OF FIGURES

Figure Page

Chapter I

1. Historical distribution and distribution at the time of ESA listing of gray wolves 5

2. Current distribution of gray wolves across the contiguous United States 6

3. Locations of radio-marked northern Minnesota gray wolf packs during the 2017-2018 MNDNR survey 11

Chapter II

1. Red Lake Indian Reservation Tribal Lands 38

2. Subset of 16 gray wolf capture locations by the Red Lake Department of Natural Resources since summer 2012 42

3. 95% MCP contours for gray wolves 51

4. Variograms and continuous time movement model fits for wolves with restricted space use 54

5. Variograms and continuous time movement model fits for gray wolf M2014-14 55

6. Variograms and continuous time movement model fits for gray wolf M2016-2710 56

7. Variograms and continuous time movement model fits for gray wolf M2017-24 56

8. Mean observation time spans for all wolves 57

9. Maximum likelihood 95% AKDE contours for gray wolves displaying constricted space use 59

10. Maximum likelihood 95% AKDE home range estimates and 95% confidence intervals gray wolves 60

11. Mean percent occurrence of each season for constrained and not constrained space use data sets 65

12. 95% KDE contours for gray wolves 75

13. 95% BBMM contours for gray wolves 79

14. 95% AKDE home range estimates as a function of 95% MCP KDE, and BBMM home range estimates for comparable wolves with constrained space use 85

15. Pairwise comparisons of 95% MCP, KDE, and BBMM home range estimates for comparable wolves with constrained space use 86

16. Pairwise comparisons of 95% MCP, KDE, and BBMM home range estimates for all wolves 87

17. Maps depicting GPS relocations for all wolves 103

18. Maps depicting all applicable 95% home range estimate contours for each individual gray wolf 106

Chapter III

1. Occupied gray wolf range in northern Minnesota during the 2017-2018 Minnesota DNR survey 125

2. Red Lake Indian Reservation Tribal Lands 128

3. Reclassified National Land Cover Data land class frequencies 132

4. Individual level gray wolf habitat use 137

5. Population level gray wolf habitat use 140

6. Individual habitat use compared to habitat available within a 30km buffer for group 2011 wolves 142

7. Individual habitat use compared to habitat available within a 30km buffer for group 2016 wolves 145

8. Interaction between season and sex for speed of gray wolves ... 161

9. Population level land class composition across buffers ... 174

10. Geographic visualization of land class distribution within individual level 30km buffers ... 176

11. Geographic visualization of land class distribution within population level 30km buffers ... 191

12. Individual habitat use by gray wolves across categories compared to availability within a 30km buffer ... 194

13. Seasonal population level habitat use by gray wolves compared to availability within a 30km buffer ... 209

14. Diel population level habitat use by gray wolves compared to availability within a 30km buffer ... 210

15. Sex-based population level habitat use by by gray wolves compared to availability within a 30km buffer ... 211

16. Boxplots of gray wolf speed across different categories ... 218

LIST OF TABLES

Table Page

Chapter II

1. Subset of 16 gray wolves collared by the Red Lake Department of Natural Resources Wildlife Program since summer 2012 ... 40

2. MCP home range estimates (km^2) for gray wolves ... 50

3. Mean MCP home range estimates (km^2) by location for gray wolves ... 53

4. Maximum likelihood AKDE home range estimates (km^2) for gray wolves ... 58

5. Mean maximum likelihood AKDE home range estimates (km^2) by location for gray wolves with restricted space use ... 61

6. Maximum likelihood AKDE home range estimates (km^2) by season for gray wolves with restricted seasonal space use ... 63

7. Mean maximum likelihood AKDE home range estimates (km^2) by season for gray wolves with restricted seasonal space use ... 66

8. Maximum likelihood AKDE home range estimates (km^2) by season and diel period for gray wolves with restricted seasonal and diel space use ... 67

9. Mean maximum likelihood AKDE home range estimates (km^2) by season and diel period for gray wolves with restricted seasonal and diel space use ... 69

10. Maximum likelihood AKDE home range estimates (km^2) by diel period for gray wolves with restricted diel space use ... 70

11. Mean AKDE home range estimates (km^2) by diel period for gray wolves with restricted seasonal and diel space use ... 71

12. Mean AKDE home range estimates (km^2) by sex for gray wolves with restricted seasonal and diel space use 71

13. Linear mixed effects main model of log_{10} transformed 95% AKDE home range estimates 72

14. Top three linear mixed effects model of log_{10} transformed 95% AKDE home range estimates 73

15. KDE home range estimates (km^2) for gray wolves... 74

16. Mean KDE home range estimates (km^2) by location for gray wolves................. 77

17. BBMM home range estimates (km^2) for gray wolves 78

18. Mean BBMM occurrence estimates (km^2) by location for gray wolves 81

19. 95% home range estimates (km^2) by estimator for gray wolves.......................... 83

20. Mean 95% home range estimates (km^2) by estimator for comparable gray wolves with restricted space use (N=7) and for all gray wolves (N=16) 84

Chapter III

1. Subset of 15 gray wolves collared by the Red Lake Department of Natural Resources Wildlife Program since summer 2012 129

2. Land class percent occurrence and reclassified land categories for the 2011 and 2016 National Land Cover Data.. 131

3. Individual level percent gray wolf habitat use 136

4. Population level percent gray wolf habitat use 139

5. Individual level gray wolf habitat selection for group 2011 143

6. Individual level gray wolf habitat selection for group 2016 146

7. Population level gray wolf habitat selection for group 2011 150

8. Population level gray wolf habitat selection for group 2016 151

9. Comparison of individual and population level gray wolf habitat selection 153

10. Comparison of individual and population level seasonal gray wolf habitat selection 154

11. Comparison of individual and population level diel gray wolf habitat selection 156

12. Mean gray wolf speed estimates by category 159

13. Linear mixed effects main model for gray wolf speed estimates 160

14. Linear mixed effects top model for gray wolf speed estimates 160

15. Top individual level gray wolf habitat selection multinomial models for group 2011 213

16. Top individual level gray wolf habitat selection multinomial models for group 2016 214

17. Top population level gray wolf habitat selection multinomial models 215

18. Top linear mixed models for gray wolf speed 216

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For my mom, who always believed in me.

ABSTRACT

Every animal requires space where they can perform activities to survive and reproduce. For land animals, components of space use include area and habitat. Because most land animals are living on a human dominated landscape, understanding home range area and habitat needs is critical to their conservation. This is particularly relevant for threatened or endangered species such as the gray wolf (*Canis lupus*). The Minnesota Department of Natural Resources estimates home ranges and habitat use of wolves in northwestern Minnesota; however, a subset of this population lives within the bounds of Red Lake Indian Reservation, where The Red Lake Band of Chippewa Indians manage wolves independent of the state. The Red Lake Department of Natural Resources Wildlife Program has been monitoring wolf population numbers using GPS collars since 2012, and my objectives were to use the GPS collar data to estimate home range and habitat use of gray wolves found within and around Red Lake Indian Reservation. I used minimum convex polygon as well as autocorrelated kernel density estimation, which reveals if a defined home range does exist and better captures the autocorrelative nature of GPS relocation data, and tested for seasonal changes in the latter estimates. I also used kernel density and Brownian bridge for home range estimator comparisons. I estimated population and individual level habitat use of gray wolves and tested for habitat selection using multinomial models, which included testing for variation in

selection related to season and sex. I investigated one aspect of movement behavior by testing if land class, season, or sex predicted movement speed. I found that the average home range of Red Lake wolves was 1716km^2 using minimum convex polygon and 291km^2 using autocorrelated kernel density estimation. Only 7 of 16 total wolves displayed a restricted home range, and I was unable to detect any impact of season on restricted home range size. For wolves with a restricted home range, kernel density, autocorrelated kernel density, and Brownian bridge provided similar results, whereas minimum convex polygon provided significantly lower results. For wolves without a restricted home range, minimum convex polygon and kernel density estimation provided similar results, whereas Brownian bridge estimation provided significantly lower results. Because home range is typically estimated to inform managers of minimum required area for a species, estimator selection should be considered carefully due to the possible underestimation of home range area. I found that gray wolves on Red Lake used mostly woody wetlands, regardless of season, time of day, or sex. I detected an overall selection of woody wetlands and an avoidance of developed areas. I found that gray wolves tend to travel slower through forested areas, likely due to foraging, and faster through developed areas, which were likely used for travel along roads. Red Lake Indian Reservation consists of primarily woody wetlands, and although there is currently no limitation of available habitat for wolves, monitoring and preservation of wooded areas should continue as wolf populations on Red Lake lands continue to increase.

CHAPTER I

GRAY WOLVES *(CANIS LUPUS)* ON A HUMAN DOMINATED LANDSCAPE

Introduction

Understanding how animals use space is critical to understanding their ecology and conservation (Powell 2000). Most animals tend to confine their activities to a single area called a home range (Burt 1943). The size of the home range varies for individuals of a species, with some individuals requiring more area to meet their needs in terms of food, water, or cover required for survival and reproduction. The type of land used by individuals to make a living within their home range is one aspect of their habitat (Hall et al. 1997). High quality habitat within home ranges is ecologically valuable to a species, allowing them to survive and reproduce (Hall et al. 1997). This becomes especially critical for species or populations in decline, or that chronically occur at low density, putting them at greater risk of extinction (Yagerman 1990). Such is the case for many large predators in the modern world, including the once transcontinental gray wolf (*Canis lupus*) in the United States (Fuller et al. 2013, Mech 1970).

Human activity impacts the environments they inhabit, but widespread land conversion in particular has led to drastic results with some habitats being altered or lost entirely (Ellis et al. 2010). In addition to indirect impacts of altered habitat, some species have also experienced direct impacts on mortality through intentional or unintentional harvest (Foin et al. 1998). Species that are identified as both at risk of extinction and sufficiently valuable become targets of conservation efforts to prevent their losses. In those cases, identification and protection of crucial habitat as well as reduction in direct mortality become critical (Yagerman 1990, Foin et al. 1998). This is the situation with the gray wolf in most of the lower 48 states of the United States, where habitat loss and intentional population control resulted in the species being listed as federally endangered under the Endangered Species Act (ESA). Although that status now varies in some states, Minnesota wolves remain a federally listed species. My study focused on the identification of space and habitat use by gray wolves in northern Minnesota, specifically on and around Red Lake Indian Reservation. The gray wolf has been an endangered species for decades, but as numbers reach population levels that are sustainable in these areas (Erb et al. 2018), wolves no longer warrant protection under the Endangered Species Act and will be managed on a state and local level (Boitani 2003, USFWS 2018). My study provides information for gray wolf management decisions on Red Lake Indian Reservation as they relate to gray wolf space and habitat needs on a landscape dominated by human activity.

Land Use by People and Animals

For terrestrial species, individuals use features on the landscape to survive and reproduce, allowing populations to persist. These landscape features are identified as habitat (Johnson 1980). Populations may persist in areas where habitat is limited or unavailable, but only if they are demographically connected to other populations promoting regionally-derived recruitment. In some cases, landscape features are altered through environmental or anthropogenic forces and species can no longer persist where they did historically. If enough alterations occur, habitat can become rare or fragmented across large areas of landscape, limiting connectivity of populations for breeding.

Human actions have modified approximately 50-70% of the earth's land surface (Tucker et al. 2018). It is estimated that 39% of potential terrestrial habitat has been altered to meet the needs of agriculture and industry and an additional 37% of this habitat has been fragmented or degraded as agricultural and industrial landscapes continue to expand (Ellis et al. 2010). The ESA was passed by Congress in 1973 upon recognition that human activity was driving some species to extinction, primarily due to loss of habitat (Noss et al. 2009). According to the United States Fish and Wildlife Environmental Conservation Online System (USFWS; ECOS; 2018), there are currently 56 terrestrial species and sub-species of mammals, including the gray wolf, that are federally protected under the ESA. The primary goal of the ESA is to "restore listed species to a point where they are secure, self-sustaining components of their ecosystem" (USFWS 1996). If the goal is "recovery", then the most important factor that will contribute to reaching that goal is the availability of habitat. The designation of critical habitat, which confers habitat protection, has been found to improve the status of listed species (McDonald et al. 2012; Hagen and Hodges 2006).

In addition to the negative impacts of habitat loss and fragmentation, some species are subjected to direct mortality caused by humans. Whether intentional or not, human induced mortality of endangered species hinders the rate of recovery, even when ample habitat is available (Messer 2010). Although species federally listed as endangered are protected from legal harvest seasons, illegal harvest and killing of some species still occurs and is particularly common for mammalian predators, especially those that attack pets or livestock (Woodroffe 2000). These mammals generally have low density populations and low population growth rates causing them to be especially vulnerable to the effects of harvest and killing (Liberg et al. 2012). Even with their higher population growth rates, lethal population control led to the federal listing of gray wolves as an endangered species decades ago, and illegal killing hinders their recovery today.

History of North American Wolves

In 1905, the United States Department of Agriculture (USDA) Biological Survey Division began working closely with the United States Forestry Service (USFS) to discover methods to control coyotes and wolves (Bacon 2012). This investigation came at the request of ranchers who complained to USFS that livestock depredation by these predators was becoming a financial burden (Edvenson 1994). Congress established the Branch of Predator and Rodent Control (PARC) in 1915 under the USDA Biological Survey Division with the intent to destroy any animal causing destruction or loss of property (Bacon 2012, Edvenson 1994). The US government began to pay bounty hunters to kill wolves, and hunters used a variety of methods including traps, pits, corrals, deadfalls, snares, den hunting, and poisoning to eradicate even non-property threatening individuals (Boitani 2003, Young and Goldman 1944). Because early European settlers had brought to America a fear and antagonism towards wolves, driven by folklore and mythology, there was not much resistance to this extreme persecution (Fritts et al. 2003, Boitani 2003). By 1930, as a result of the bounty, the gray wolf, which historically ranged throughout the United States (Fig 1a), had almost entirely disappeared from the contiguous 48 states (Fig 1b), with small populations remaining in Northern Minnesota and in Isle Royale National Park of Michigan (Mech 1970, Boitani 2003).

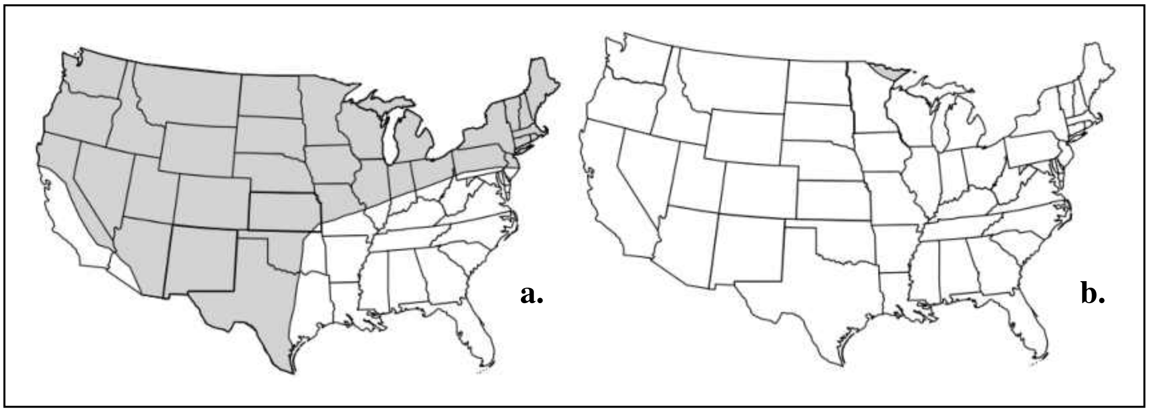

Figure 1a. Historical distribution of gray wolves across the 48 contiguous United States.
Figure 1b. Distribution of gray wolves across the 48 contiguous United States in 1974 at the time of ESA listing (USFWS 2006).

As time went on, human dispositions towards wolves became less negative (Browne-Nunez and Taylor 2002), and famed conservationist Aldo Leopold was among the first prominent Americans to speak out about his change of mind regarding the eradication of wolves (Fritts 2003). Bounties for wolves were eventually eliminated and by the 1970's several non-governmental groups were formed with the intent of conserving the wolves remaining in the lower 48 states (Fritts et al. 2003). In 1974, gray wolves in Minnesota and Michigan gained legal government protection under the ESA, which was passed only one year prior (Boitani 2003). Although Wisconsin wolves were considered locally extinct at the time, the ESA protection included Wisconsin in 1975 as wolves in Minnesota began to recolonize the Minnesota/Wisconsin border (Wydeven 2011). In 1978, protection under the ESA extended to wolves throughout the contiguous United States (Boitani 2003).

In addition to the protection of gray wolves under the ESA, US conservationists explored additional methods of promoting wolf recovery. These included the reintroduction of gray wolves into Yellowstone National Park. In January 1995, after a 70-year absence, 8 gray wolves were transported to Yellowstone from Alberta, Canada, and by 1996, 31 wolves had been reintroduced (Dax 2015, Lowry 2009). The reintroduction of wolves into Yellowstone was a human-driven success, although some populations of wolves have made their own successful reintroductions, and wolf populations are expanding across the United States (USFWS 2019; Fig 2).

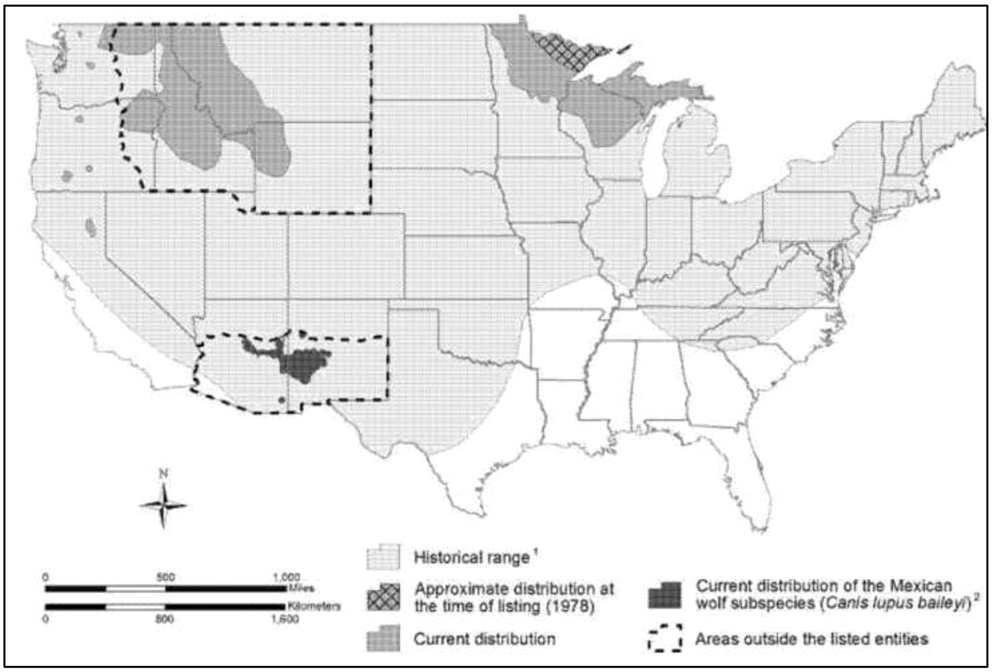

Figure 2. Current distribution of gray wolves across the contiguous United States (USFWS 2019).

Since being listed as endangered in 1974, some areas have seen such increases in gray wolf populations that the status has been reduced to threatened or even recovered (USFWS 2018). However, the path to recovery has not been an easy one. In the past 40 years, the landscape where wolves once found habitat has changed dramatically (Tucker et al. 2018), and wolves are now living on a human dominated landscape. Most forests are now heavily managed and agricultural lands have expanded. These landscapes act as ideal habitat to support white-tailed deer populations, which are primary prey for gray wolves (Nixon et al. 1991, Stenlund 1955). The higher populations of prey near agriculture and in young forests potentially support larger wolf populations (Mladenoff et al. 2009). Although wolves living in remote areas can avoid accidental or illegal, intentional killing by people, the incentive of food draws wolves closer to where people live and increases the likelihood of human-wolf conflicts (Mladenoff et al. 2009, Mladenoff et al.1997). The overlap of space use between humans and wolves adds more conflict to the broader and already controversial topic of how people should share the landscape with wildlife. Situations like these increase the risk of rifts among people who have different beliefs about how to manage expanding wolf populations. To minimize potential conflict and promote wolf survival, we must develop an understanding of the habitat needs of wolves in human dominated landscapes.

Gray Wolf Ecology

Understanding habitat requirements and space use begins with understanding the ecology of a species. The gray wolf is a broadly distributed and versatile habitat generalist that inhabits the Northern Hemisphere as an apex predator (Mech and Boitani 2003a, Mech 1970). As carnivores, wolves consume prey in various sizes ranging from snowshoe hare to bison (Peterson and Ciucci 2003). Wolves generally live in packs, allowing them to hunt large ungulates, but individuals and pairs can successfully capture smaller prey (Mech and Boitani 2003b). Packs usually consist of a pair of breeding adults and their pups and, in some instances, other adults who may also breed (Mech 1970, Young and Goldman 1944). Most wolf packs maintain fewer than 8 members, and pack size is primarily dependent upon prey availability (Mech and Boitani 2003b, Mech 1970).

Wolves live 6-8 years in the wild, but some have been reported to reach 13 years old (Mech 1988). Wolves breed from late January to early March and have a 9-week gestation period (Mech 1970, Brown 1936), with birthing of pups usually occurring in April or May (Busch 2018). Average litter sizes are 4-6 pups (Mech 1970). In early spring, shortly before giving birth, wolves will establish a den site (Busch 2018). Non-breeding pack members travel more throughout the home range than breeders, who spend more time closer to the den site (Jedrzejewski 2004, Mech 1970, Ruprecht 2012). The pack stays around the den until late summer when juvenile pups are 8-10 weeks old and able to move about (Mech 1970). During this time, they use rendezvous sites to rest and nurse (Joslin 1967, Fuller 1989, Mech 1970, Milakovic et al. 2011). By late autumn or early winter, pups no longer require specific sites for rest, and the pack returns to its wayfaring lifestyle, where they consistently travel throughout their home range until the next denning season (Mech 1970). Because yearling pups are often still with the pack when a new litter is born, winter pack numbers tend to be larger. Pups will stay with their natal packs until they reach sexual maturity at 22 months. At maturation, they will either rival the current wolf hierarchy, or disperse to find mates or a new pack (Mech and Boitani 2003b, Mech 1970, Young and Goldman 1944). As an itinerant species, wolf dispersals can exceed 600km (Mech 1970, Van Camp and Gluckie 1979, Fritts 1983).

Wolves are territorial and members of a pack are generally intolerant of outside wolves who approach territory boundaries (Mech 1970). A territory for a pack or a dispersing wolf is a defended area, concordant with or located within the home range. Home ranges, which are the areas where the packs or animals regularly traverse and forage, can sometimes overlap, whereas territories usually do not (Mech 1970, Burt 1943). Often, adjacent packs are separated spatially or temporally, and the territory and home range for the pack are concordant (Mech 1970). Wolf home range sizes are mostly determined by the availability of land and prey (Fuller et al. 2003). When prey densities are low, average pack home range size tends to increase, and can be more than 1000km^2 (Mech 1988, Mech et al. 1998). In contrast, wolf home ranges average 100-200km^2 in areas where prey density is high (Fuller et al. 2003). Packs continuously move throughout their home ranges during both summer and winter, using low-traffic dirt roads, game trails, and fire breaks as travel routes (Thompson 1952, Mech 1970, Zimmerman et al. 2014). Because of the need to care for pups at den and rendezvous sites, area use within the home ranges may be constricted during summer (Mech 1970). Movements tends to follow waterways, and wolves may travel across ice during winter (Mech 1970, Joslin 1966, as cited in Mech 1970).

Minnesota Wolves

When wolves were extirpated in most of the contiguous 48 states, a small population of several hundred wolves remained in northern Minnesota, despite the bounty that remained in place until 1965 (Mech 1970, Boitani 2003). Minnesota wolves received federal protection under the ESA in 1974 when they were listed as endangered and remain listed as threatened today. Wolves in Minnesota were briefly removed from the Endangered Species List in January of 2012, after the USFWS declared populations sustainable (50 Fed. Reg. 04420). During this time, wolf management was handled on a state level, and in the fall of 2012, the Minnesota Department of Natural Resources (MNDNR) implemented a 3 month wolf harvest season as a way to control wolf populations, with 413 of the estimated total 2,921 wolves having been harvested (Stark and Erb 2013, Erb 2008). Two more harvest seasons occurred in the fall of 2013, with 238 of the estimated total 2,211 wolves having been harvested (Stark and Erb 2014, Erb et al. 2013) and, in the fall of 2014, with 272 of the estimated 2,423 total wolves having been harvested (Minnesota Department of Natural Resources, Erb et al. 2014). In December of 2014, a federal court ruling placed the wolves back on the Endangered Species List after legal complaints were made by the Humane Society of the United States and other animal welfare groups, claiming that Minnesotan wolves would not continue to recover if susceptible to intentional human-induced mortality. Their current threatened status prevents hunting and killing of wolves for any reason other than self-defense. In cases where people feel that their livestock are in danger of predation by wolves, Federal workers can remove wolves once proof of endangerment is provided (50 Fed. Reg. 04420).

In March 2019, USFWS again declared wolf populations sustainable and claimed that gray wolves across the contiguous United States no longer meet the requirements for listing under the ESA (78 Fed. Reg. 35664). The Center for Biological Diversity brought a suit to the USFWS, claiming that the lack of a nationwide gray wolf recovery plan violates the ESA, and wolves should remain protected until a plan is in place (US Dept. of Int. v. The Center for Biological Diversity 2018).

According to the 2018 Distribution and Abundance of Wolves in Minnesota report published by the MNDNR, an estimated 465 wolf packs currently exist in Minnesota, with an average of 4.85 wolves per pack during winter (Erb et al. 2018, Fig 3). Wolf pack numbers decreased from 508 wolf packs in 2017, but this is not considered to be a statistically significant decrease and MNDNR believes that Minnesota wolf numbers are currently stable (Erb et al. 2017; Erb et al. 2018).

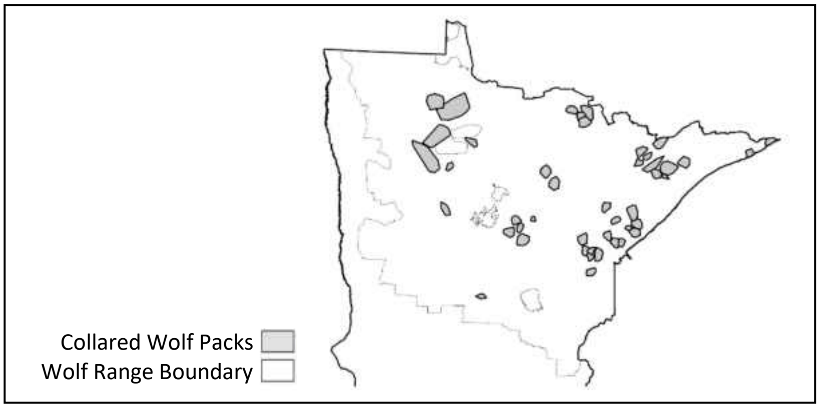

Figure 3. Locations of radio-marked wolf packs in Northern Minnesota during the 2017-2018 MNDNR survey (Erb et al. 2018).

Current average space use for Minnesota wolf packs is 158.97km^2 based on the estimation method used by MNDNR, and sizes have been relatively stable since 2003 (Erb at el. 2018). Typical land cover for wolf territories includes an average of 55% woody wetlands and deciduous forest (Erb at el. 2018). Prior studies have shown that recovering wolf populations in Minnesota are primarily using forest and wetlands as habitat and generally avoid anthropogenic features such as agriculture and high-traffic roads (Mladenoff et al. 2009, Oakleaf et al. 2006). Although there is a general avoidance of human dominated landscapes, Mladenoff et al. (2009) found that agricultural land, which can support denser prey populations, accounted for 5.3% of wolf pack home ranges. This spatial overlap with human land use increases the likelihood of conflict between Minnesotans and wolves (Mladenoff et al. 1997).

Human-wolf conflict occurs directly, because wolves and humans compete for resources, and indirectly, because humans disagree with each other over issues related to wolf management (Madden 2004). In Minnesota (a part of the Great Lakes Region), direct human conflict occurs mostly because of wolf depredation of livestock (Ruid et al. 2009). Instances of depredation have increased with the expansion of wolf populations (Fritts 1982, as cited in Harper et al. 2008, Harper et al. 2005). As of 2018, the threatened status of wolves protects them from anyone who is not a USFWS official, but when federal protection is removed, state managers will manage conflict involving livestock depredation (Mech 1998, Mech et al. 2000).

Although those who are directly impacted by wolf depredation (e.g. some livestock producers) tend to support lethal control, attitudes of those less affected have shifted towards empathy for wolves, which are seen as a symbol of wildness and nature (Williams et al. 2006). The high reproductive potential of wolves, in combination with their high dispersal capability, ensure that there are few places where wolves could be restored without requiring some form of control, but these shifted empathetic attitudes make decisions about how to control populations difficult (Mech 1995). Indirect human-wolf conflict, resulting from the disagreement over how to proceed with wolf management, could potentially be reconciled with the identification and preservation of wolf habitat away from human activities and by understanding the region-specific attitudes of people who may or may not have direct conflict with wolves (Mech 2017).

Red Lake Wolves

Red Lake Indian Reservation is a sovereign nation with its own government that is independent of the state of Minnesota. This includes management of Tribal natural resources. Specifically, when wolves are federally delisted, Red Lake has a wolf management plan that was approved by the Red Lake Tribal Council on September 14, 2010 by Resolution No. 158-

10. The Red Lake Band of Chippewa Indians Gray Wolf Management Plan (RLDNR 2010) prohibits wolf harvest of any kind for any reason and designates Red Lake lands to be a wolf sanctuary. In contrast, as of this thesis, the Minnesota Wolf Management Plan (MNDNR 2001) has been shown to allow harvest to control wolf populations. The plan is to be revised in 2020 in consideration of the time since it was last updated (Minnesota Department of Natural Resources). Historically, Ojibwe people have felt a spiritual union to the gray wolf, ma'iingan, and this leads current Red Lake Tribal residents to have little support for lethal population control (David 2009). Prior to the arrival of European settlers, when Native Americans would hunt wolves, they would do so with utmost respect and apologies to the spirits of the wolves (Fritts et al. 2003). That feeling persists in current times: a 2009 survey administered to Red Lake members revealed that roughly 80% of members would not support harvest and very few considered wolf numbers to be too high (RLDNR 2010). However, despite the overwhelming spiritual respect for ma'iingan, there is concern that uncontrolled populations could lead to negative impacts on deer populations, which are a food source for many members (Shelley 2010, RLDNR 2010). At this time, the decision to implement harvest seasons on Red Lake Indian Reservation has not been considered.

There are approximately 11 known wolf packs with an unknown number of individuals per pack using lands owned by the Red Lake Band. Current estimates of home ranges for these packs average 236km^2 (RLDNR, unpublished data 2020). However, these estimates need to be updated and confirmed using more accurate methods. Habitat selection and movement patterns are currently unknown. Preliminary analyses show wolves avoiding areas of concentrated development on Red Lake lands. (RLDNR, unpublished data 2012), but how they are using the broader landscape remains uncertain. This information is needed by

Red Lake wildlife managers to ensure that wolves on Red Lake can continue to thrive and maintain a prominent role in the regional ecosystem and Red Lake Band culture.

Research Questions and Objectives

As top predators and an important component of ecosystems, and because of their conservation status, there have been many research studies on the life history, habitat, and home ranges of gray wolves across the globe (Mech and Boitani 2003b, Musiani et al. 2010). Most critical to their conservation is habitat availability, and as wolves and human populations come into contact, it is essential to understand how the two can coexist (Mech 2017). Conflicting attitudes towards wolves (e.g. Red Lake Indian Reservation residents and residents in the surrounding areas) mandates particular attention to how wolves use the landscape. If and when wolves are removed from the Endangered Species List, long term, conflicting management plans that result from the differences in attitudes can have serious state-wide implications. Given the connectivity of the landscape and the territoriality and wide dispersal potential of gray wolves, we can assume that exchange of individuals occurs across the reservation boundaries. My research examined home range and habitat selection of gray wolves on and around Red Lake Indian Reservation. This provides some insight into how wolves are using space on Red Lake as well as how often and how far Red Lake wolves are using space surrounding tribal lands, where state management practices contradict those of Red Lake. Seasonal space use comparisons will be especially important when state managers implement seasonal harvest. My primary objectives were to:

1. **Estimate Red Lake wolf home range areas.**
2. **Estimate Red Lake wolf habitat use and selection.**

Data Collection

The Red Lake Department of Natural Resources Wildlife Program (RLDNR-WP) implemented a wolf monitoring project in summer 2012 with the intention of recording gray wolf population numbers and pack areas within Red Lake Indian Reservation boundaries (RLDNR 2010). Since the project began, 27 gray wolves have been captured and collared with global positioning system (GPS) units. The collar data from a subset of 16 wolves was found to be sufficient for analysis in this study. The Red Lake project is ongoing and wolf capture and data collection will continue through the foreseeable future. My analysis is based on GPS location data collected from May 2012 through August 2018.

Methodological Considerations

The first step in estimating animal space use is determining the extent of the landscape encountered by the animals and whether there is evidence for a defined home range within that land use. Subsequent analyses quantify the landscape features within the area or home range. There are several space use estimators from which home ranges are inferred, with each having its set of advantages and disadvantages. One of the simplest estimators to calculate is minimum convex polygon (MCP). This estimator connects the outermost points from a set of GPS fixes creating the smallest convex polygon possible around the points. The area inside is then often considered the home range (Mohr 1957, Hayne 1949). This is the current method used by the MNDNR to estimate gray wolf home ranges and pack numbers in Minnesota (MNDNR 2017). The problem with the method is that it overestimates space use, especially for animals with larger home ranges (Douglas-Hamilton et al. 2005). It does not account for uneven use of space within the boundaries and subsequently it does not necessarily meet the commonly accepted definition of home range as the area traversed during normal activities, excluding explorations beyond those areas, provided by Burt (1943). The polygon estimate is not calculated based on probability and although this method is still commonly used, it is well documented that it is not appropriate for estimating home range (Borger et al. 2006).

Kernel density estimation (KDE) addresses some of the limitations associated with MCP (Borger et al. 2006) and incorporates a probabilistic model, therefore giving a more accurate home range estimate (Worton 1989, Borger et al. 2006). Despite being a better estimator than MCP, it is statistically biased; it assumes location points are independently and identically distributed in a probabilistic sense, and so it does not account for spatial or temporal autocorrelation of GPS fixes (Silverman 1986, Noonan et al. 2018). Autocorrelation can be removed from samples prior to using KDE by subsampling data, but this removes biological information because animals do not move non-randomly (De Solla et al. 1999).

Non-independence in GPS location data can be somewhat accounted for with a Brownian bridge movement model (BBMM) which uses the sequence of GPS fixes in a discrete time fashion to estimate the probability path for the animal (Horne et al. 2007). Analyzing the points sequentially rather than independently gives a more accurate estimate of space use than KDE, but it still does not capture the autocorrelation in the data completely (Horne et al. 2007), thus leaving out information that can be used to get an even more accurate space use estimate. Continuous-time movement models use statistical methods to account for and correct the bias associated with autocorrelated data (Fleming et al. 2015, Noonan et al. 2018). This method is the most appropriate method for estimating space use from autocorrelated data. A constrained home range, as defined by Burt (1943), can be inferred from this analysis using the autocorrelated kernel density estimator (AKDE) of

Fleming et al. 2015. If there is evidence for a defined area of use, a more accurate estimate of home range can be obtained. Even with insufficient evidence of a limited area range (home range), continuous-time movement models like AKDE can estimate a probability of occurrence distribution (Calabrese et al. 2016). Brownian-bridge models actually estimate only the latter (occurrence probability along a trajectory of discrete relocation points) and not an asymptotic (i.e. limited area) probabilistic home range, which should represent space use over the course of multiple instances of trajectories, and not simply the single one recorded during the sampling period (Fleming et al. 2015). However, these occurrence estimates are routinely interpreted as home range estimates (Fleming et al. 2015, Calabrese et al. 2016) and are therefore included in this study. For analysis of space use, I implemented MCP for comparison to MNDNR home range estimates and AKDE to obtain more accurate home range estimates. I also implemented KDE and BBMM to understand the implications of using each estimator because each method works under a different set of assumptions.

Having an accurate estimate of home range is essential for habitat use, selection and movement pattern analyses. Habitat use and selection analyses requires knowing what animals have available to them across the landscape. Only then can I analyze what they are definitively using, and what they are using in relation to what is available. The MNDNR uses remote sensing imagery to determine available habitat within Minnesota gray wolf home ranges. Specifically, they use National Land Cover Database classified LandSat Thematic Mapper imagery (Yang et al. 2018) provided by the United States Geological Survey (USGS). This land cover data includes classified categories that are ecologically important to wolves and was used for the identification of available habitat in the habitat selection analysis.

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CHAPTER II

HOME RANGE OF RED LAKE GRAY WOLVES (*CANIS LUPUS*)

Abstract

An animal's home range is the area it uses to gather food, mate, and rear young. Although all species require sufficient area to perform these activities, adequate area is particularly important for those that are threatened, as is the case with the gray wolf (*Canis lupus*) in northeastern Minnesota. The Minnesota Department of Natural Resources estimates home ranges of wolves in this region; however, a subset of this population lives within the bounds of Red Lake Indian Reservation. The Red Lake Indian Reservation is a sovereign nation where wolves are managed independent of the state Red Lake lands are declared to be a wolf sanctuary. The Red Lake Department of Natural Resources Wildlife Program has been monitoring wolf population numbers using GPS collars since 2012, but the home ranges of wolves on the reservation had not been estimated. Here, I used both traditional and modern methods to estimate home ranges to inform management. I used minimum convex polygon as is used by the Minnesota Department of Natural Resources, as well as autocorrelated kernel density estimation, which better captures the autocorrelative nature of GPS relocation data, and importantly, reveals if a defined home range does exist. I used the latter to test if home range area changes seasonally. Additionally, I used kernel density and Brownian bridge

to understand the implications of using one method versus another. I found that the average home range of Red Lake wolves was 1716km^2 using minimum convex polygon and 291km^2 using autocorrelated kernel density estimation. Of the 16 wolves used in the study, only 7 displayed a restricted home range, and I was unable to detect any impact of season on restricted home range size. I found that for wolves with a restricted home range, kernel density, autocorrelated kernel density, and Brownian bridge performed similarly, whereas minimum convex polygon provided significantly lower results. For those without a restricted home range, minimum convex polygon and kernel density estimation performed similarly, whereas Brownian bridge estimation provided significantly lower results. Because home range is typically estimated to inform managers of minimum required area for a species, the underestimation of home range could have dire effects, and estimator selection should be considered carefully.

Introduction

Space use patterns of gray wolves (*Canis lupus*) in Minnesota have been studied extensively (Fritts 1983, Fuller 1989, Fuller et al. 1992, Mech 1970) since the species' near eradication in 1933 (Mech 1970, Boitani 2003). One fundamental and crucial component of space use is the amount of area an animal needs to make a living (survive and reproduce), or its home range (Powell 2000). Burt (1943) defined home range as "the area traversed by the individual in its normal activities of food gathering, mating, and caring for young". As Minnesota wolf populations recover and expand, it will be critical to have a thorough understanding of these spatial requirements, particularly in areas that were once traversed by wolves and which have now changed drastically as humans continue to dominate and alter the landscape (Ellis et al. 2010, Mech 2017).

Current Minnesota wolf populations are living on a landscape dominated by industrialization and agriculture (Ellis et al. 2010, Erb et al. 2018), and although wolves are habitat generalists (Mech 1970), there is much to learn about how they use space in this dynamic environment. Gray wolves were initially eradicated because of the perceived conflict between wolves and colonizing farmers and ranchers (Mech 1970, Boitani 2003). Although current attitudes towards wolves are highly variable and possibly more accepting, agriculture has increased significantly, so, in addition to the changed landscape and availability of habitat, human-wolf conflict is still a primary issue for recovering populations (Mladenoff et al. 1997, Harper et al. 2005, Mech 2017). Quantifying the area currently used by wolves will not only allow us to understand the space needed to make a living, but also help us learn how wolves and humans can share the landscape with minimal conflict.

The Minnesota Department of Natural Resources (MNDNR) estimates home range sizes every five years for wolves in Minnesota using data from several agencies (e.g. USGS, Voyageurs National Park; Erb et al. 2018). The current average home range size for these wolves is estimated to be 159km^2 (Erb et al. 2018). Although the MNDNR receives GPS collar information from the Red Lake Department of Natural Resources (RLDNR) for use in its state home range average, home ranges for wolves found exclusively on Red Lake Indian Reservation have not been precisely estimated. Current approximate average home range estimates for Red Lake wolves are 236km^2 (RLDNR, unpublished data 2020). Distinguishing between wolves across the state and wolves found on Red Lake Indian Reservation is important because The Red Lake Indian Reservation, as a sovereign nation, manages wolves independent of the state, and management objectives will likely diverge upon removal of Endangered Species Act protections. A crucial difference between state and reservation management is the use of lethal population control (MNDNR 2001, RDLNR 2010). The Red Lake Band of Chippewa Indians have a great spiritual connection to gray wolves and prohibit harvest of any kind (Shelley 2010, RDLNR 2010). This drives the desire to know about wolf space requirements across Red Lake lands, as well as where, and to what extent, Red Lake wolves cross reservation boundaries and become subject to Minnesota state management practices.

The RLDNR Wildlife Program (RLDNR-WP) has been tracking gray wolves since 2012 using GPS technology, which allows for more frequent and precise tracking of animal movement than has previously been available with very high frequency (VHF) radio telemetry (Kays 2015). However, a problem occurs with more frequent sampling when the methods used to analyze the data for home range estimation do not account for the increased sampling frequency (Noonan et al. 2018).

The MNDNR uses the traditional minimum convex polygon (MCP; Mohr 1947) method for home range estimation (Erb et al. 2018). This method along with other traditional methods such as kernel density estimation (KDE; Silverman 1986, Worton 1989), assume that the relocation points are independently and identically distributed (IID). However, animal movement is a continuous process (Fleming et al. 2015), which means that locations are not all independent, but rather, temporally autocorrelated with greater similarity of relocation points that are closer together in time (Fleming et al. 2015, Calabrese et al. 2016). Autocorrelation within a time series of points can occur with respect to the sequence of locations, velocity, and acceleration, which provide additional information about probability of future locations (Fleming et al. 2015). Although MCP and KDE are still commonly used for estimating home range (Laver and Kelly 2008), the usual result of methods that do not account for autocorrelation is a seemingly more precise home range estimation than warranted by the information actually contained in the data (Fleming et al. 2014, Fleming et al. 2015, Fleming and Calabrese 2017, Noonan et al. 2018). This is because points are assumed to convey independent information when, in actuality, they do not, inflating the apparent sample size. They also fail to account for the probability of locations along a movement trajectory that are associated with autocorrelated velocities. Because traditional estimators cannot reflect the true probability of space use, the area contours they produce, which are interpreted as home ranges, are often smaller than those produced by methods that account for uncertainty. With the increased use of GPS tracking technology capable of finer temporal sampling, more studies are collecting autocorrelated data (Kays et al. 2015). Previously, autocorrelation had been considered a problem, primarily because of the violation of assumptions of traditional home range estimators (Fieberg 2007, Fieberg 2010). However, autocorrelation should not be considered problematic, but rather as an additional source of information available for more accurately estimating home range and movement trajectories (Fleming et al. 2015, Noonan et al. 2018).

A continuous-time movement model (ctmm) leverages the additional information found in autocorrelated data to estimate a more accurate home range. One approach using the R package ctmm (Fleming et al. 2014, Fleming et al. 2015, Calabrese et al. 2016) begins by estimating a variogram from time series location data, which measures the variability, or specifically the semivariance in locations as a function of time lag between locations; this approach is commonly used in geosciences for spatial pattern estimation (Fleming et al. 2014, Calabrese et al. 2016). The ctmm approach accounts for the autocorrelation between data points and is robust (within limits) to uneven sampling intervals within an animal relocation dataset (Fleming et al. 2014). Most importantly, when considering home range estimation, the variogram will reveal if there is a constrained area of use, which is interpreted as a defined home range, if it exhibits an asymptote (Fleming et al. 2014). When the variogram reaches an asymptote, or sill, at some time lag, locations no longer convey information about future locations (i.e. they are statistically independent; Fleming et al. 2015, Calabrese et al. 2016). We can infer from this that the animal is no longer expanding their space use as time lags increase beyond that point but is instead moving within a constrained area of use, or a defined range.

Once existence of a defined home range is established, a ctmm from a list of candidate models that represent different hypotheses about movement dynamics is fit to the empirical variogram using maximum likelihood, and the best fit model is identified using Akaike Information Criterion (AIC). The predicted sill from this model (if it has a sill) is used for estimating home range area (Fleming et al. 2014, Calabrese et al. 2016). This produces what is referred to as autocorrelated kernel density estimation (AKDE). This approach has the added benefit over non-movement based KDE approaches because the movement model itself contains information about the uncertainty in locations along a sampled trajectory, and thus in the home range estimate itself. In other words, in addition to producing probability contours that estimate intensity of use of locations within the estimated home range, AKDE also estimates the confidence intervals of those contours (Fleming et al. 2015).

KDE fits a probability density function (a kernel) over each GPS location, then averages across all locations to create a smooth probability density surface (Silverman 1986, Worton 1989). The smoothing parameter for KDE is the bandwidth, and the optimal bandwidth minimizes the mean integrated squared error between the true mean and the estimated kernels (Fleming et al. 2015). Optimal bandwidth for a typical Gaussian reference-function KDE is calculated from the covariance of the kernels and is appropriate for uncorrelated data (Silverman 1986, Fleming et al. 2015). Conceptually, AKDE works the same way as a Gaussian reference-function KDE (Fleming et al. 2015). The difference in AKDE estimation comes from the calculation of the optimal bandwidth, which is derived from the mean of the data and the autocorrelation function (Fleming et al. 2015). The autocorrelation function comes from a fitted ctmm (Fleming et al. 2014, Calabrese et al. 2016), and the result is a home range estimate that is more accurate and includes statistically derived confidence intervals (Fleming et al. 2015, Calabrese et al. 2016).

Conversely, if the variogram shows no evidence of a home range (i.e. it has no asymptote), a model can still be fit to the variogram and used for the estimation of occurrence (i.e. an estimated reconstruction of the realized trajectory during the sampling period). In this case, the best fit model may conform to any of the candidate models that are associated with a restricted spatial extent, but more importantly, any model that assumes constrained space use (has an asymptote) will fail to predict the observed expanding spatial extent with increasing lag (Calabrese et al. 2016). Although occurrence is often treated as equivalent to home range, they are distinctly different aspects of space use (Fleming et al. 2015, Calabrese et al. 2016). Home range estimation methods predict how much area an animal is likely to spend time in over an extended period of time, whereas occurrence estimation methods interpolate within the period of data collection to infer the specific trajectory taken during that period, given that location sampling is not continuous, even if the actual trajectory is (Fleming et al. 2015, Calabrese et al. 2016). The Brownian bridge movement model (BBMM; Horne et al. 2007), for example, is a commonly used occurrence estimator that is frequently cited as a home range estimator (Fleming et al. 2015, Calabrese et al. 2016). This model does account for autocorrelation by estimating trajectories using discrete time steps (Horne et al. 2007). However, the model assumes Brownian motion between observed relocations, but with no spatial limits (Horne et al. 2007). This means that there is an assumption that the animal can randomly walk without limits, thus eliminating the possibility of a constrained home range and deeming this method inappropriate as a home range estimator (Fleming et al. 2015). Occurrence estimates are more generally useful for estimating the path taken by an animal, which is useful both for identifying corridors and habitat choices along the way.

Objectives

In this study, I used GPS collar data from the RLDNR to estimate space use for wolves captured on Red Lake Indian Reservation. These estimates provided RLDNR wildlife managers information about home ranges for wolves on Red Lake lands and gave insight into the extent Red Lake wolves cross reservation boundaries into state management areas. To estimate home ranges, I implemented the traditional MCP method, which has been previously used by the RLDNR and the MNDNR. I also implemented the recently developed AKDE, which accounts for the autocorrelated nature of GPS collar data and provides statistically derived estimates of home ranges. I further tested for season, diel period, and sex effects on AKDE home range estimates but were limited to those wolves with sufficient sampling duration. I implemented the commonly used KDE and BBMM home range estimators and assessed differences between MCP, AKDE, KDE and BBMM estimates. My specific objectives were to:

1. **Estimate home ranges of Red Lake gray wolves using the traditional MCP method for comparison to current MNDNR estimates, and using AKDE, the most recently developed modern estimator relative to current GPS technology.**
2. **Test for effects of variables known to influence wolf home range size (season, diel period, sex) on AKDE estimated home ranges derived for wolves that display constrained space use.**
3. **Estimate home ranges of Red Lake gray wolves using additional commonly used traditional probabilistic (KDE) and modern probabilistic (BBMM) methods and test for significant differences between estimates derived from all home range estimators to identify implications of using one estimator versus another.**

Methods

Study Area

The Red Lake Indian Reservation (48.0512° N, 95.0010° W; Fig 1) is in northwestern Minnesota and is home to the Red Lake Band of Chippewa Indians. The reservation covers 3,259.81 km² with a majority in Clearwater and Beltrami counties. This area is known as the Diminished Reservation and surrounds Lower Red Lake and the western half of Upper Red Lake, which has a surface area of 2,280.03km^2 and makes up 35% of the Diminished Reservation coverage. There are smaller, scattered pieces of tribal land known as Restored Ceded Lands spread throughout six other counties: Koochiching, Polk, Pennington, Marshall, Red Lake, Roseau, and Lake of the Woods. A larger section of Restored Ceded Lands, the Northwest Angle, is farther to the north in Lake of the Woods county and is accessible only through Canada or by water. The current population on the reservation is 5,162, with a majority of the people living in one of four communities within the Diminished Reservation: Red Lake (largest), Redby, Ponemah, and Little Rock. Ecologically, there are three main vegetation zones across Red Lake lands including second growth deciduous and pine forest, marsh/wet prairie/oak savannah, and boreal swamp conifer (RLDNR 2010). Red Lake lands consist of approximately 1,384km^2 of forest or forested wetlands, 971km^2 of lakes, and 1,886km^2 of wetlands. Red Lake lands have been harvested extensively for hardwood over the past several decades, producing early stage successional communities that support a variety of gray wolf prey species including white-tailed deer (*Odocoileus virginianus)*, moose (*Alces alces*), snowshoe hares (*Lepus americanus*), beavers (*Castor canadensis*), and muskrats (*Ondatra zibethica*; RLDNR 2010, Mech 1970).

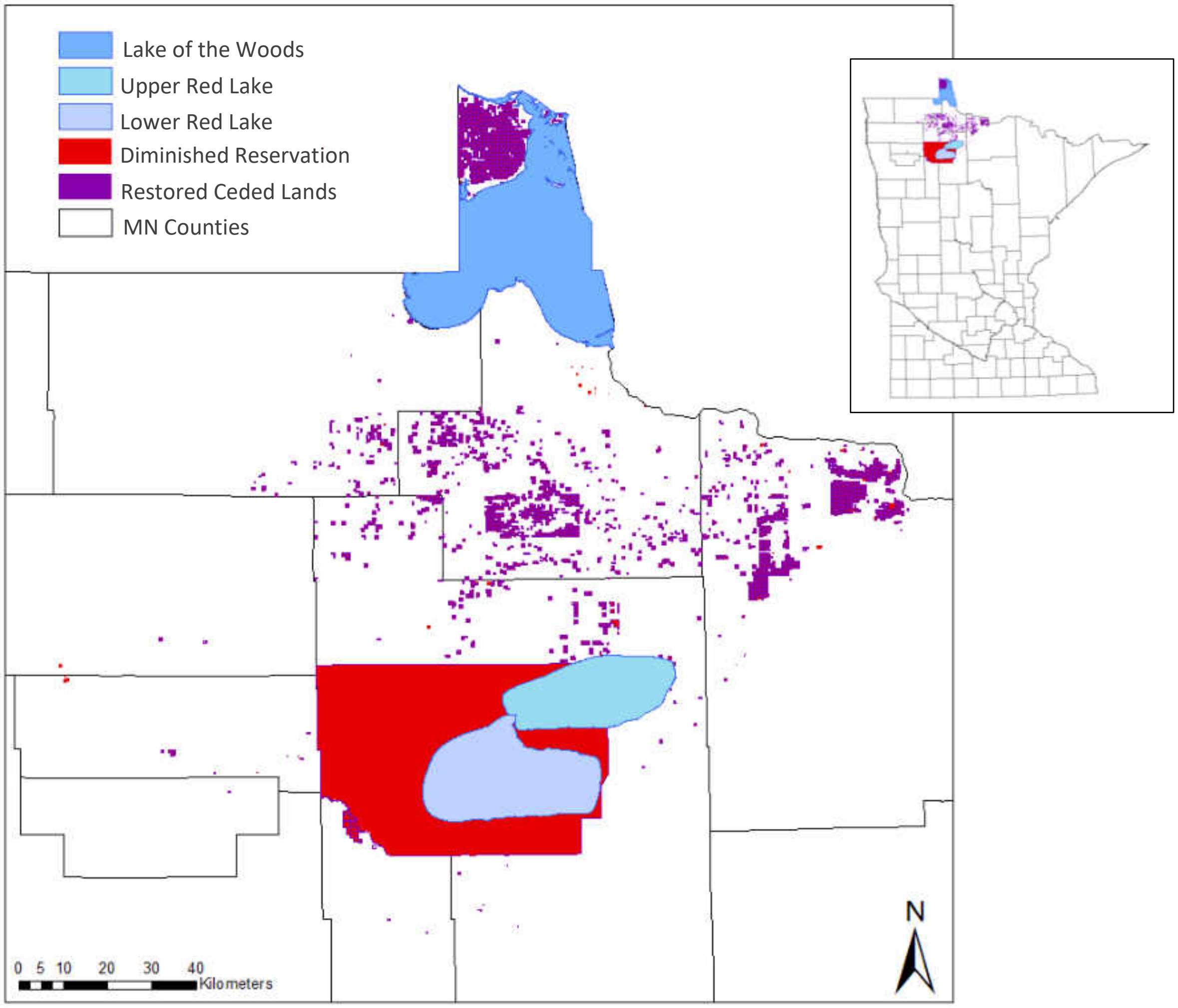


Figure 1. Red Lake Indian Reservation Tribal Lands. The Diminished Reservation includes all of Lower Red Lake and part of Upper Red Lake. The Restored Ceded Lands are distributed across the region, mostly to the north of the Diminished Reservation. These lands include the Northwest Angle, which is on the northern tip of Minnesota. This area is separated from the rest of the state by Lake of the Woods (MnDOT 2013, USGWS 2015, RLDNR 2017).

Data Collection

I obtained GPS collar relocation data that was collected from gray wolves on Red Lake Indian Reservation from May 2012 to August 2018 by RLDNR-WP personnel. GPS collars were programmed to record locations every four hours for approximately two years; however, collar sampling intervals and durations varied due to technical and physical interruptions. Although the RLDNR has collected relocation data on 27 gray wolves, only 16 of the wolves had relocation data that were sufficient in both sampling interval and duration to be used in this study (i.e. at least 300 relocations and/or at least 55 days of observation time; Table 1). See Appendix A for visualization of relocation data collected from the wolves used in this study. The following methods describe field protocols that were used by RLDNR-WP personnel.

RLDNR Wolf Capture and Handling

Summer wolf capture season was mid-May to mid-September. Trapping began following the birthing of pups, which occurs in late April or early May in this area (J. Huseby, personal communication). Winter capture season was mid- November to mid-February. My study was based on seven summer capture periods (2012-2018) and six winter capture periods (2013-2018). Capture of wolves was approved for RLDNR-WP by the MNDNR and the USFWS. Procedures followed trapping and collaring training from USFWS federal trappers and wildlife handling training from Global Wildlife Resources (GWR; The Wildlife Science Center, Forest Lake, MN). Professional training from the GWR was received in 2009 by select RLDNR-WP personnel who created and implemented the following protocols. The basis for the protocols came from the GWR training, and incorporated methods from the United States Department of Agriculture Animal and Plant Health Inspection Service Wildlife Services (USDA-APHIS-WS) and the MNDNR. All protocols followed humane wildlife handling regulations as indicated in the Red Lake Band of Chippewa Indians Gray Wolf Management Plan (2010).

Table 1. Subset of 16 gray wolves collared by the Red Lake Department of Natural Resources Wildlife Program since summer 2012. Wolf ID indicates the sex of the captured animal by beginning with either F (female) or M (male) and year of capture. Capture location occurred within the Diminished Reservation (Dim. Res.), the Restored Ceded Lands (Ced. Lands), or at the Northwest Angle (NW Angle).

Wolf ID	Date Captured	Observation Time Span (days)	Number of Relocations	Capture Location
M2012-01	6.05.2012	291	245	Dim. Res.
F2013-22	5.18.2013	56	310	Ced. Lands
F2013-2459	5.19.2013	418	935	Ced. Lands
F2013-04	6.09.2013	61	307	Dim. Res.
M2013-06	7.14.2013	106	380	Dim. Res.
M2013-15	7.17.2013	190	724	Dim. Res.
F2013-23	7.23.2013	145	767	Ced. Lands
M2013-07	8.12.2013	151	616	Dim. Res.
M2013-10	9.16.2013	211	1469	NW Angle
M2014-14	9.11.2014	426	2679	Dim. Res.
F2015-16	8.08.2015	575	4360	Dim. Res.
M2016-2710	2.07.2016	455	1561	Res. Ced.
F2016-17	8.28.2016	74	1681	Dim. Res.
F2017-2723	3.02.2017	261	2141	Dim. Res.
M2017-24	8.21.2017	682	4936	Dim. Res.
M2018-25	2.18.2018	80	462	Dim. Res.

RLDNR-WP personnel used laminated, rubber padded, grapple-drag foothold traps (#7 EZ Grip, Livestock Protection Company, Alpine, Texas) during the summer. The trigger sensitivity of the foothold spring was altered to reduce the occurrence of non-target captures (i.e. smaller animals such as skunks or raccoons). Because of the intense summer heat, they set these traps in areas where any captured animal would have access to shade. Animals caught in a foothold trap in cold weather are at risk of hypothermia if the trap prevents blood circulation to the foot. For this reason, cable restraints (SNARE605, The Snare Shop, Lidderdale, Iowa) were used during the winter. The restraints were equipped with double safety stops to prevent accidental mortality.

RLDNR-WP personnel attempted to capture wolves in the three separate areas of Red Lake Indian Reservation. Most capture efforts occurred in the Diminished Reservation, with some attempts occurring in the Restored Ceded Lands and the Northwest Angle, as time and logistics allowed. Both foothold trap and cable restraint locations were based primarily on recent wolf activity and track surveys. Low traffic, minimum maintenance backroads and fire breaks throughout reservation lands, which are known to be used for travel by wolves (Mech 1970, Zimmerman et al. 2014, Thompson 1952), were surveyed for wolf scat and tracks as evidence of wolf presence (Joslin 1967, Ausband et al. 2014), and traps were set accordingly. However, traps were also set in areas of interest, regardless of wolf sign or lack thereof. An area of interest was any area where wolves have been known to exist historically, or where they are likely to be, based on the habitat and environment. The Diminished Reservation is made up of several distinct but contiguous areas (e.g. Butcher Knife, The Narrows, etc.). Trap sites were separated on the Diminished Reservation according to these areas, with 3-10 individual trap locations within each area, depending on landscape structure (i.e. areas with more grass coverage had fewer trap locations because foothold traps cannot be hidden as easily in the grass). There was an assumption that wolves occupying an area make up a pack separate from the wolves occupying another area; therefore, an individual collared wolf was considered representative of a pack. Once a wolf was collared in an area, traps were removed to reduce the chance of collaring more than one wolf in a pack during a single trapping term. In general, traps were set in two to three different areas at once, for up to two weeks at a time, or until a wolf was captured. There were typically 150 foothold trap locations and 30 cable restraint trap locations throughout all reservation areas during each summer and winter trapping term. Figure 2 depicts the trap and capture locations for the subset of 16 wolves that were used for the purposes of this study.

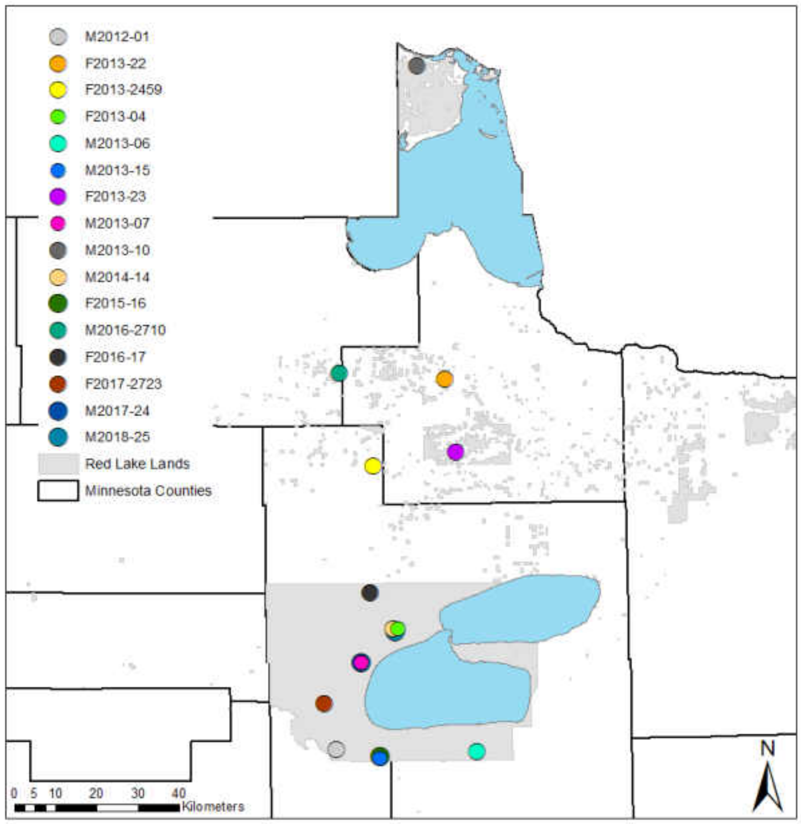


Figure 2. Subset of 16 gray wolf capture locations by the Red Lake Department of Natural Resources since summer 2012. This subset includes 11 wolves captured within the Diminished reservation, 4 wolves captured within the Restored Ceded Lands, and 1 wolf captured at the Northwest Angle.

Traps were baited with a variety of scent lures (e.g. wolf or coyote urine, Prairie Fire, Call of the Wild) purchased from several vendors (Forsyth Animal Lures, F&T Fur Harvesters, Cumberland Northwest Trappers, Schmitt Enterprises Inc, Ram Connection Co., and Wildlife Control Suppliers) at the time of deployment, and every three days thereafter. Personnel checked traps at least once every 24 hours per USFWS regulations. In the event of an incidental capture, they released the animal at the site without sedation, unless sedation was necessary to maintain safety. Incidentals were evaluated on a case by case basis when determining if the trap could be reset in the same spot using the same trap (e.g. a skunk incidental would require trap relocation and replacement due to scent contamination). Every captured wolf was processed, but only wolves that were large enough to support the collars were fitted with a GPS unit. For yearling wolves, the collar was modified with retrofitted padding, which deteriorates as the animal grows.

RLDNR Wolf Processing

When a wolf was captured, RLDNR-WP personnel visually estimated the weight of the wolf and prepared an appropriate mixture of ketamine (mL; anesthetic) and xylazine (mL; sedative which decreases the animal's heart rate, respiration, and digestion). A manual syringe pole, which is adjustable and ranges from 42 inches to 8 feet in length was fixed with a 14-gauge needle to administer an intramuscular (IM) injection of the sedative into a hind quarter. Once the wolf was sedated (2-6 minutes post injection), an accurate weight was obtained, and additional sedative was administered if necessary. An ophthalmic ointment was applied to prevent corneal desiccation and the wolf was fitted with an eye mask to decrease optic stimulation and stress. The eye mask doubled as a safety muzzle if the wolf were to show signs of consciousness. Wolf reflexes were checked every 5 minutes and an IM injection of 1.5 mL of ketamine was administered if the wolf was prematurely responsive. Temperature, heart rate, and respiration were monitored continuously. Doxapram was administered in the case of respiratory distress and Diazepam in the case of seizure. Sex, age, body condition, full body and tail length (cm) and head, chest, and neck circumference (cm) were recorded. Every wolf was photographed for identification and given both a 5 mL IM injection of a vitamin B complex and a 1.5 mL/15lbs IM injection of penicillin to promote health.

Wolves of every size and age were tagged with an identifying yellow RLDNR ear tag; males received a left ear tag and females received a right ear tag. At the completion of processing, wolves received a weight-based IM injection (mL) of yohimbine to reverse the effects of xylazine. This was administered no sooner than 45 minutes after the last dose of ketamine to maximize the effects of the yohimbine. Wolves were visually monitored throughout recovery (45 minutes to 1 hour) and any pertinent behavioral observations were recorded. Monitoring continued until the wolf left the processing site, in which the wolf was documented as recovered, and the time of recovery was recorded.

Wolves were fitted with collars regardless of age, sex, weight, or bodily condition. Two brands of collars were used: 830-gram Iridium G22110E GPS collars (Advanced Telemetry Systems, Isanti, Minnesota) and 1130-gram IridiumTrackM GPS collars (Lotek, Newmarket, Ontario). The collars also had very high frequency (VHF) radio transmitter capabilities operating on frequencies of 155-157 hertz, which remained intact for 3-4 years post deployment. VHF capabilities were essential because they provided a way to locate a collar via radio telemetry if the GPS unit failed. Collars were tested immediately before fitting them to ensure accurate data collection and programmed to report location points every four hours for a duration of approximately two years. When the GPS unit battery became low, the collar would drop from the animal and was recovered by RLDNR-WP.

Data Analysis

Minimum Convex Polygon

I estimated 50% core area and 95% broader home range (Benson and Patterson 2015, Hinton et al. 2016) MCP polygons (km^2) for each of the 16 wolves using the R package adehabitatHR (Calenge 2006; R Version 3.6.1,www.rproject. org).

Autocorrelated Kernel Density Estimation

I formatted the GPS relocation data to conform to the specification defined in the R package move (Kranstauber et al. 2019) as recommended for ctmm input (Calabrese et al. 2016; R Version 3.6.1, www.r-project.org). Once in the appropriate format, the data were imported into R as telemetry objects using the ctmm package. This created a spatial data frame with wolf ID, a timestamp, x and y coordinates, and projection for each relocation point (Calabrese et al. 2016). I chose Universal Transverse Mercator (UTM), zone 15, which includes Red Lake for the coordinate system projection, as recommended by the authors of the ctmm package, because it facilitates planar calculations.

I visualized the autocorrelation in each data set by estimating empirical variograms, which plot the semivariance in relocations as a function of time lag (Fleming et al. 2014). The candidate movement models fit to the variograms are variants of continuous-time stochastic models, which include the independently identically distributed process (IID), the Ornstein-Uhlenbeck (OU) process, and the Ornstein-Uhlenbeck Foraging (OUF) process (Calabrese et al. 2016, Noonan et al. 2018). The IID process is used in KDE and assumes no autocorrelation in position or velocity (Silverman et al.1986). The OU process assumes autocorrelation in position only (Uhlenbeck and Ornstein 1930). The OUF process assumes autocorrelation in both position and velocity

(Fleming et al. 2014). Additionally, the models can either be anisotropic (semivariance pattern consistent with directionality) or isotropic (semivariance pattern changes with directionality). The models were fit using the effective sample size of the relocation data, which represents the number of independent pieces of information within the relocation data and reflects the sample size adjustment, which accounts for non-independence of sequential points (Fleming et al. 2015). I used the best fit model, identified using AIC, along with the relocation data as input for AKDE (Fleming et al. 2015) in the R package ctmm (Calabrese et al. 2016; R version 3.6.1) to estimate 50% core area and 95% broader home ranges (Benson and Patterson 2015, Hinton et al. 2016) as well as home ranges over time periods of interest for those wolves that displayed constrained space use.

Time period of interests, here-after referred to as time period, were based upon seasons expected to be biologically relevant to wolves and when I hypothesized I would see differences in space use (breeding: January 15-March 14, denning: March 15-July 31, rendezvous: August 1-October 14, wayfaring: October 15-January 14) and diel period (day or night), as well as combinations of season and diel period. Day and night were determined using sunrise and sunset times based on the date and the longitude and latitude for each relocation.

Effects on AKDE Home Range

I tested for the effects of season, diel period, and sex (fixed effects) on AKDE home range estimates using a general linear mixed effects model with wolf ID, here-after referred to as wolf, as a random effect. I developed a main effects-only model and a model that included main effects and all two-way interactions using the R package nlme (Pinheiro et al. 2019; R version 3.6.1). I used a best subsets approach to model selection

(Hosmer and Lemeshow 2000), implemented in the R package MuMin (Barton 2019, R version 3.6.1) using AICc (AIC corrected for small sample size; Burnham and Anderson 2002) as the model comparison criterion. This allowed us to identify which combination of the hypothesized variables best predicted AKDE home range size. I used $\log_{10}$ transformed AKDE home range estimates as the response variable to meet the assumptions of normality.

Kernel Density Estimation

I estimated 50% core area and 95% broader home range (Benson and Patterson 2015, Hinton et al. 2016) KDE contours (km^2) for each of the 16 wolves using the R package adehabitatHR (Calenge 2006; R Version 3.6.1, www.r-project.org). I used the H-reference (H-ref) bandwidth method, which uses a default bandwidth calculated from the kernel covariance (Silverman 1986, Fleming et al. 2015). Although this method can over-smooth and thus overestimate home range (Worton 1995), it is more appropriate for autocorrelated data because the alternative bandwidth method, cross-validation, assumes independence of location data (Fleming et al. 2015).

Brownian Bridge Estimation

I estimated 50% core area and 95% broader home range BBMM contours for each of the 16 wolves (Horne et al. 2007) using the R package BBMM (Neilson et al. 2013; R version 3.6.1).

Home Range Estimator Comparison

I used paired (by individual wolf) two-tailed t-tests to compare 95% home range estimates for each estimator against each other. I interpreted BBMM occurrence estimates as home range estimates and included it in the comparison based on the current and common use of the method as a home range estimator. Because AKDE home range estimates were only obtained for wolves with constrained space use, I could not compare all individual wolf MCP, KDE, and BBMM estimates to the AKDE estimates. Instead, I compared the AKDE estimates for the wolves who displayed constrained space use to the MCP, KDE, and BBMM estimates for the same wolves. Since MCP, KDE, and BBMM do not assume constrained space use, I compared these estimates to each other for all wolves. However, I compared the MCP, KDE, and BBMM estimates for only the wolves with constrained space use to see how the estimators compare when there is known constrained space use. I performed all t-tests on $\log_{10}$ transformed home range estimates to meet both the assumptions of normality and equality of variances.

Results

Primary Home Range Estimation

Minimum Convex Polygon

The 95% MCP home range estimates for gray wolves ranged from 43km^2 to 6192km^2 (Table 2, Fig 3) and the 50% MCP home range estimates ranged from 14km^2 to 1450km^2 (Table 2). Wolves across all Red Lake lands had an average 95% MCP home range of 1716km^2 and an average 50% MCP home range of 264km^2 (Table 3).

Autocorrelated Kernel Density Estimation

Of the 16 wolves, 7 (5 males and 2 female) had variograms with a sill that was indicative of constrained space (Fig 4). An additional 3 wolves (males) had variograms that did not display a sill but had visual indications in their geographic relocations of potential shifts in space use. Accordingly, the data from these 3 wolves were each broken into 2 parts. Both parts of 1 wolf yielded a variogram indicative of constrained space use (Fig 5), while the other 2 wolves each had 1 variogram with a sill indicative of constrained space use (Fig 6a, Fig 7a) and 1 that showed no sill (Fig 6b, Fig 7b).

Due to the divisions of the data set for the 3 male wolves, the 16 wolves provided 19 total data sets, 12 of which were from males and 7 from females. Data sets from males had an average observation time span of 212 days while female data sets had an average observation time span of 227 days (Fig 8a).

There were 11 data sets with constrained space use with an average observation time span of 294 days. These constrained data sets were primarily from males with 9 male data sets having an average observation time span of 243 days. There were 2 data sets from females with an average observation time span of 237 days. However, the 2 females had vastly different observation time spans (Fig 8b).

There were 8 data sets with no constrained space use and an average observation time span of 185 days. There were only 3 male data sets having an average observation time span of 122 days. There were 5 data sets from females with an average observation time span of 223 days (Fig 8b).

The 11 constrained space use data sets had had continuous time movement models fit to the semivariance (Fig 5-6), and 95% AKDE (Table 4, Figure 9) and 50% AKDE (Table 4) home ranges were estimated from the ctmms. Uncertainty of estimation was relatively consistent among individual wolves, with M2013-06 having the least uncertainty and M2017-24 having the greatest uncertainty (Fig 10). Wolves across all Red Lake lands had an average 95% AKDE home range of 291km^2 and an average 50% AKDE home range of 84km^2 (Table 5).

Table 2. MCP home range estimates (km^2) for gray wolves on Red Lake Indian Reservation.

Wolf	**95% MCP**	**50% MCP**	**Time Span (days)**	**Number of Relocations**	**Capture Location**
M2012-01	132	34	290	245	Dim. Res.
F2013-22	43	14	56	310	Ced. Lands
F2013-2459	289	103	418	935	Ced. Lands
F2013-04	2123	269	61	307	Dim. Res.
M2013-06	48	15	106	380	Dim. Res.
M2013-15	174	53	190	724	Dim. Res.
F2013-23	190	46	145	764	Ced. Lands
M2013-07	344	130	151	616	Dim. Res.
M2013-10	167	41	211	1469	NW Angle
M2014-14	1005	331	426	2679	Dim. Res.
F2015-16	5561	261	575	4360	Dim. Res.
M2016-2710	4184	148	455	1561	Ced. Lands
F2016-17	3161	1450	74	1681	Dim. Res.
F2017-2723	2709	669	261	2137	Dim. Res.
M2017-24	6192	605	682	4936	Dim. Res.
M2018-25	1140	59	80	462	Dim. Res.

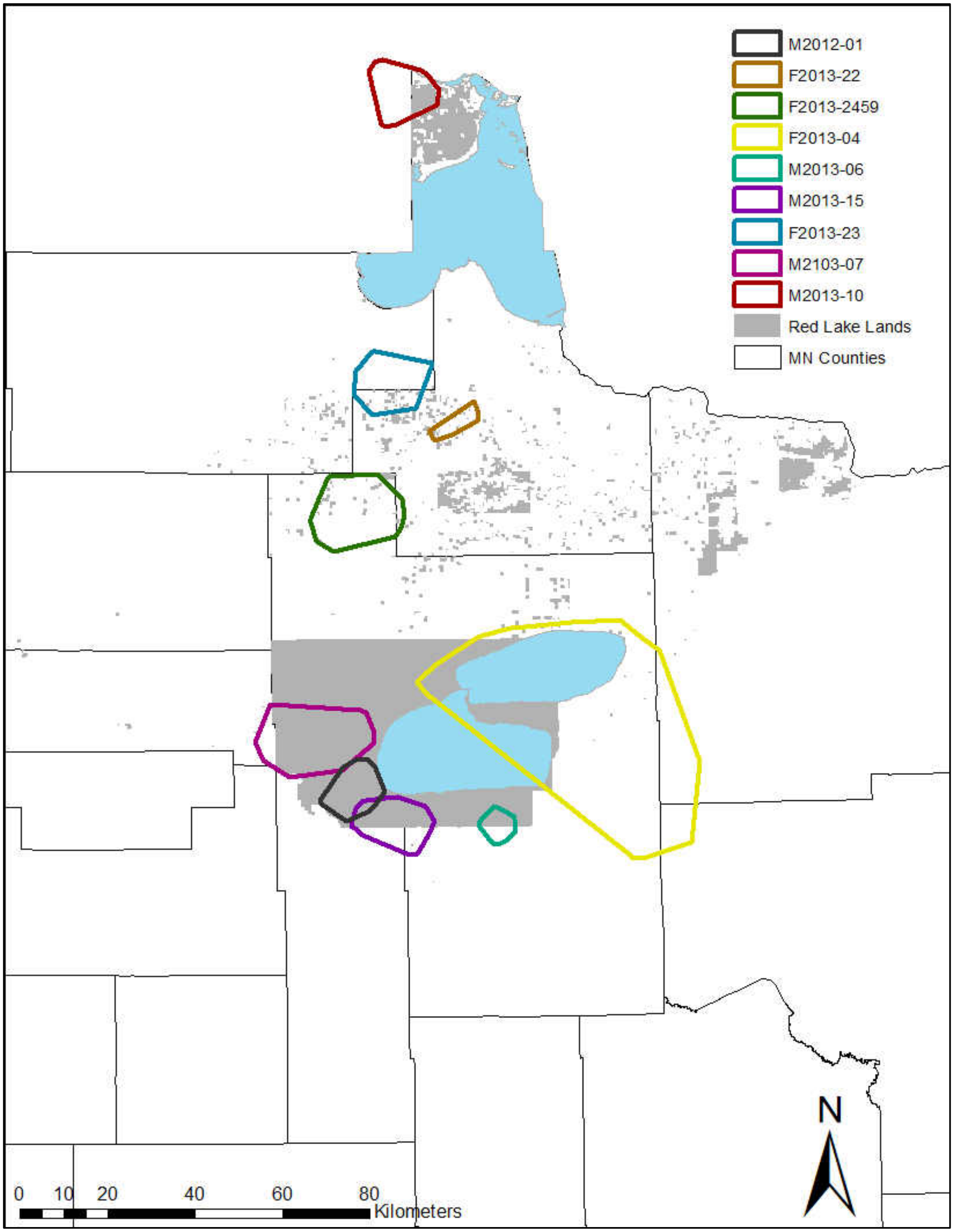


Figure 3a. 95% MCP polygons for gray wolves captured from 2012-2013 on Red Lake Indian Reservation.

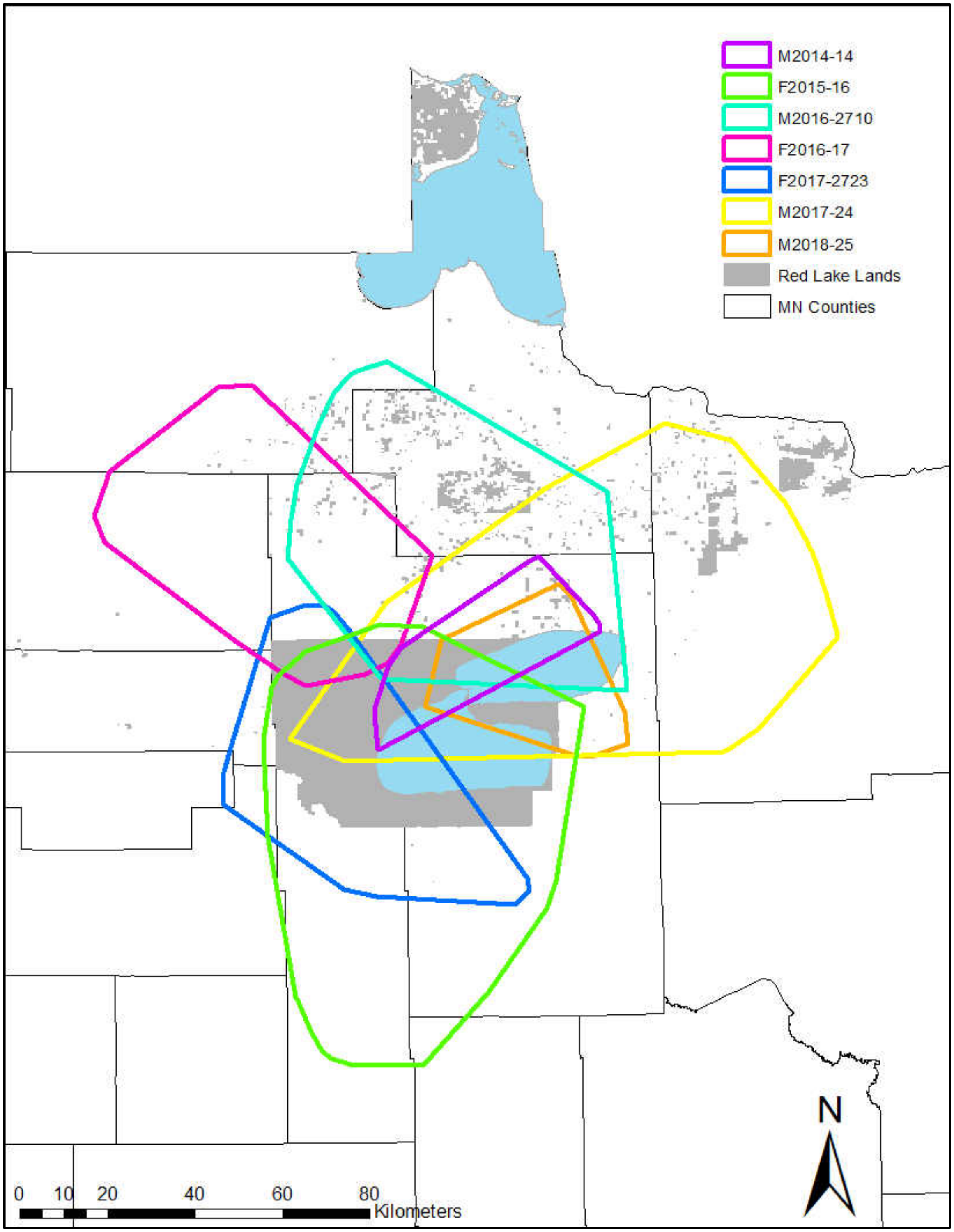
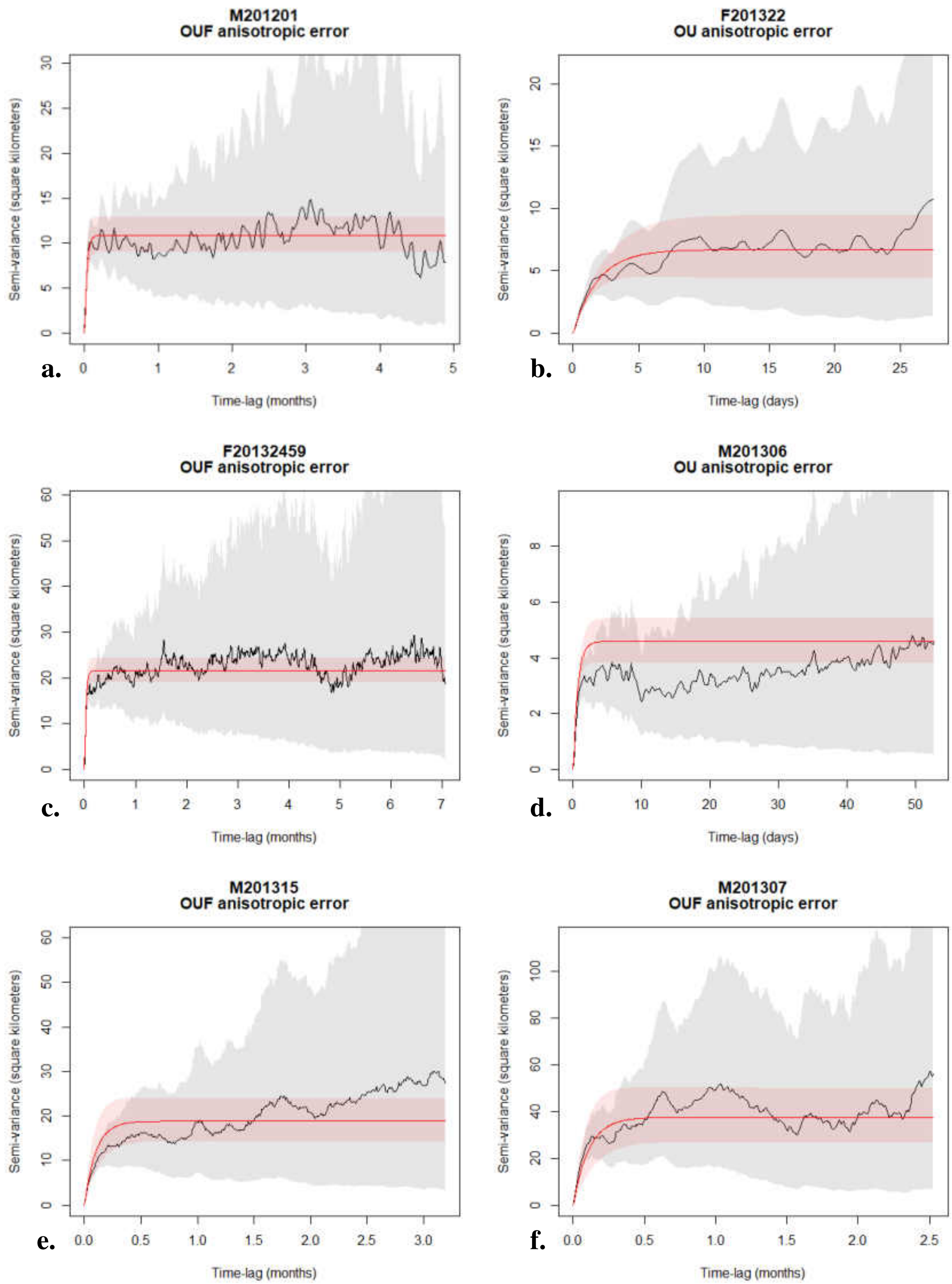
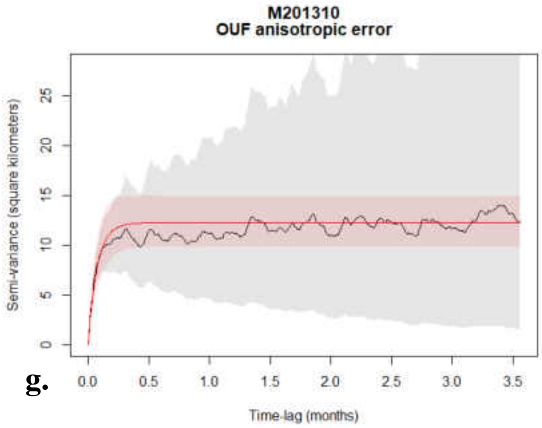


Figure 3b. 95% MCP polygons for gray wolves captured from 2014-2018 on Red Lake Indian Reservation.

Table 3. Mean MCP home range estimates (km^2) by location for gray wolves on Red Lake Indian Reservation.

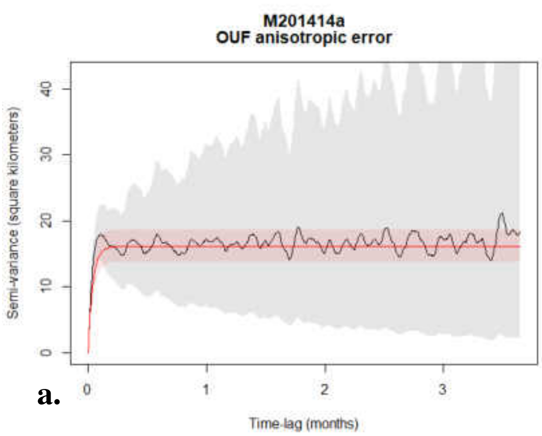
				95% CI				95% CI	
Location	**N**	**95% Mean**	**SE**	**Lower**	**Upper**	**50% Mean**	**SE**	**Lower**	**Upper**
All Red Lake Lands	16	1716	517	703	2729	264	94	80	448
Diminished Reservation	11	2054	655	770	3337	352	129	100	605
Restored Ceded Lands	5	975	803	0	2549	70	24	23	118


M201201
OUF anisotropic error
F201322
OU anisotropic error
F20132459
OUF anisotropic error
M201306
OU anisotropic error
M201315
OUF anisotropic error
M201307
OUF anisotropic error
Semi-variance (square kilometers)
Time-lag (months)
Time-lag (days)
a.
b.
c.
d.
e.
f.

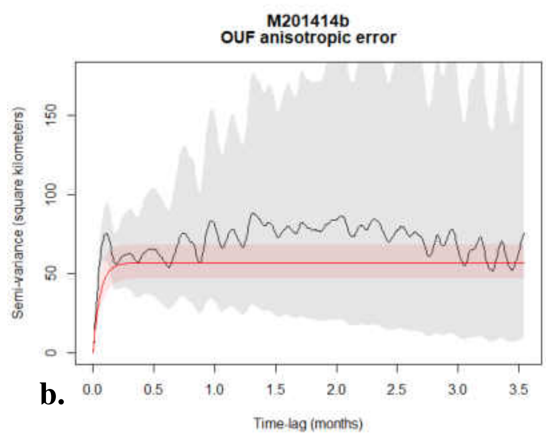


g.

Figure 4. Variogram and continuous time movement model fit for wolf **a.** M2012-01, **b.** F2013-22, **c.** F2013-2459, **d.** M2013-06, **e.** M2013-15, **f.** M2013-07, and **g.** M2013-10. The black line represents the average semivariance of the points within the gray cloud. The semivariance reaches a sill representing constrained space use. The red line is the model fit with confidence intervals.



a.



b.

Figure 5. Variogram and continuous time movement model fit for wolf M2014-14 broken into part **a.** M2014-14a and **b.** M2014-14b. The semivariance reaches a sill for both parts indicating two separate areas of constrained space use.

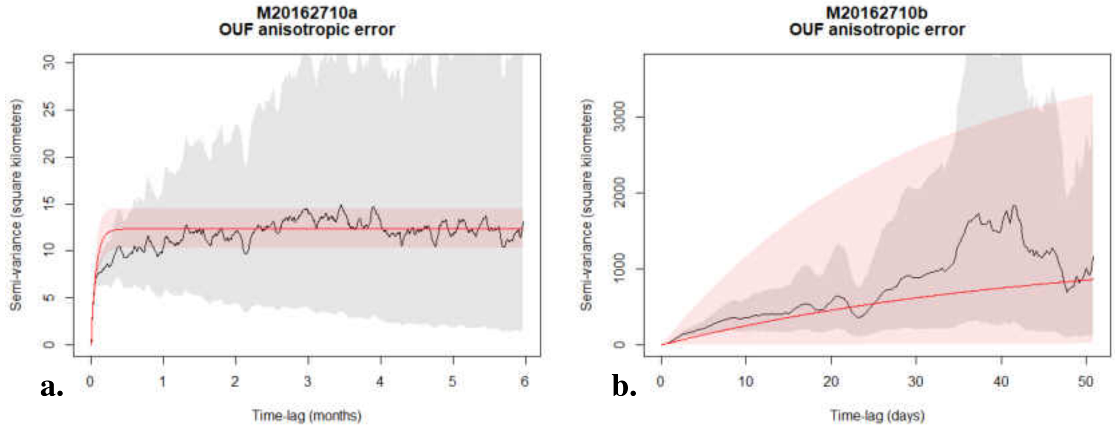


Figure 6. Variogram and continuous time movement model fit for wolf M2016-2710 broken into part **a.** M2016-2710a and **b.** M2016-2710 b. The semivariance reaches a sill for only M2016-2710a indicating partial constrained space use.

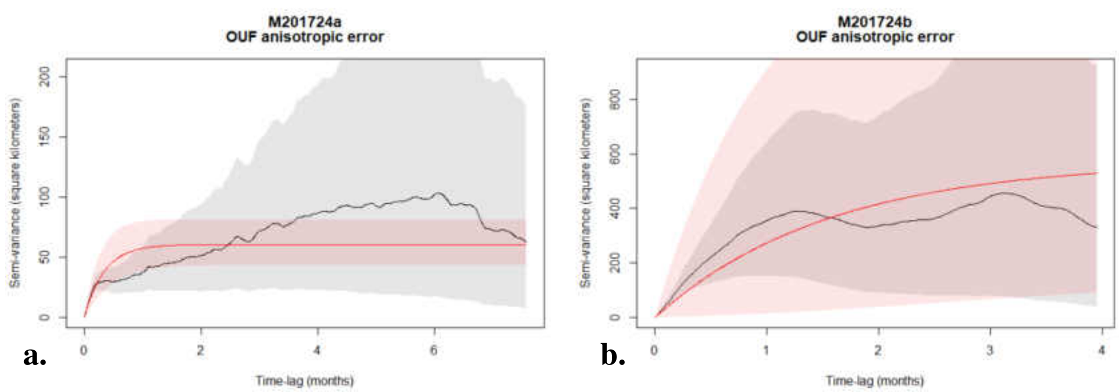


Figure 7. Variogram and continuous time movement model fit for wolf M2017-24 broken into part **a.** M2017-24a and **b.** M2017-24b. The semivariance reaches a sill for only M2017-24a indicating partial constrained space use.

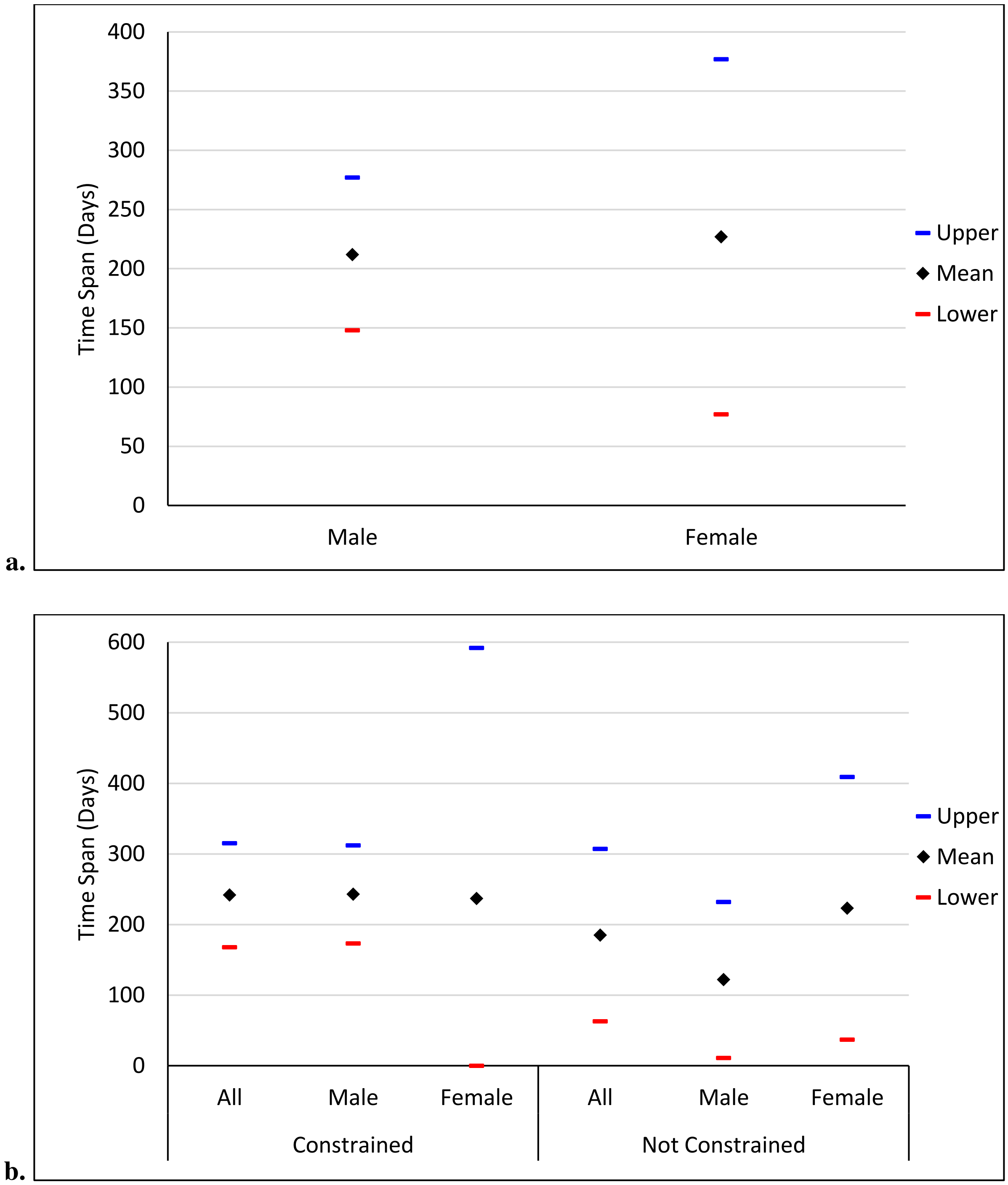


Figure 8. Mean observations time spans for **a.** all male and female data sets and for **b.** constrained and not constrained data sets.

Table 4. AKDE home range estimates (km^2) of the 11 data sets derived from the 10 gray wolves with constrained space use on Red Lake Indian Reservation.

Wolf	95% AKDE	95% CI Lower	95% CI Upper	50% AKDE	95% CI Lower	95% CI Upper	Time Span (days)	Number of Relocations	Effective Sample Size	Model Type	Capture Location
M2012-01	165	137	195	40	33	47	291	245	83	OUFa	Dim. Res.
F2013-22	72	47	102	16	10	22	56	310	16	OUa	Ced. Lands
F2013-2459	297	262	333	76	67	85	418	935	157	OUFa	Ced. Lands
M2013-06	72	60	85	13	11	15	106	380	74	OUa	Dim. Res.
M2013-15	280	212	357	61	47	78	190	724	32	OUFa	Dim. Res.
M2013-07	481	342	642	129	92	173	151	616	24	OUFa	Dim. Res.
M2013-10	183	147	223	44	35	53	211	1469	48	OUFa	Ced. Lands
M2014-14a	230	197	266	263	201	332	217	1511	92	OUFa	Dim. Res.
M2014-14b	448	368	535	56	48	65	210	1168	61	OUFa	Dim. Res.
M2016-2710a	195	163	230	46	39	55	354	1403	76	OUFa	Ced. Lands
M2017-24a	782	559	1043	177	127	237	449	3697	23	OUFa	Dim. Res.

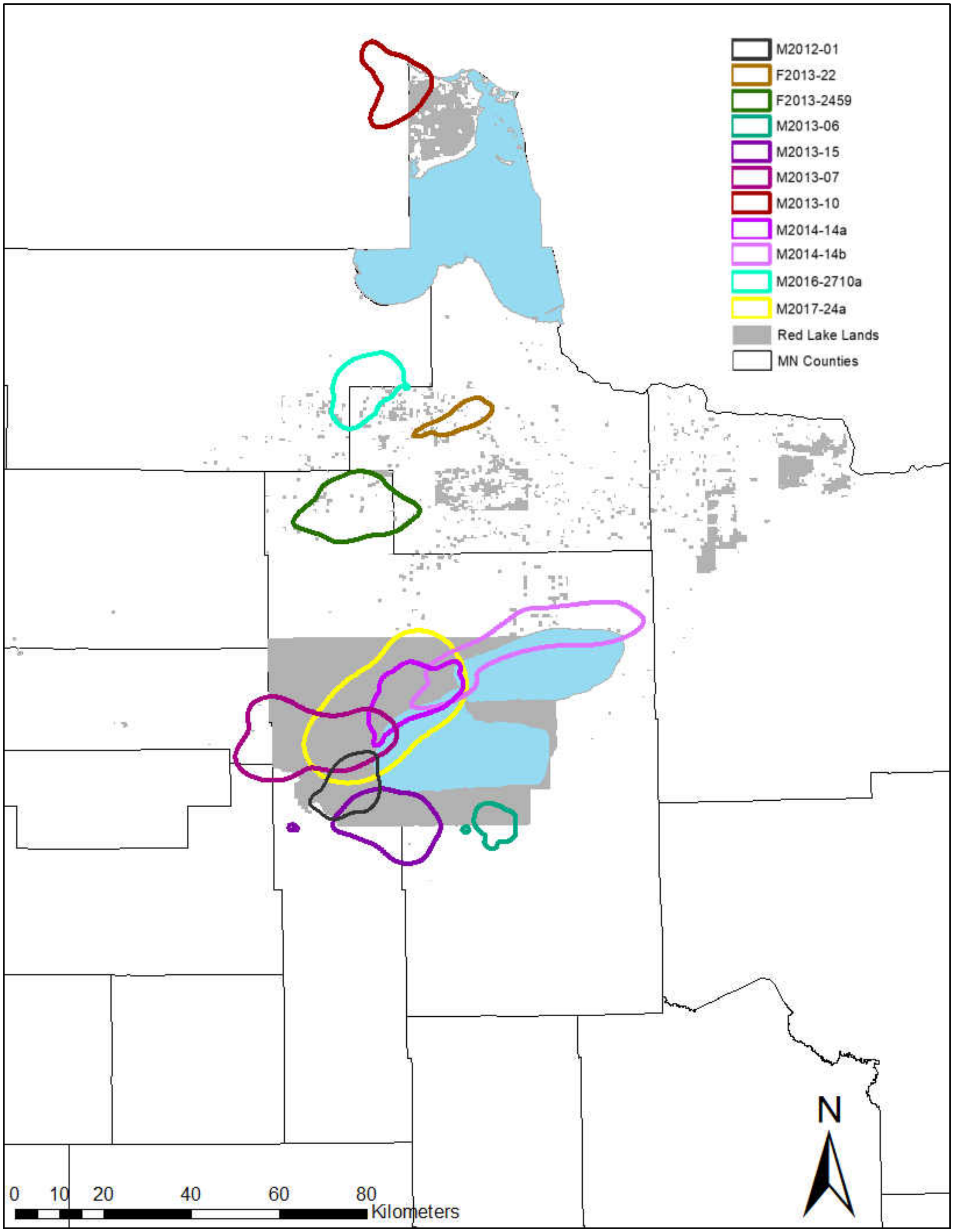


Figure 9. 95% AKDE home range contours of the 11 data sets derived from the 10 gray wolves with constrained space use on Red Lake Indian Reservation.

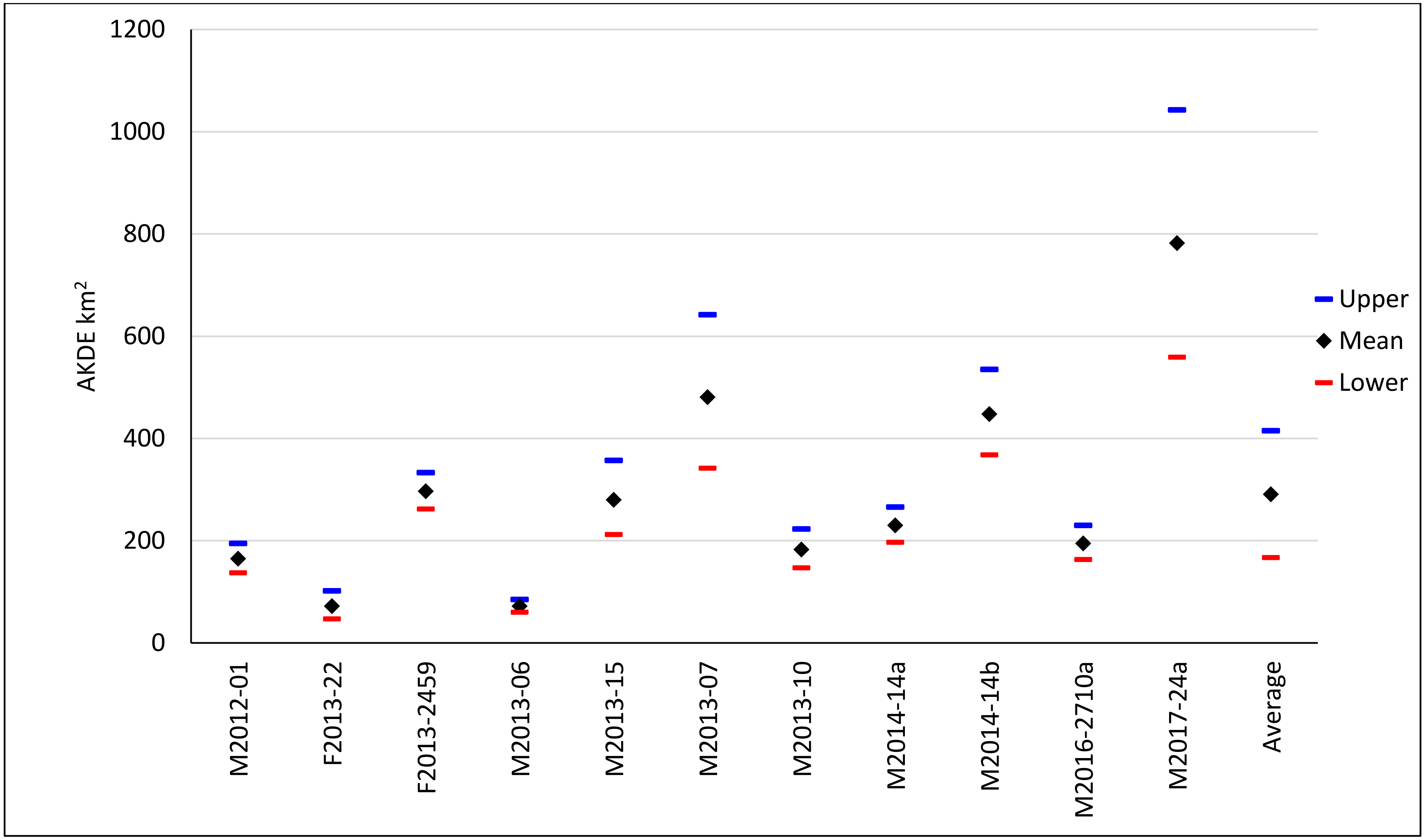


Figure 10. 95% AKDE home range estimates and 95% confidence intervals of the 11 data sets derived from the 10 gray wolves with constrained space use on Red Lake Indian Reservation.

Table 5. Mean AKDE home range estimates (km^2) by location of the 11 data sets derived from the 10 gray wolves with constrained space use on Red Lake Indian Reservation.

				95% CI				95% CI	
Location	**N**	**95% Mean**	**SE**	**Lower**	**Upper**	**50% Mean**	**SE**	**Lower**	**Upper**
All Red Lake Lands	11	291	63	167	415	84	23	38	129
Diminished Reservation	7	351	91	174	529	106	34	40	172
Restored Ceded Lands	4	187	46	97	277	46	12	21	70

All 11 constrained space use data sets displayed additional constrained space use during at least one season (based on the dates I used to delineate seasons) and were used for 95% AKDE and 50% AKDE seasonal home range estimation (Table 6). Collection of these data occurred primarily during wayfaring season (Fig 11), however, all average seasonal home ranges fell within a small window between 215km^2 and 258km^2 for 95% AKDE estimates and between 50km^2 and 58km^2 for 50% AKDE estimates (Table 7). All 11 constrained space use data sets also displayed additional constrained space use during at least one diel period and were used for 95% AKDE and 50% AKDE seasonal and diel period home range estimation (Table 8). Average seasonal and diel home ranges were between 174km^2 and 268km^2 for 95% AKDE estimates and between 42km^2 and 64km^2 for 50% AKDE estimates (Table 9). Independent of season, 10 of the 11 data sets with constrained space use displayed constrained space use for both diel periods and were used for 95% AKDE and 50% AKDE diel period home range estimation (Table 10). Average diel home ranges across the entire sampling period were 239km^2 at night and 242km^2 during daylight hours for 95% AKDE estimates and 55km^2 at night and 56km^2 during daylight hours for 50% AKDE estimates (Table 11).

Average 95% AKDE home ranges across the entire sampling period were 185km^2 for females and 315km^2 for males and average 50% AKDE home range estimates were 54km^2 for females and 117km^2 for males (Table 12).

Table 6. AKDE home range estimates (km^2) by season of the 11 data sets derived from the 10 gray wolves with constrained space use on Red Lake Indian Reservation.

Wolf	Season	95% AKDE	95% CI Lower	95% CI Upper	50% AKDE	95% CI Lower	95% CI Upper	Time Span (days)	Number of Relocations	Effective Sample Size	Model Type
M2012-01	Breeding	NA	NA	NA	NA	NA	NA	59	69	NA	NA
	Denning	165	114	223	39	27	53	65	61	24.9	OUFa
	Rendezvous	167	124	215	23	29	50	75	61	43.3	OUFi
	Wayfaring	147	100	203	37	25	50	92	54	24.6	OUFa
F2013-22	Denning	72	47	102	16	10	22	56	310	15.6	OUa
F2013-2459	Breeding	NA	NA	NA	NA	NA	NA	59	42	NA	NA
	Denning	262	213	315	68	55	82	192	339	66.2	OUFa
	Rendezvous	345	279	418	66	53	19	75	256	57.8	OUFa
	Wayfaring	322	247	407	78	60	99	92	298	36	OUFa
M2013-06	Denning	37	23	55	7	4	10	17	73	13.4	OUa
	Rendezvous	54	46	63	9	8	11	75	270	81.2	OUa
	Wayfaring	NA	NA	NA	NA	NA	NA	14	37	NA	NA
M2013-15	Breeding	NA	NA	NA	NA	NA	NA	10	13	NA	NA
	Denning	NA	NA	NA	NA	NA	NA	13	62	NA	NA
	Rendezvous	154	116	197	37	28	48	75	354	30	OUFa
	Wayfaring	338	215	488	76	48	110	92	295	14.4	OUFa
M2013-07	Rendezvous	NA	NA	NA	NA	NA	NA	64	338	NA	NA
	Wayfaring	467	307	660	129	85	182	87	278	17.5	OUFa
M2013-10	Breeding	147	101	202	30	21	42	59	471	18.8	OUFa
	Denning	NA	NA	NA	NA	NA	NA	32	302	NA	NA
	Rendezvous	NA	NA	NA	NA	NA	NA	28	169	NA	NA
	Wayfaring	137	106	173	32	24	40	92	527	34.7	OUFa

Continued

M2014-14a	Breeding	282	195	384	72	50	99	59	396	20.1	OUFa
	Denning	236	147	347	59	37	87	33	166	14.1	OUFa
	Wayfaring	176	143	212	49	40	59	92	701	54.6	OUFa
M2014-14b	Denning	529	406	668	82	63	104	107	597	35.6	OUFa
	Rendezvous	539	375	733	130	90	176	75	422	20.4	OUFa
	Wayfaring	128	83	183	26	17	38	28	149	16.4	OUFa
M2016-2710a	Breeding	NA	NA	NA	NA	NA	NA	48	69	NA	NA
	Denning	214	156	281	51	37	66	139	379	27.9	OUFa
	Rendezvous	171	120	231	33	23	45	75	300	21.9	OUFa
	Wayfaring	144	108	186	38	29	50	92	414	29.9	OUFa
M2017-24a	Breeding	NA	NA	NA	NA	NA	NA	59	318	NA	NA
	Denning	545	365	758	121	81	169	139	754	17.2	OUFa
	Rendezvous	NA	NA	NA	NA	NA	NA	130	1642	NA	NA
	Wayfaring	NA	NA	NA	NA	NA	NA	121	983	NA	NA

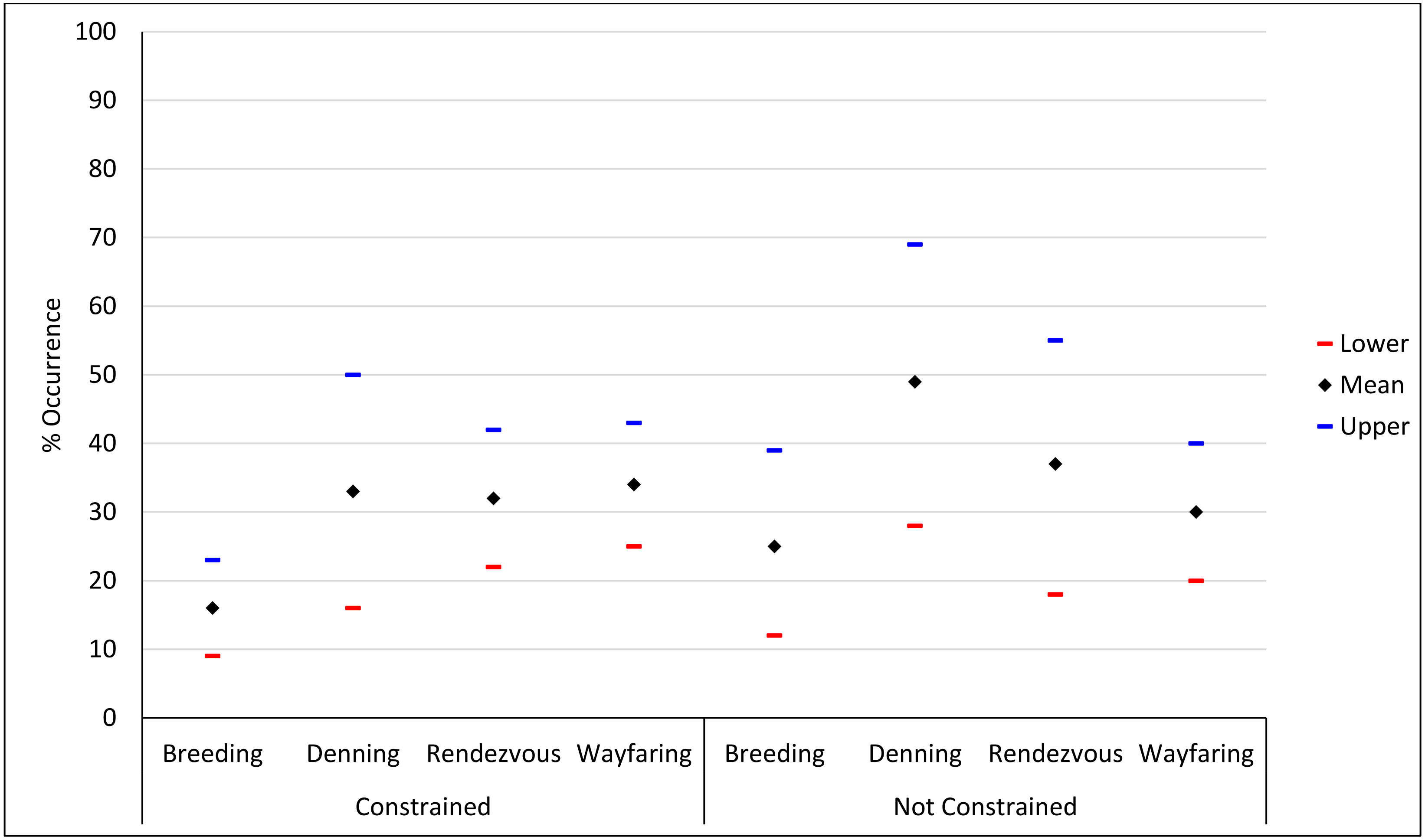


Figure 11. Mean percent occurrence of each season in the constrained and not constrained data sets.

Table 7. Mean AKDE home range estimates (km^2) by season of the 11 data sets derived from the 10 gray wolves with seasonal constrained space use on Red Lake Indian Reservation.

				95% CI				95% CI	
Season	**N**	**95% Mean**	**SE**	**Lower**	**Upper**	**50% Mean**	**SE**	**Lower**	**Upper**
Breeding	2	215	29	158	271	51	9	33	69
Denning	8	258	71	117	398	55	14	28	82
Rendezvous	6	238	87	67	409	50	22	7	92
Wayfaring	8	232	63	108	357	58	17	24	92

Table 8. AKDE home range estimates (km^2) by season and diel period of the 11 data sets derived from the 10 gray wolves with constrained seasonal and diel space use on Red Lake Indian Reservation.

Wolf	Season	Diel Period	95% AKDE	95% CI Lower	95% CI Upper	50% AKDE	95% CI Lower	95% CI Upper	Number of Relocations	Effective Sample Size	Model Type
M2012-01	Rendezvous	Day	177	119	248	42	28	59	30	30	IIDi
		Night	152	100	215	35	23	50	31	24.9	OUFi
	Wayfaring	Night	124	76	184	32	20	48	39	17.2	OUFa
F2013-22	Denning	Day	74	50	101	17	11	25	200	18.8	OUa
		Night	67	47	91	14	10	20	110	25.4	OUFa
F2013-2459	Breeding	Night	98	57	149	25	15	38	26	14.9	OUFa
	Denning	Day	300	233	375	83	65	104	168	49.6	OUFa
		Night	228	183	278	53	42	64	171	62.4	OUa
	Rendezvous	Day	345	272	426	74	57	91	130	57.6	OUFa
		Night	358	279	447	64	49	79	126	46.2	OUa
	Wayfaring	Day	318	227	423	81	58	108	120	25.7	OUa
		Night	330	247	424	79	59	101	178	32.6	OUFa
M2013-06	Denning	Day	37	22	55	7	4	10	47	13.8	OUa
		Night	38	19	63	8	4	12	26	14.5	OUFa
	Rendezvous	Day	51	41	62	9	7	11	136	61.7	OUa
		Night	59	47	72	12	9	14	134	57.8	OUa
M2013-15	Rendezvous	Day	138	99	184	34	25	45	175	23.9	OUFa
		Night	172	128	223	42	31	54	179	28.7	OUi
M2013-07	Wayfaring	Day	429	302	578	112	79	151	91	26.3	OUFa
		Night	459	296	658	127	82	182	187	16.9	OUFa

Continued

M2013-10	Breeding	Day	157	110	213	32	23	44	170	21.5	OUFa
		Night	141	98	191	28	19	38	301	20	OUFa
	Wayfaring	Day	130	100	164	30	23	38	189	38.6	OUFi
		Night	141	109	177	33	25	41	338	37.9	OUFa
M2014-14a	Breeding	Day	269	185	369	69	47	95	144	21.1	OUFa
		Night	284	202	379	73	52	97	2523	22.7	OUFa
	Denning	Day	187	129	257	49	34	68	70	22.6	OUFa
		Night	236	148	344	57	36	84	96	15	OUFi
	Rendezvous	Day	243	151	356	64	40	93	103	14	OUFa
	Wayfaring	Day	179	144	217	48	38	58	264	56.6	OUFa
		Night	174	141	211	49	40	60	437	56.2	OUFa
M2014-14b	Denning	Day	529	407	666	57	67	109	296	37.2	OUFa
		Night	532	417	662	80	63	100	301	42.6	OUFa
	Rendezvous	Day	509	367	672	130	94	171	181	26.8	OUFa
		Night	519	371	692	120	85	159	241	24.4	OUFa
	Wayfaring	Day	75	48	107	71	11	25	46	18.7	OUFa
		Night	121	83	166	25	17	34	103	20	OUFa
M2016-2710a	Denning	Day	208	147	279	51	36	68	177	24.3	OUFi
		Night	232	160	317	53	36	72	202	22.1	OUi
	Rendezvous	Day	181	122	251	34	279	47	131	19.1	OUFa
		Night	150	104	205	31	22	43	169	20.3	OUFa
	Wayfaring	Day	162	120	211	40	29	52	167	29.3	OUFa
		Night	134	99	175	37	27	48	247	28.2	OUFa
M2017-24a	Denning	Day	531	366	724	120	82	164	368	19.4	OUFa
		Night	543	359	764	119	78	167	386	16.3	OUFa

Table 9. Mean AKDE home range estimates (km^2) by season and diel period of the 11 data sets derived from the 10 gray wolves with constrained seasonal and diel space use on Red Lake Indian Reservation.

					95% CI				95% CI	
Season	**Diel Period**	**N**	**95% Mean**	**SE**	**Lower**	**Upper**	**50% Mean**	**SE**	**Lower**	**Upper**
Breeding	Day	2	213	24	166	260	51	8	35	66
	Night	3	174	29	117	232	42	8	26	58
Denning	Day	7	267	76	119	415	55	14	27	83
	Night	7	268	100	71	465	55	19	17	92
Rendezvous	Day	7	235	76	87	383	55	20	16	94
	Night	6	235	85	68	402	51	19	14	88
Wayfaring	Day	6	216	66	86	345	64	15	34	93
	Night	7	212	66	83	341	54	18	19	90

Table 10. AKDE home range estimates (km^2) by diel period of the 11 data sets derived from the 10 gray wolves with constrained diel space use on Red Lake Indian Reservation.

		95%	**95% CI**		**50%**	**95% CI**		**Number of**	**Effective**	**Model**
Data Set	**Diel Period**	**AKDE**	**Lower**	**Upper**	**AKDE**	**Lower**	**Upper**	**Relocations**	**Sample Size**	**Type**
M2012-01	Day	182	146	221	46	37	56	123	67.8	OUFa
	Night	128	100	158	33	26	40	122	62.9	OUFa
F2013-22	Day	74	50	101	17	11	23	200	18.8	OUa
	Night	67	47	91	14	10	20	110	25.4	OUFa
F2013-2459	Day	309	267	354	83	72	95	434	128.4	OUFa
	Night	293	255	334	73	63	83	501	130.5	OUa
M2013-06	Day	61	51	73	12	10	14	199	77.4	OUFi
	Night	82	67	99	15	12	18	181	64.5	OUi
M2013-15	Day	266	196	346	59	44	77	337	28.1	OUFa
	Night	295	221	380	64	48	83	387	30.6	OUa
M2013-07	Day	445	317	594	115	82	153	252	24.9	OUFa
	Night	481	350	634	130	94	171	364	27.6	OUFa
M2013-10	Day	188	151	229	45	36	55	562	49.9	OUFa
	Night	180	144	220	43	35	53	907	46.5	OUFa
M2014-14a	Day	227	194	262	55	47	64	581	96.6	OUFa
	Night	235	202	271	57	49	65	930	96	OUFa
M2014-14b	Day	470	388	558	86	71	103	523	66.9	OUFa
	Night	441	367	521	77	64	91	645	71	OUFa
M2016-2710a	Day	197	164	234	46	38	55	609	71.7	OUFa
	Night	189	157	224	46	38	54	794	72.2	OUFa

Table 11. Mean AKDE home range estimates (km^2) by diel period of the 11 data sets derived from the 10 gray wolves with constrained diel space use on Red Lake Indian Reservation.

				95% CI				95% CI	
Diel Period	**N**	**95% Mean**	**SE**	**Lower**	**Upper**	**50% Mean**	**SE**	**Lower**	**Upper**
Day	10	242	41	161	323	56	9	38	75
Night	10	239	42	156	322	55	10	35	75

Table 12. Mean AKDE home range estimates (km^2) by sex of the 11 data sets derived from the 10 gray wolves with constrained diel space use on Red Lake Indian Reservation.

				95% CI				95% CI	
Sex	**N**	**95% Mean**	**SE**	**Lower**	**Upper**	**50% Mean**	**SE**	**Lower**	**Upper**
Female	2	185	113	0	405	54	32	0	116
Male	9	315	73	172	458	117	36	47	187

Effects on AKDE Home Range

I ran a main effects (season, diel period, and sex) only model with wolf as a random effect to test for the effect of these specific factors on wolf AKDE home range. None of the main effects has significant effects on AKDE home range. (Table 13).

Table 13. Linear mixed main effects model for log_{10} transformed AKDE estimates for Red Lake Indian Reservation gray wolves.

	Estimate	**log_{10} Estimate**	**SE**
(Intercept)	105.624	4.660	0.628
Denning	1.420	0.351	0.235
Rendezvous	1.553	0.440	0.241
Wayfaring	0.929	-0.073	0.217
Night	1.003	0.003	0.114
Male	1.470	0.385	0.654

I performed best subsets model selection on a full linear regression model including all main effects and two-way interactions. The best subsets model selection supported 3 top models with AICc delta < 2. These models included season, sex, and the season by sex interaction as best predictors of AKDE home range (Table 14). The top model with the lowest AICc was the null, intercept only model, suggesting that none of the predictors, at least for this data set, explain the variance in AKDE home range estimates. There is further evidence for this, considering the similarity of null and model residual deviances in this set of top models, and the similarity of individual estimates of home range as seen previously.

Table 14. The top 3 linear mixed models for Red Lake Indian Reservation gray wolf AKDE home range based on Akaike's Information Criterion (AICc) and Akaike weights (ω_i). Predictor variables were all categorical and included season (SSN), diel period (DP), and sex (SEX) as well as all 2-way interactions as fixed effects and wolf as a random effect. Response variable was $\log_{10}$ AKDE home range estimates.

	Model Variables				**log**				**Residual**
Rank	**SSN**	**SEX**	**SSN:SEX**	**K**	**Likelihood**	**AICc**	**ΔAICc**	**ω_i**	**Deviance**
1				1	-37.87	82.30	0.00	0.42	0.42
2		+		2	-37.37	83.70	1.41	0.21	0.42
3	+	+	+	4	-28.81	84.10	1.76	0.17	0.31

Home Range Estimator Comparison

Kernel Density Estimation

The 95% KDE home range estimates for gray wolves ranged from 75km^2 to 4889km^2 (Table 15, Fig 12), and the 50% KDE home range estimates ranged from 12km^2 to 828km^2 (Table 15). Wolves across all Red Lake lands had an average 95% KDE home range of 1591km^2 and an average 50% KDE home range of 244km^2 (Table 16).

Table 15. KDE home range estimates (km^2) for gray wolves on Red Lake Indian Reservation.

Wolf	95% KDE	50% KDE	Time Span (days)	Number of Relocations	Capture Location
M2012-01	181	44	290	245	Dim. Res.
F2013-22	92	15	56	310	Ced. Lands
F2013-2459	337	82	418	935	Ced. Lands
F2013-04	3813	814	61	307	Dim. Res.
M2013-06	75	12	106	380	Dim. Res.
M2013-15	275	57	190	724	Dim. Res.
F2013-23	208	39	145	764	Ced. Lands
M2013-07	447	121	151	616	Dim. Res.
M2013-10	174	38	211	1469	NW Angle
M2014-14	1118	242	426	2679	Dim. Res.
F2015-16	4278	291	575	4360	Dim. Res.
M2016-2710	1870	178	455	1561	Ced. Lands
F2016-17	3837	828	74	1681	Dim. Res.
F2017-2723	2946	488	261	2137	Dim. Res.
M2017-24	4889	533	682	4936	Dim. Res.
M2018-25	920	114	80	462	Dim. Res.

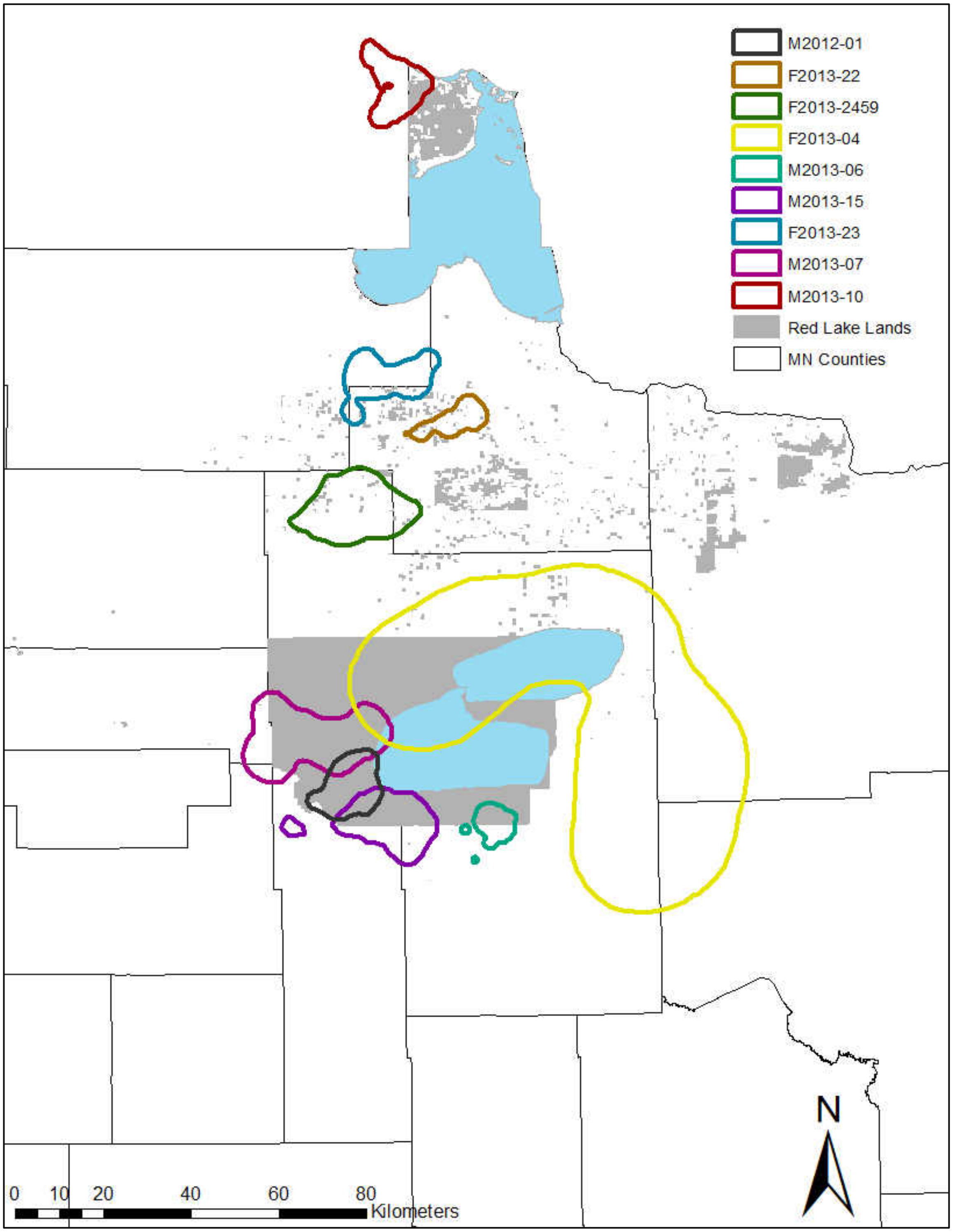


Figure 12a. 95% KDE contours for gray wolves captured from 2012-2013 on Red Lake Indian Reservation.

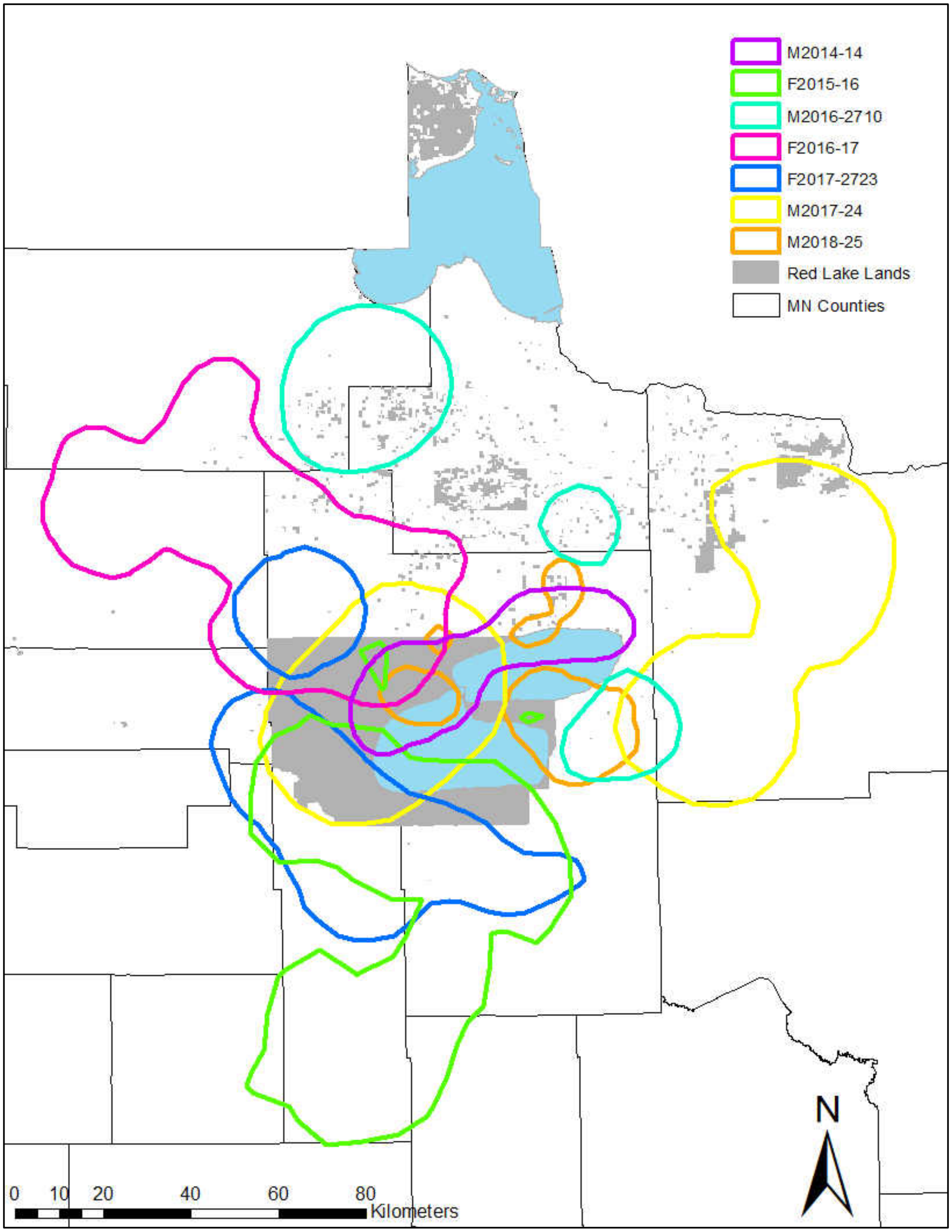


Figure 12b. 95% KDE contours for gray wolves captured from 2014-2018 on Red Lake Indian Reservation.

Table 16. Mean KDE home range estimates (km^2) by location for gray wolves on Red Lake Indian Reservation.

				95% CI				95% CI	
Location	**N**	**95% Mean**	**SE**	**Lower**	**Upper**	**50% Mean**	**SE**	**Lower**	**Upper**
All Red Lake Lands	16	1591	437	736	2447	244	70	108	379
Diminished Reservation	11	2071	567	959	3182	322	91	144	500
Restored Ceded Lands	5	536	336	0	1194	70	29	14	127

Brownian Bridge Estimation

The 95% BBMM home range estimates for gray wolves ranged from 55km^2 to 1993km^2 (Table 17, Fig 13), and the 50% BBMM home range estimates ranged from 7km^2 to 92km^2 (Table 17). Wolves across all Red Lake lands had an average 95% BBMM home range of 461km^2 and an average 50% BBMM home range of 57km^2 (Table 18). BBMM home range estimation uses information from the relocation data differently from the home range estimators, resulting in different numbers of relocations used in the estimation.

Table 17. BBMM home range estimates (km^2) for gray wolves on Red Lake Indian Reservation.

Wolf	95% BBMM	50% BBMM	Time Span (days)	Number of Relocations	Capture Location
M2012-01	284	50	290	241	Dim. Res.
F2013-22	55	7	56	302	Ced. Lands
F2013-2459	417	92	418	919	Ced. Lands
F2013-04	424	57	61	303	Dim. Res.
M2013-06	83	13	106	375	Dim. Res.
M2013-15	198	43	190	717	Dim. Res.
F2013-23	93	14	145	761	Ced. Lands
M2013-07	325	70	151	611	Dim. Res.
M2013-10	130	24	211	1442	NW Angle
M2014-14	388	82	426	2660	Dim. Res.
F2015-16	1993	165	575	4351	Dim. Res.
M2016-2710	549	59	455	1547	Ced. Lands
F2016-17	403	25	74	1664	Dim. Res.
F2017-2723	636	72	261	2120	Dim. Res.
M2017-24	1069	104	682	4929	Dim. Res.
M2018-25	329	38	80	459	Dim. Res.

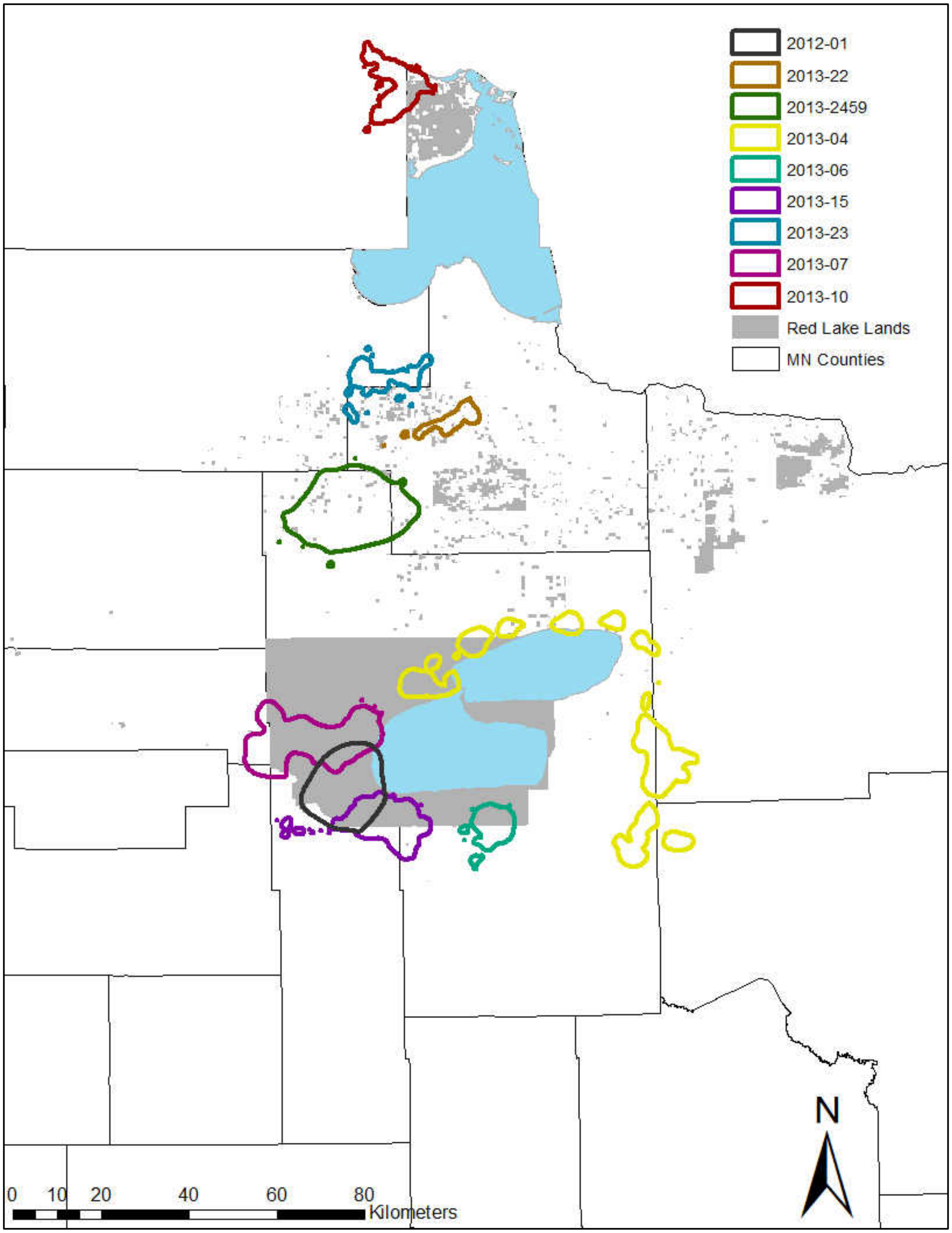


Figure 13a. 95% BBMM contours for gray wolves captured from 2012-2013 on Red Lake Indian Reservation.

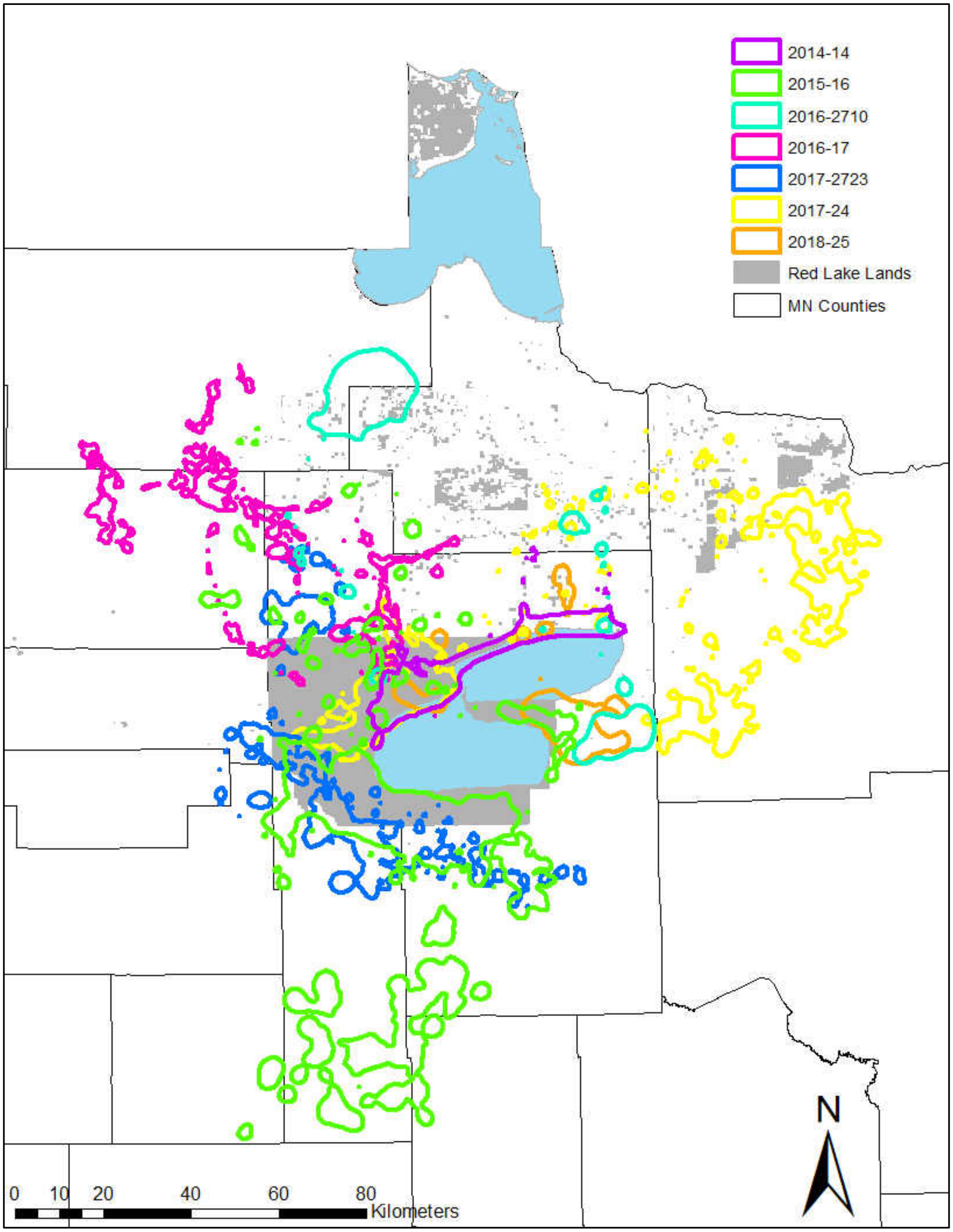


Figure 13b. 95% BBMM contours for gray wolves captured from 2014-2018 on Red Lake Indian Reservation.

Table 18. Mean BBMM home range estimates (km^2) by location for gray wolves on Red Lake Indian Reservation.

Location	N	95% Mean	SE	95% CI Lower	95% CI Upper	50% Mean	SE	95% CI Lower	95% CI Upper
All Red Lake Lands	16	461	120	226	696	57	10	37	77
Diminished Reservation	11	558	163	237	878	65	13	41	90
Restored Ceded Lands	5	249	99	56	442	39	16	8	74

Home Range Estimator Comparison

I used the 7 wolves with constrained space use and AKDE estimates derived from their complete data sets to compare AKDE, MCP, KDE, and BBMM home range estimates (Table 19). Mean areas for the 7 wolves ranged from 171km^2 to 226km^2 across estimators (Table 20).

When comparing AKDE to MCP, the estimators had a nearly linear relationship indicating correlation of their values (Fig 14a). The paired t-test indicated that the means were significantly different ($t_{df=6} = 4.157$, $p = 0.006$). When comparing AKDE to KDE, the estimators also had a nearly linear relationship indicating a high correlation of their values (Fig 14b). The paired t-test indicated that the means were not significantly different ($t_{df=6} = 1.223$, $p = 0.268$). When comparing AKDE to BBMM, the estimators appeared to have a linear relationship indicating correlation of their values (Fig 14c). The paired t-test indicated that the means were not significantly different ($t_{df=6} = 0.321$, $p = 0.759$). When comparing MCP to KDE, the estimators had a linear relationship indicating correlation of their values

(Fig 15a). The paired t-test indicated that the means were significantly different ($t_{df=6} = 3.913$, $p = 0.007$). When comparing MCP to BBMM, the estimators also appeared to have a linear relationship indicating correlation of their values (Fig 15b). The paired t-test indicated that the means were not significantly different ($t_{df=6} = 0.321$-1.898, $p = 0.107$). When comparing KDE to BBMM, the estimators had a nearly linear relationship indicating a high correlation of their values (Fig 15c). The paired t-test indicated that the means were not significantly different ($t_{df=6} = 0.736$, $p = 0.49$). At least for wolves with constrained space use, AKDE, KDE, and BBMM produced similar area estimates, whereas MCP produced different home range estimates from AKDE and KDE, but similar home range estimates to BBMM.

I compared MCP, KDE, and BBMM estimates for all 16 wolves with average home range from 244km^2 to 1716km^2 across estimators (Table 20). When comparing MCP to KDE for all wolves, the estimators had a linear relationship indicating correlation of their values (Fig 16a). The paired t-test indicated that the means were not significantly different ($t_{df=15} = 1.303$, $p = 0.212$). When comparing either MCP or KDE to BBMM, there were no obvious pattern of collinearity in the estimates (Fig 16b-c). The paired t-test between MCP and BBMM also indicated that the overall difference between the estimates was significantly different ($t_{df=15} = 2.909$, $p = 0.011$). The paired t-test between KDE and BBMM indicated that the overall difference between the estimates was significantly different ($t_{df=15} = 4.083$, $p = 0.001$). When there was no known constrained space use, MCP and KDE produced similar home range estimates, whereas both MCP and KDE produced different home range estimates from BBMM. See Appendix B for geographic visualization of applicable home range estimates for individual wolves.

Table 19. 95% area estimates (km^2) by estimator for gray wolves on Red Lake Indian Reservation.
*Wolves used to compare all four home range estimators.

	AKDE		MCP		KDE		BBMM		
Wolf	**Home Range**	**Number of Relocations**	**Home Range**	**Number of Relocations**	**Home Range**	**Number of Relocations**	**Home Range**	**Number of Relocations**	**Time Span (days)**
M2012-01*	165	245	132	245	181	245	284	241	291
F2013-22*	72	310	43	310	92	310	55	302	56
F2013-2459*	297	935	289	935	337	935	417	919	418
F2013-04	NA	NA	2123	307	3813	307	424	303	61
M2013-06*	72	380	48	380	75	380	83	375	106
M2013-15*	280	724	174	724	275	724	198	717	190
F2013-23	NA	NA	190	764	208	764	93	761	145
M2013-07*	481	616	344	616	447	616	325	611	151
M2013-10*	183	1469	167	1469	174	1469	130	1442	211
M2014-14	NA	NA	1005	2679	1118	2679	388	2660	426
M2014-14a	230	1511	NA	NA	NA	NA	NA	NA	217
M2014-14b	448	1168	NA	NA	NA	NA	NA	NA	210
F2015-16	NA	NA	5561	4360	4278	4360	1993	4351	575
M2016-2710	NA	NA	4184	1561	1870	1561	549	1547	455
M2016-2710a	195	1403	NA	NA	NA	NA	NA	NA	354
F2016-17	NA	NA	3161	1681	3837	1681	403	1664	74
F2017-2723	NA	NA	2709	2137	2946	2137	636	2120	261
M2017-24	NA	NA	6192	4936	4889	4936	1069	4929	682
M2017-24a	782	3697	NA	NA	NA	NA	NA	NA	449
M2018-25	NA	NA	1140	462	920	462	329	459	80

Table 20. Mean 95% area estimates (km^2) by estimator for comparable gray wolves with constrained space use (N=7) and for all gray wolves (N=16) on Red Lake Indian Reservation.

Home Range				**95% CI**	
Estimator	**N**	**Mean**	**SE**	**Lower**	**Upper**
Constrained					
AKDE	7	221	55	114	329
MCP	7	171	43	87	255
KDE	7	226	51	126	326
BBMM	7	213	51	114	313
All					
MCP	16	1716	517	703	2729
KDE	16	1591	437	736	2447
BBMM	16	461	120	226	696

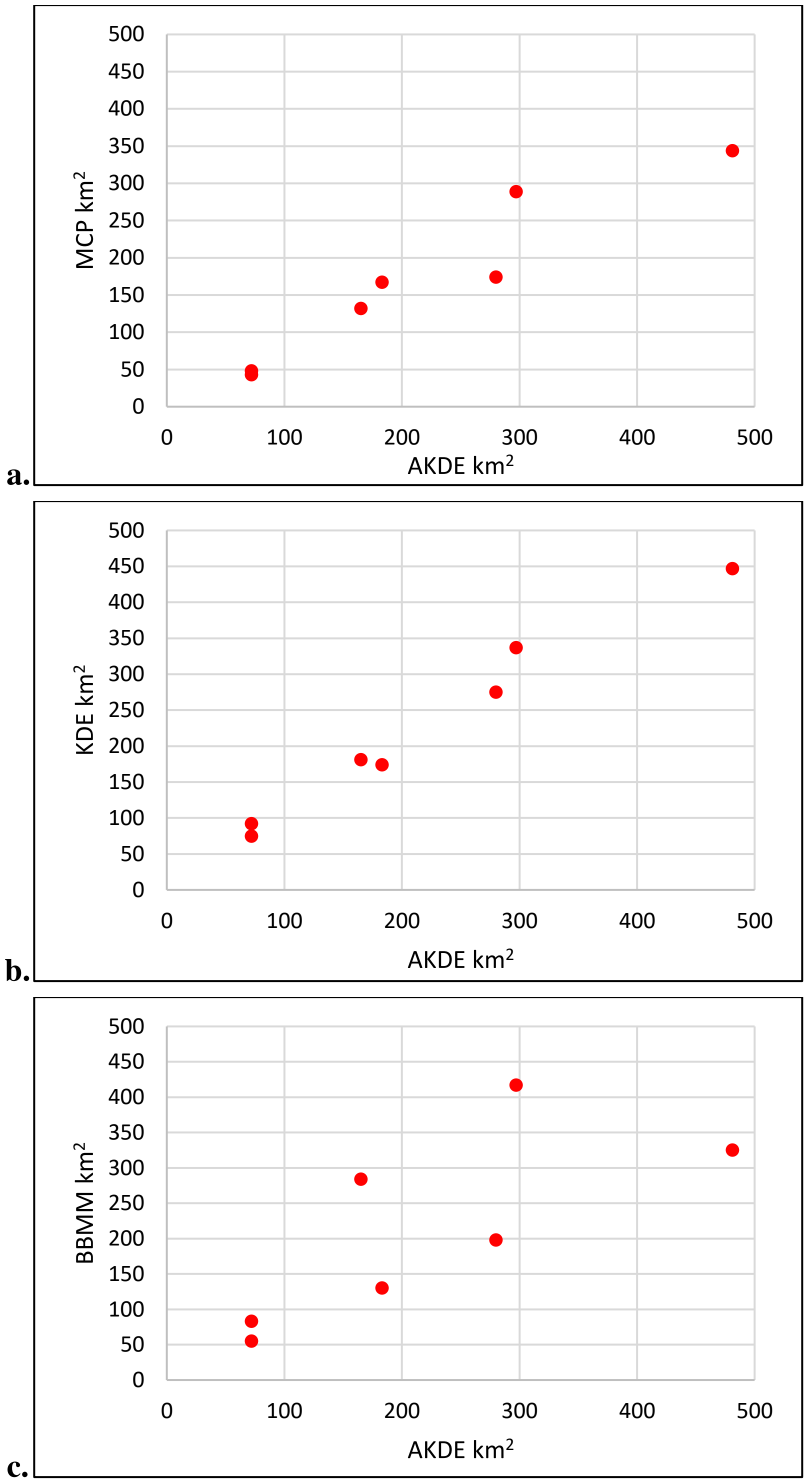


Figure 14. 95% AKDE home range estimates as a function of 95% **a.** MCP, **b.** KDE, and **c.** BBMM home range estimates for comparable data sets derived from gray wolves with constrained space use on Red Lake Indian Reservation.

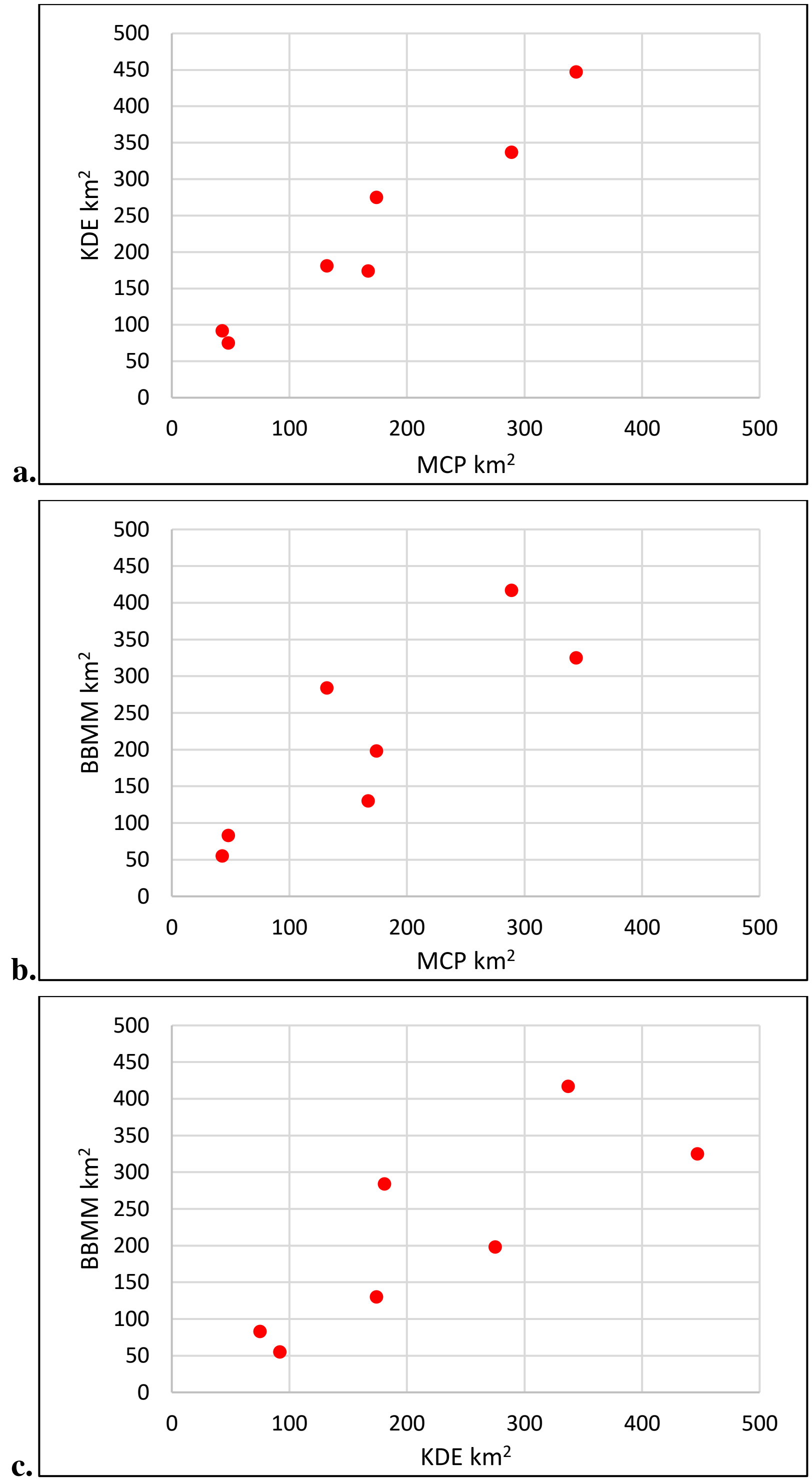
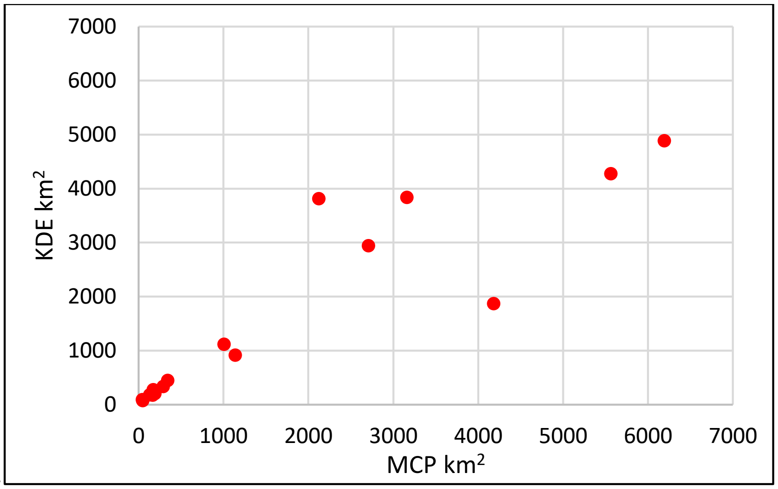
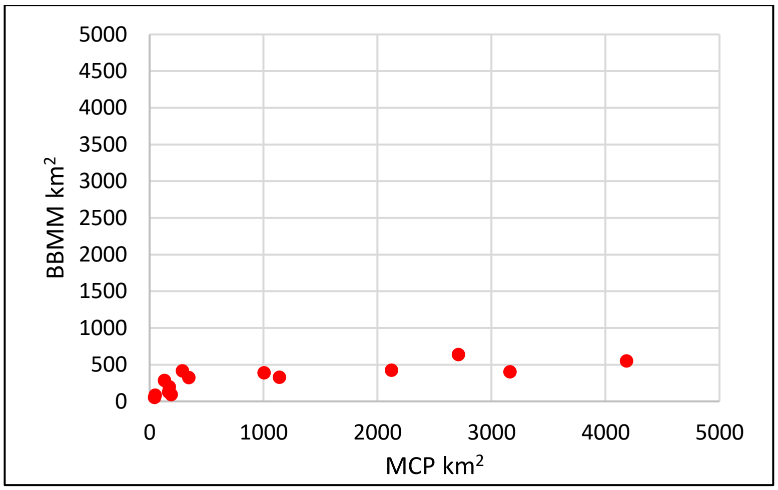


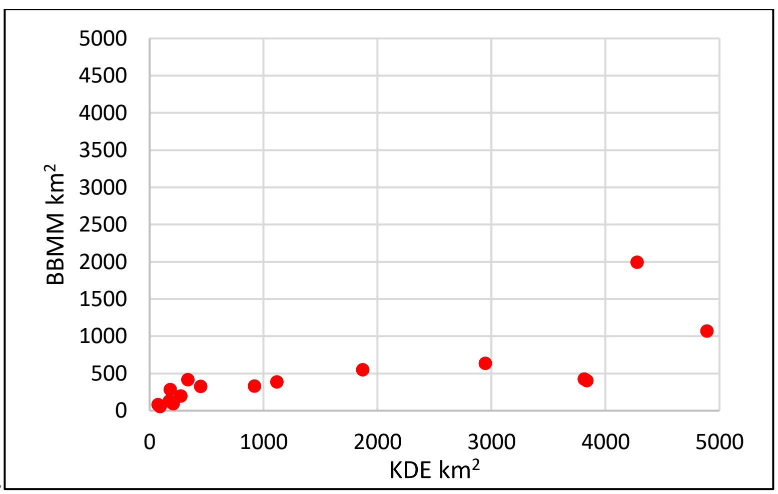
Figure 15. 95% MCP home range estimates as a function of 95% **a.** KDE and **b.** BBMM home range estimates and **c.** 95% KDE home range estimates as a function of 95% BBMM home range estimates for comparable data sets derived from gray wolves with constrained space use on Red Lake Indian Reservation.



a.



b.



c.

Figure 16. 95% MCP home range estimates as a function of 95% **a.** KDE and **b.** BBMM home range estimates and **c.** 95% KDE home range estimates as a function of 95% BBMM home range estimates for all data sets derived from gray wolves on Red Lake Indian Reservation.

Discussion

Primary Home Range Estimation

MCP home range estimates (95%) for wolves captured in 2012 and 2013 ranged from 43km^2-167km^2, with wolf F2013-04 having a home range estimated far outside that range at 2123km^2. Surprisingly, this wolf had data collection circumstances similar to that of the wolf F2013-22, who had a collar that was online for 56 days and recorded 310 GPS locations. Similarly, F2013-04 had a collar that was online for 61 days and recorded 307 GPS locations. Both wolves were captured in early denning season, however, the difference in their MCP estimated home range is 2080km^2. This is likely due both to the season and to the difference in life stage for each wolf. During denning season, the pack home range is concentrated around the den after the birthing of pups (Mech 1970). Because wolf F2013-22 was a yearling at the time of capture, she was likely still with her natal wolf pack (Mech and Boitani 2003) and was displaying the condensed space use denning behavior. Conversely, F2013-04, an adult at the time of capture, was potentially a dispersing wolf who was not yet part of an established wolf pack. However, it could also be possible that she was a part of a pack but was not the breeding female, in which case her movements would be expanded, potentially beyond pack territory borders, as she foraged for food (Jedrzejewski 2001, Ruprecht 2012). In this case, MCP would not be an accurate estimator for this wolf because the estimate is derived from the smallest convex polygon created by the outermost relocation points (Mohr 1947, Hayne 1949), some of which would not be representative of a home range with normally traversed areas.

MCP home range estimates (95%) for wolves captured from 2014 to 2018 ranged from 1005km^2-6192km^2. With an exception of wolf F2013-04, the estimates for wolves captured from 2014-2018 were larger than those of 2012 and 2013. The largest home range of the earlier years was 167km^2; this was 838km^2 less than the smallest home range of the later years. This could potentially be explained by the weather patterns in the earlier years versus the later years. The winters of 2012-13 and 2013-14 were particularly harsh in Minnesota with lower temperatures and greater snowfall (MNDNR 2019). When harsh, cold and snowy weather occurs, white-tailed deer, a primary food source for Red Lake wolves, display yarding behavior where they congregate at high densities in conifer stands near food sources for thermal protection and energy conservation (Ozoga and Gysel 1972, Messier and Barette 1985). Because the deer were likely congregated in this manner during the harsh winters of 2012 and 2013, the smaller wolf home range estimates are likely a reflection of the wolves remaining in the areas where they found tight groups of their prey.

Conversely, winters after 2013 were not as harsh as they had previously been (MNDNR 2019), and wolves during these years of milder weather were likely required to search more broadly to find deer that more widely dispersed rather than congregating. The difficulty of finding deer was compounded by decline in deer density after the previous harsh winters impacted deer food availability and, subsequently, deer survival (DeLgiudice et al. 2002, Erb et al. 2018).

The MNDNR estimates of home range using MCP reflect the same trend, with average space use estimated to be ~20km^2 larger in 2014 than they were in the previous 2 years when winters were harsh (Erb et al. 2018). Although the MNDNR estimates for northeastern Minnesota wolves follow a similar trend to Red Lake estimates, the MNDNR estimates are substantially smaller than those of Red Lake wolves. The current MNDNR average estimate over years 2012-2018 is 160km^2 (Erb et al. 2018). This is a 1556km^2

difference from the average estimate of 1716km^2 for Red Lake wolves over the same time period. This is more than likely due to the land composition of Red Lake lands, including the Diminished Reservation, the Restored Ceded Lands, and the Northwest Angle. All of these areas are comprised of vast, uninterrupted forested areas (USGS 2011, USGS 2016), which is the preferred land cover of Minnesota wolves (Erb et al. 2018). This allows Red Lake wolves to have more extensive areas of use compared to the wolves in northeastern Minnesota, where forested areas are much more fragmented with agricultural land (USGS 2011, USGS 2016), likely minimizing home range sizes. The MNDNR estimates were based on data collected from wolves captured primarily from this northeast area (Erb et al. 2018), and possibly explains the difference in home range estimation sizes. Because home range sizes for Red Lake wolves are substantially larger, Red Lake Indian Reservation may be limited in the number of wolf packs it can support, potentially causing more wolves to disperse from the Reservation than if ranges were smaller.

Parcels of the Restored Ceded Lands are relatively small and sparsely distributed north of the Diminished Reservation, and wolves that were captured within the Restored Ceded Lands expectedly have home ranges that hugely encompass lands managed by the state. Although wolves on the Diminished Reservation have less exposure to state management regulations, a majority of the wolves there do have home ranges that extend beyond the boundary of the Reservation to some extent. In some instances, this is because the area that the wolf uses is large enough to reach the boundary, but in other instances the wolves are living near the boundary.

Using AKDE, which, unlike MCP, works under the assumption of constrained space use, I found that not all of the wolves had exhibited defined home ranges. Wolves who did not display constrained space use in their variograms were primarily females. Additionally, females were observed primarily during denning season, and it is likely the behavior during this season that resulted in no constrained space use for this group. The variogram only reveals constrained space use when the area of use no longer expands over time, and although wolves spend most of the time concentrated around the den site during denning season, they will periodically travel to different areas within the home range (Jedrzejewski 2001, Ruprecht 2012). If the areas these wolves traveled to did not reach the extent of their home ranges, but continued to expand throughout the season, I would be less likely to see constrained space use, or a sill, in their variograms.

There were 2 females with constrained space use who were also observed mostly during denning season. However, one female was a yearling and the other was a breeding female. Both of these wolves would be less likely to expand area use far beyond the den site (Ruprecht 2012), thus displaying constrained space use. It was primarily males who displayed constrained space use, and these wolves were observed mostly during wayfaring season when movement is continuous throughout the entirety of the home ranges. Because I was observing these wolves during the time when they were likely traveling to the extents of their ranges, space use no longer expanded over time and I was able to see the constrained space use, or sill, in their variograms.

There did not appear to be any correlation between observation time span and whether or not I could detect constrained space use. I saw no constrained space use in one wolf with an observation time span of 101 days, whereas another wolf with 106 days of observation time did display constrained space use. However, the former was observed primarily during denning season whereas the latter was observed primarily during rendezvous season, when the wolves are moving around the home range with their pups. Accordingly, the detection of a home range using ctmm and AKDE appeared to be better suited when observation of the wolf occurred during a time period or season during which the animal is moving throughout their home range.

Although I did not detect a home range in some wolves, this does not necessarily mean that these wolves will not ever exhibit defined home ranges. As stated previously, I perhaps needed more observation time throughout the year during additional seasons. Furthermore, wolves are capable of traversing long distances (Van Camp and Gluckie 1979, Fritts 1983) and will sometimes spend months away from their packs (Mech 1970). If the duration of observation included these types of movements, I may not have been able to detect an area of constrained space use. Alternatively, there may have actually been no constrained space use. For example, I would not be as likely to see defined home ranges if I had been tracking young adult wolves (wolf age was only discernible between pup, juvenile, and adult so age within the adult life stage was unspecified) who, at maturation, often disperse from their pack in search of new mates or a new pack (Mech and Boitani 2003). This was discussed as a potential reason for the inflated MCP estimates for wolf F2013-04, who was not found to display a constrained home range using AKDE.

Constrained home range estimates derived from AKDE reflected the territorial nature of Minnesota wolves (Mech 1973). Range overlap was minimal and occurred primarily at the borders of the ranges. These areas of overlap are referred to as buffer zones, and it is here where wolves spend time patrolling and scent marking their territories (Peters and Mech 1975, Mech 1994). I potentially saw another refection of territoriality in the multiple constrained ranges of wolf M2014-14. I know that wolf M2014-14 was initially occupying a constrained home range to the north of Lower Red Lake from September of 2014 to April 2015 but shifted its range to the north of Upper Red Lake from April 2015 to the end of its tracking duration. I also know that by August of 2017, the area to the north of Upper Red Lake, which was previously used by M201414-14, was occupied by M2017-24, another male wolf of at least 1 year old. It is possible M2017-24 was in this area prior to when the RLDNR-WP began tracking him, causing M2014-14 to shift his home range to the east of where M2017-24 was now living.

Effects on AKDE Home Range

Season, diel period, and sex were not the best predictors of AKDE home ranges for my data. I may not have seen effects simply due to the GPS sampling duration and low sample of wolves that had relocations spanning all seasons. Males and females may exhibit different seasonal dynamics as well, and there were few females represented in the denning season. Finally, I employed fixed dates to define seasons, and these may not have coincided precisely with realized conditions that would have led to changes in movement behavior.

Home Range Estimator Comparison

Animals with constrained space use as defined by the continuous-time movement models had similar home range estimates using AKDE, KDE, and BBMM. Although KDE is a simpler method, AKDE has the benefit of providing confidence intervals. I estimated BBMM area because it is often used as a surrogate for home range estimation, and although estimates were similar to AKDE, BBMM contours are more useful for inferring trajectories and linking land cover type to movement paths (Fleming et al. 2015, Calabrese et al. 2016). Range estimates for these wolves with constrained ranges were consistently smaller using MCP than when using AKDE, KDE, and BBMM, resulting in an underestimation of space use. Although MCP is still commonly used and is the simplest of the estimator methods, it is not an appropriate estimator for wolves with constrained space use.

Animals with no constrained space use had range estimates derived from MCP, KDE, and BBMM. Estimates using MCP were similar to KDE estimates, and ranges derived from both of these methods were higher than those from BBMM, resulting in an underestimation of space use. This supports the idea that BBMM estimates should not be interpreted as home range, particularly when there is no defined area of use.

As GPS technology continues to advance, issues related to the use of methods that do not account for the autocorrelative nature of relocation data will become more apparent. Although MCP and KDE will always be valuable for assessing overall space use, AKDE, which accounts for autocorrelation and identifies constrained space use as defined by Burt (1943), is the most accurate and appropriate method for estimating defined home ranges.

Management Implications

This study provided the RLDNR with updated and refined estimation of home ranges for Red Lake gray wolves. Additionally, it provided insight into the spatial distribution of gray wolves across Red Lake lands, from which gray wolf home ranges can be inferred. Most importantly, it revealed that Red Lake wolves will inevitably be subjected to Minnesota management practices. Current wolves have home ranges that widely encompass state managed lands. Additionally, Red Lakes wolves will likely disperse into state managed lands as the available area becomes saturated by wolf packs with large home ranges. To fully understand the impact of Minnesota management practices on Red Lake wolves, future studies should include seasonal home range estimation with more sufficient sample sizes than were available in this study to determine the extent of wolf home ranges during state harvest seasons, and further population monitoring to estimate the amount of area within Red lake lands available to wolves based on wolf home range sizes.

This study also provided insight into the potential consequences of using an inappropriate method for home range estimation. Space use is a critical component of animal ecology and conservation (Powell 2000) and incorrect estimates can have unanticipated and undesired effects. This is more likely to occur when the animal has no constrained space use and can be avoided by using continuous time movement models to determine if there is or is not constrained space use. If there is not constrained space use, common methods such as KDE and BBMM will give significantly different estimates and are appropriate for answering different biological questions. For example, KDE is more appropriate for questions pertaining to home ranges, and BBMM is more appropriate for occurrence estimation. The continuous-time movement modeling approach developed by Calabrese, Fleming, and Gurarie (Calabrese et al. 2016) can do both.

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Appendix A

Maps Depicting GPS Relocations for All Wolves

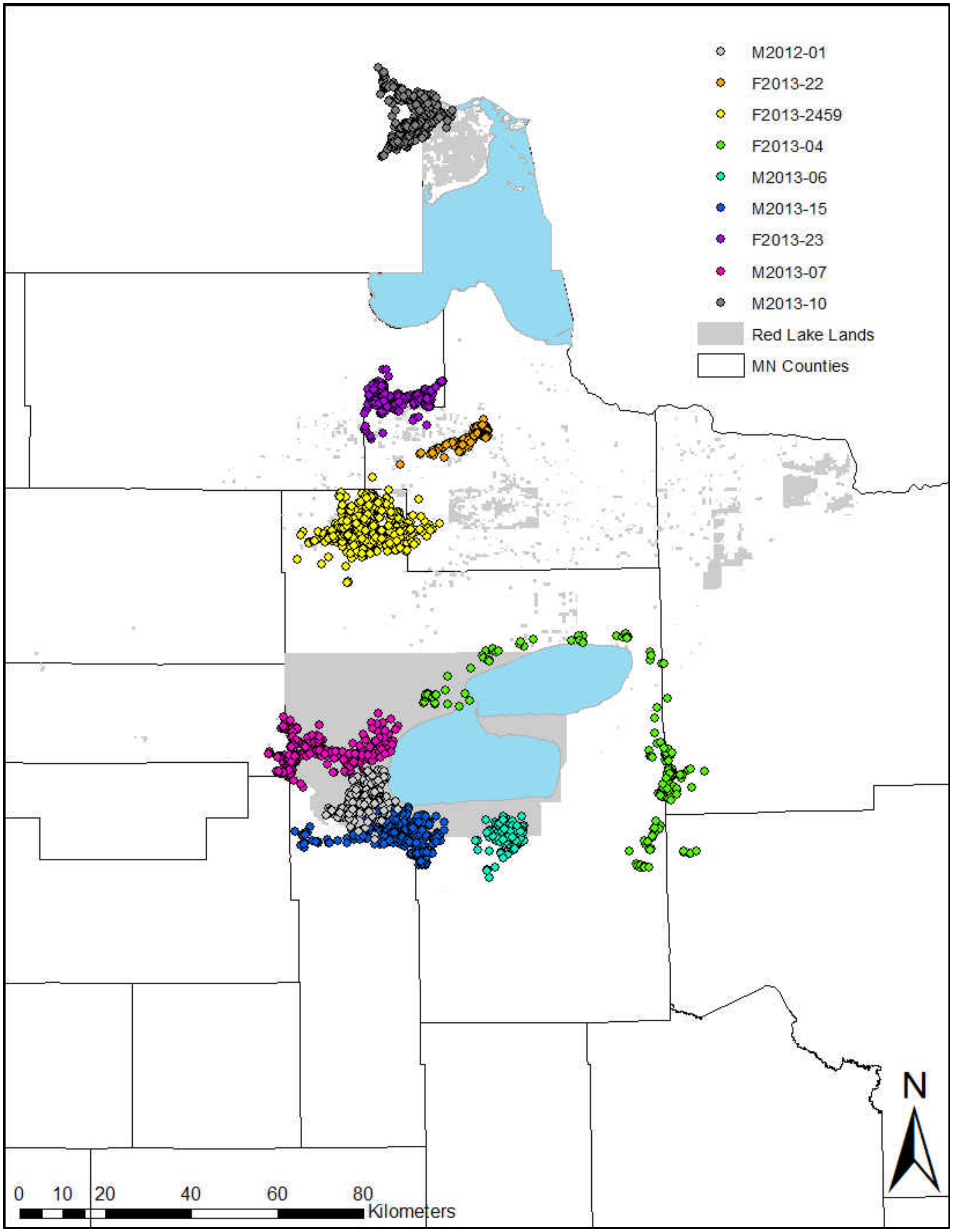

Figure 17a. GPS Relocations for gray wolves captured from 2012-2013 on Red Lake Indian Reservation.

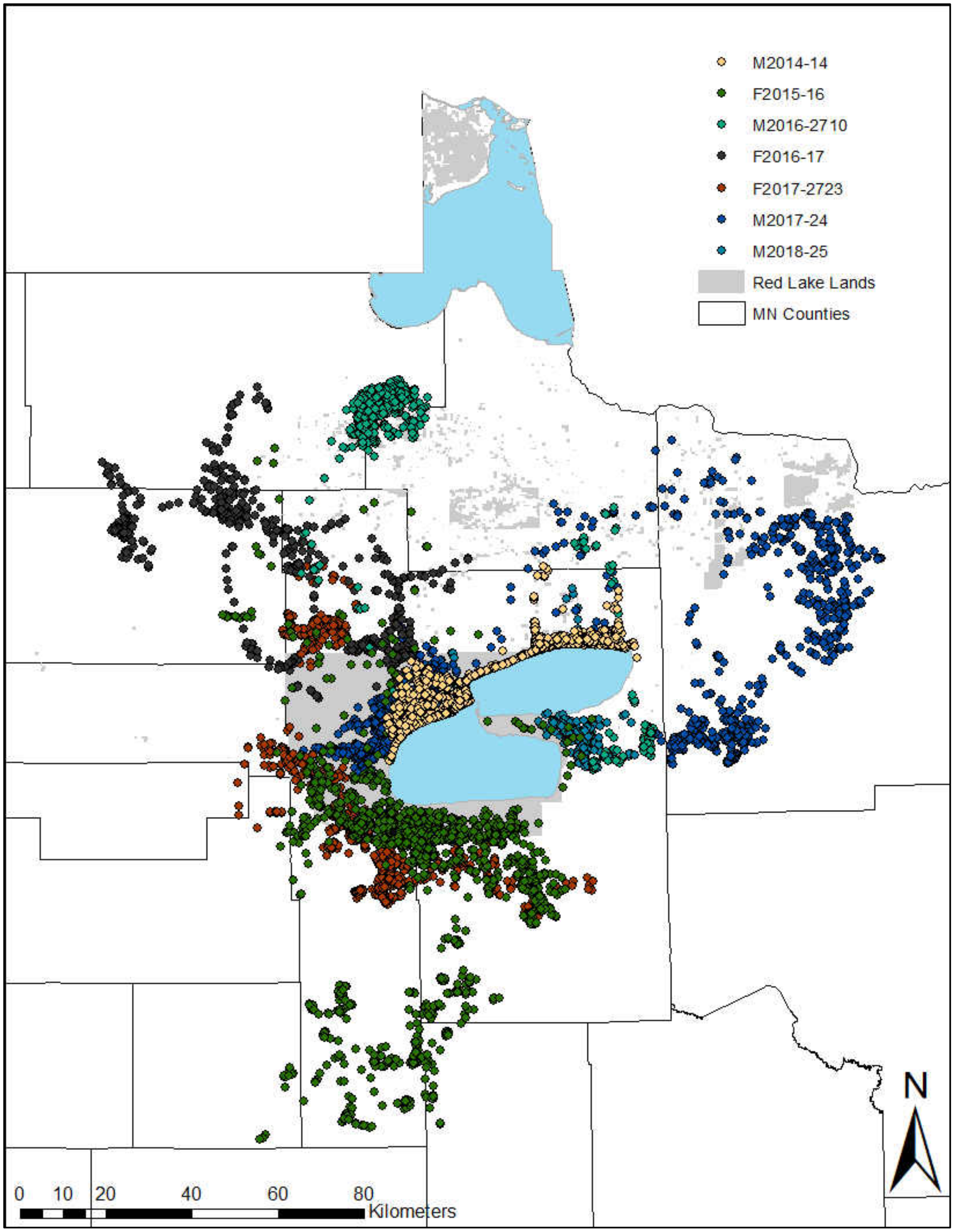

Figure 17b. GPS Relocations for gray wolves captured from 2014-2016 on Red Lake Indian Reservation.

Appendix B

Maps Depicting all Applicable 95% Home Range Estimate Contours for Each Individual Wolf

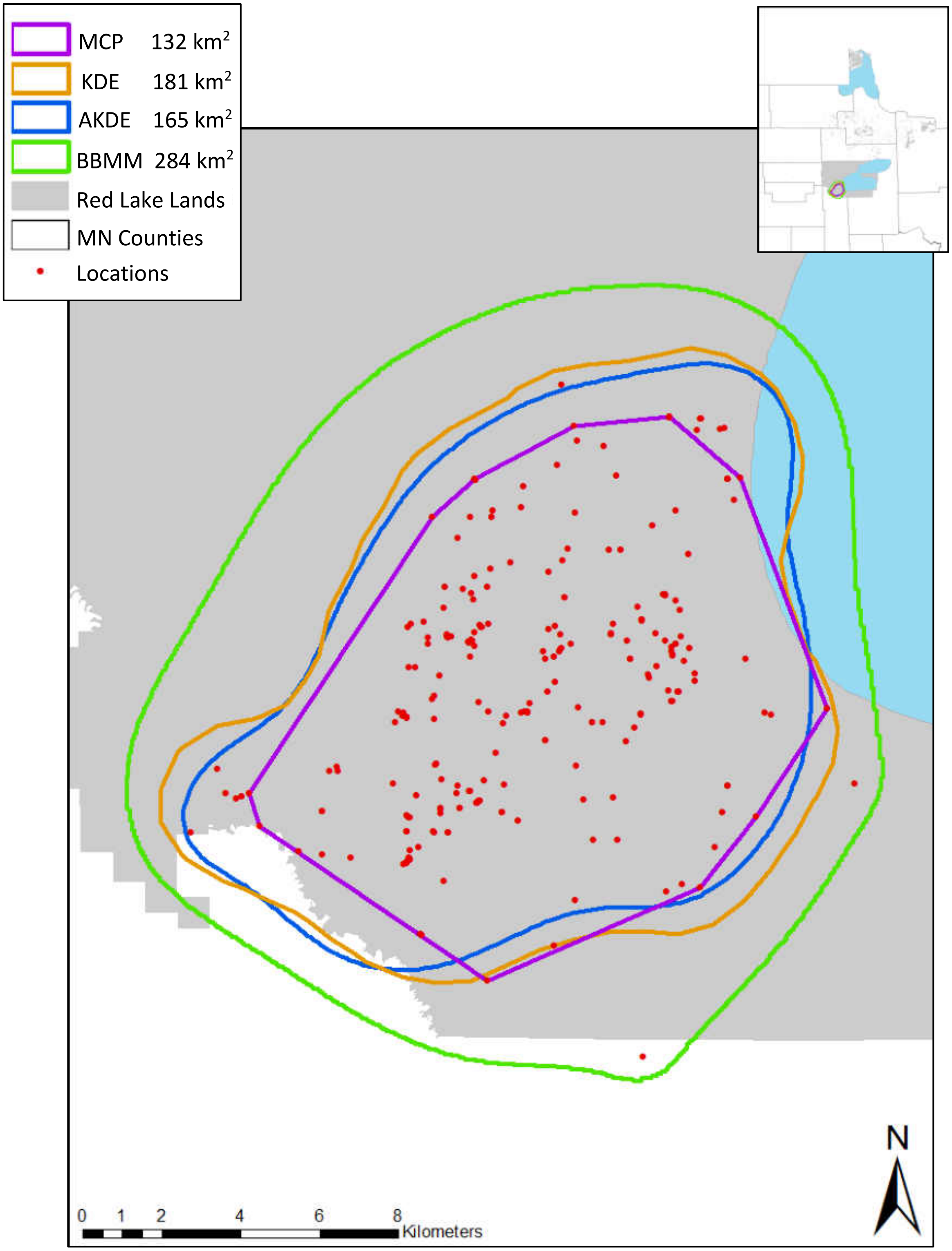

Figure 18a. All applicable 95% home range estimate contours derived from GPS relocation data received from wolf M2012-01 from 6/11/12 to 3/27/13.

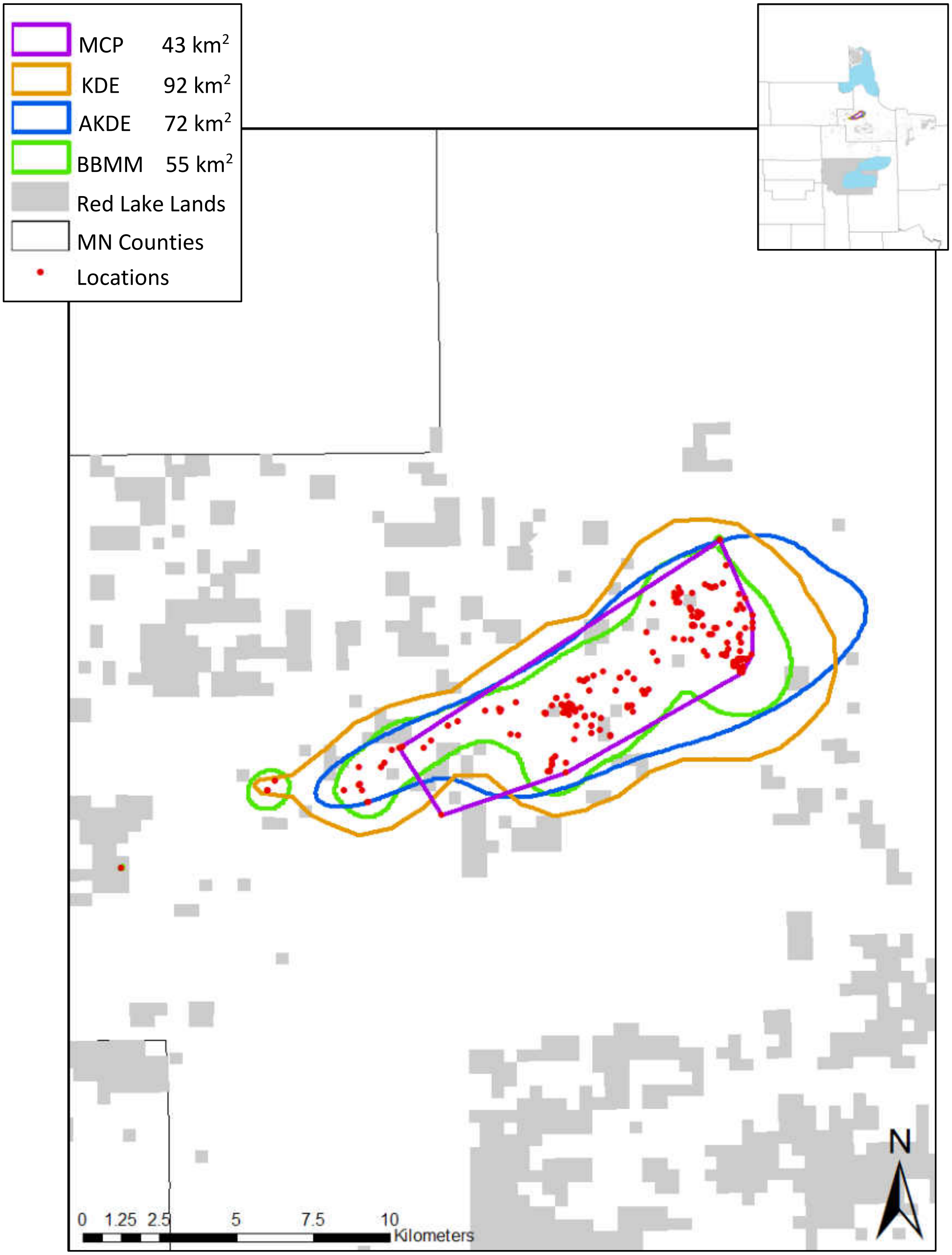

Figure 18b. All applicable 95% home range estimate contours derived from GPS relocation data received from wolf F2013-22 from 5/19/13 to 7/14/13.

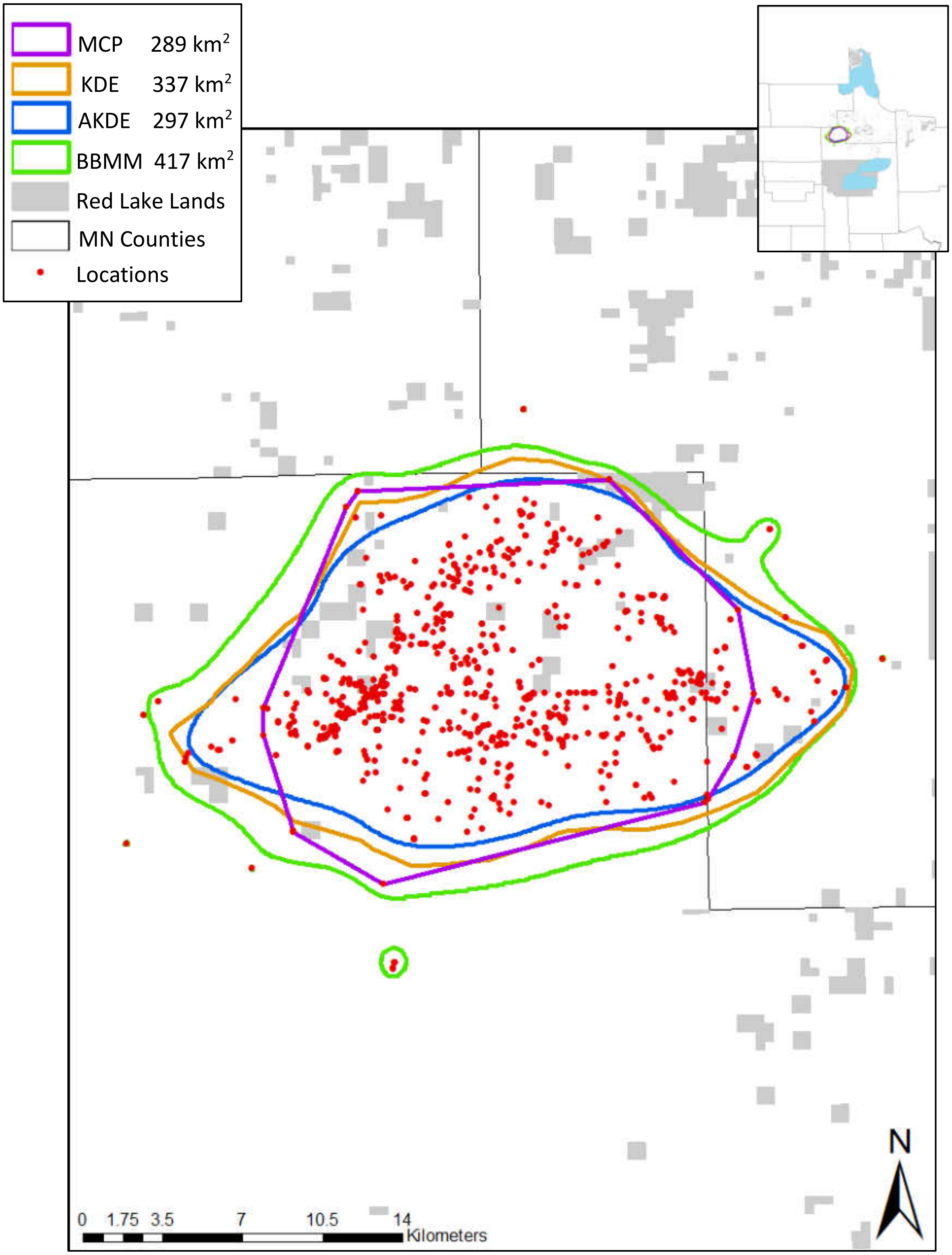

Figure 18c. All applicable 95% home range estimate contours derived from GPS relocation data received from wolf F2013-2459 from 5/19/13 to 7/11/14.

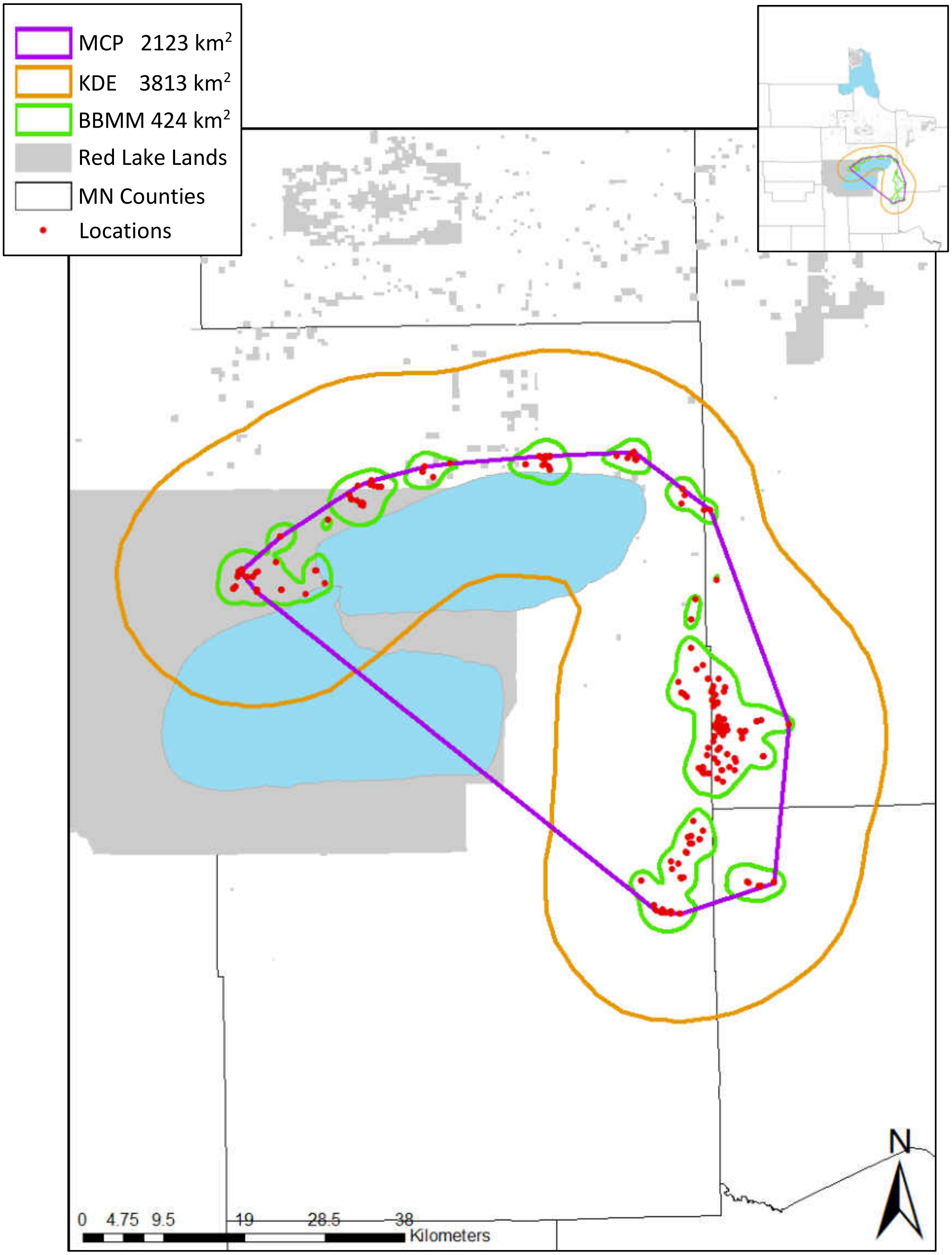

Figure 18d. All applicable 95% home range estimate contours derived from GPS relocation data received from wolf F2013-04 from 6/9/13 to 8/8/13.

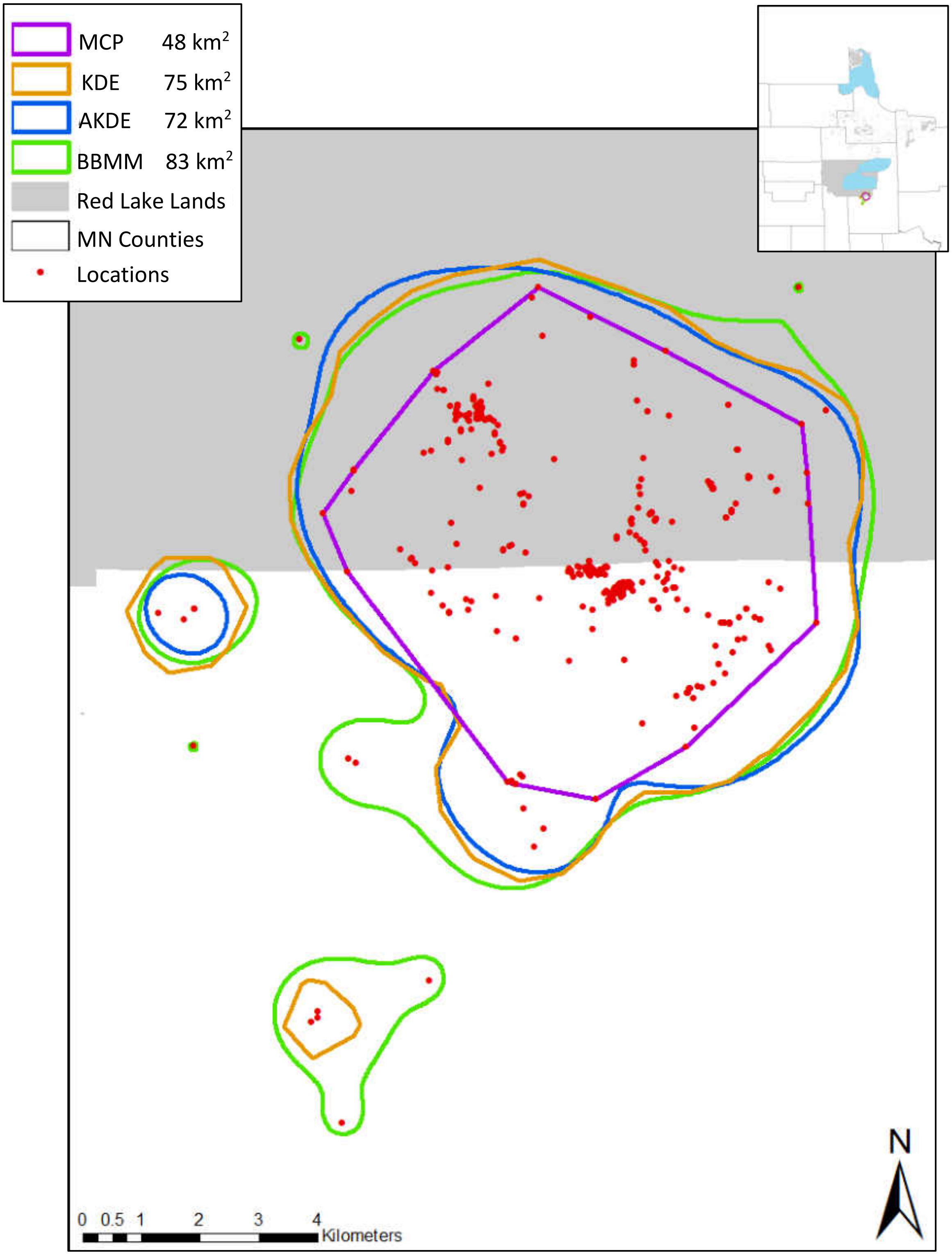

Figure 18e. All applicable 95% home range estimate contours derived from GPS relocation data received from wolf M2013-06 from 7/14/13 to 10/28/13.

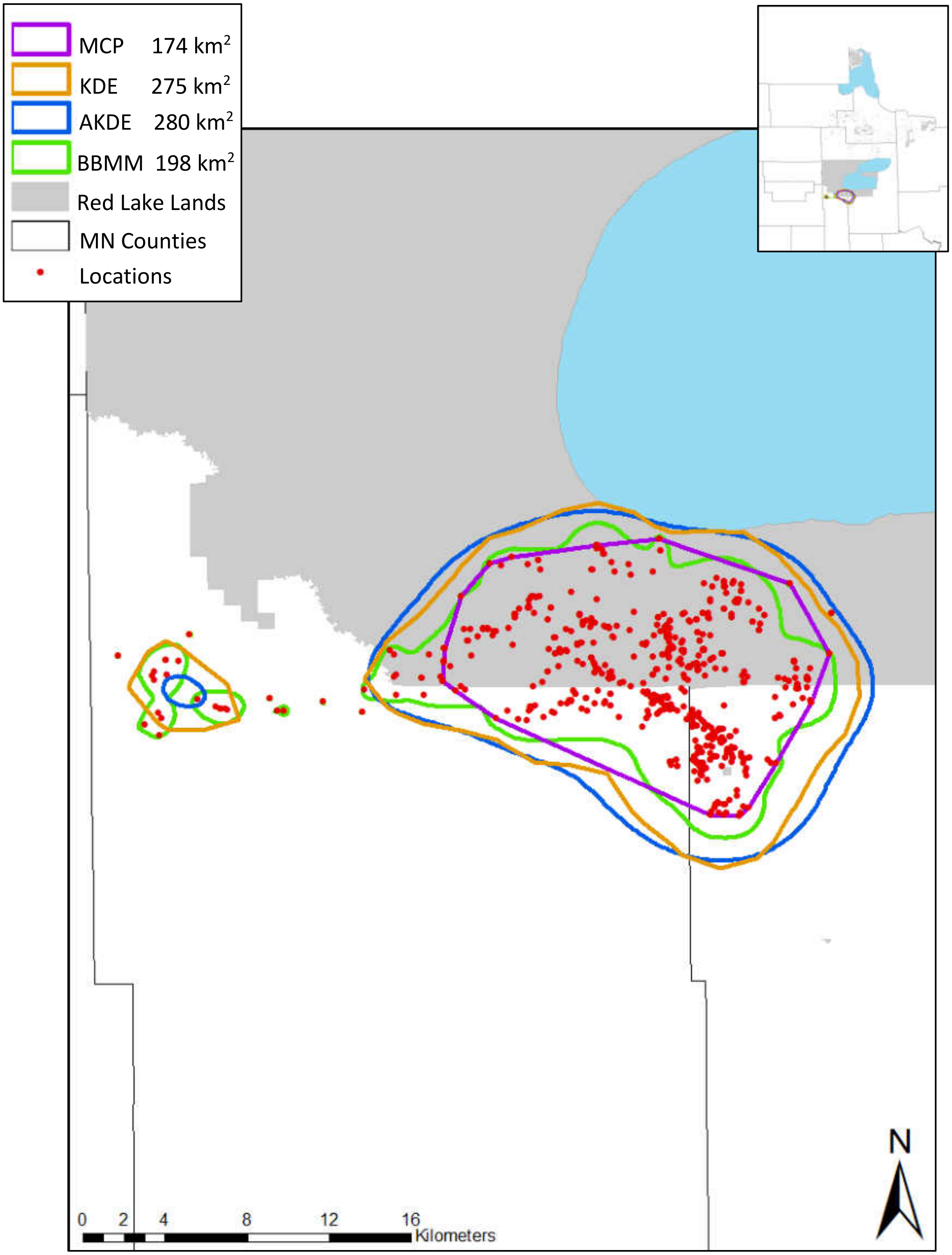

Figure 18f. All applicable 95% home range estimate contours derived from GPS relocation data received from wolf M2013-15 from 7/19/13 to 1/23/14.

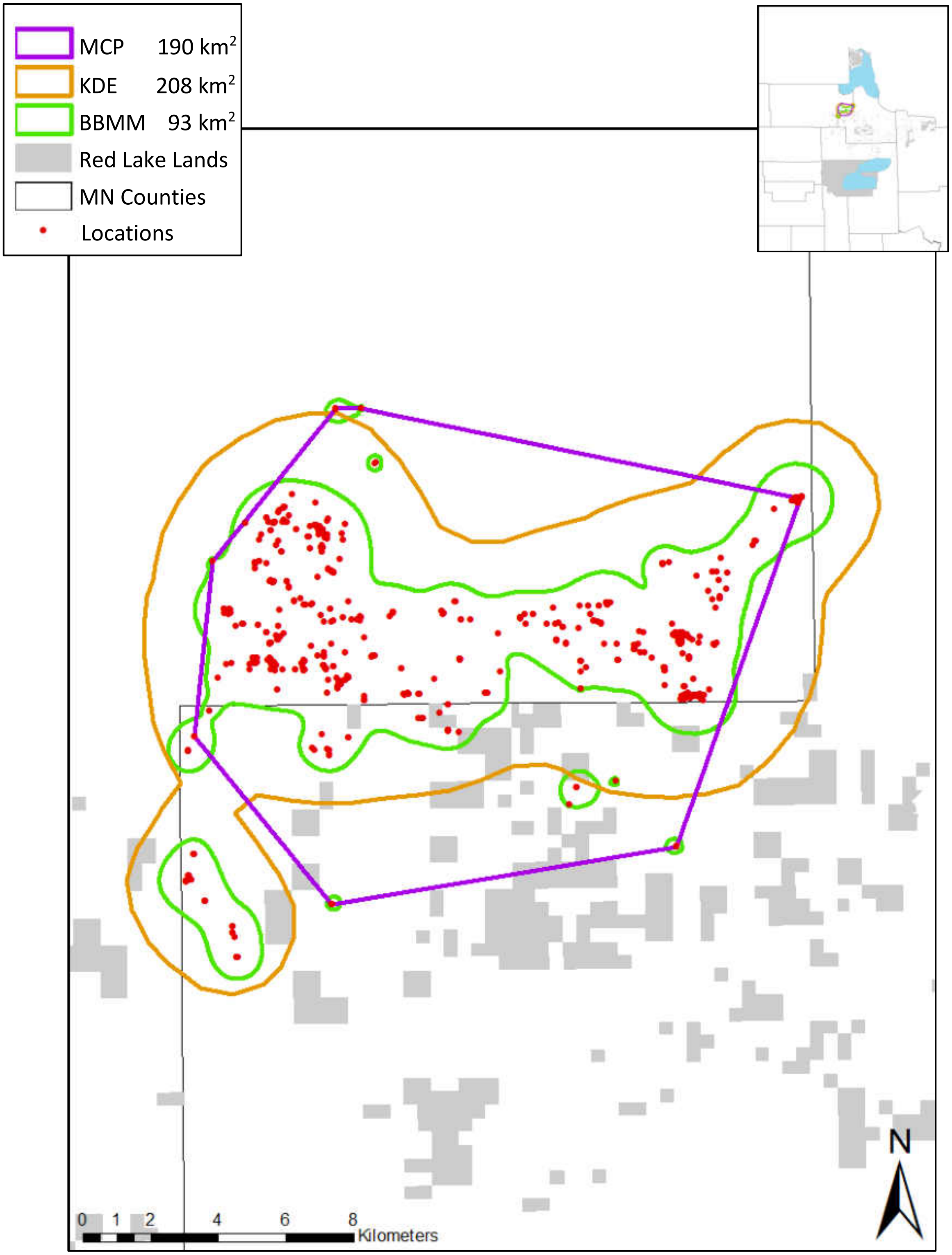

Figure 18g. All applicable 95% home range estimate contours derived from GPS relocation data received from wolf F2013-23 from 7/24/13 to 12/15/13.

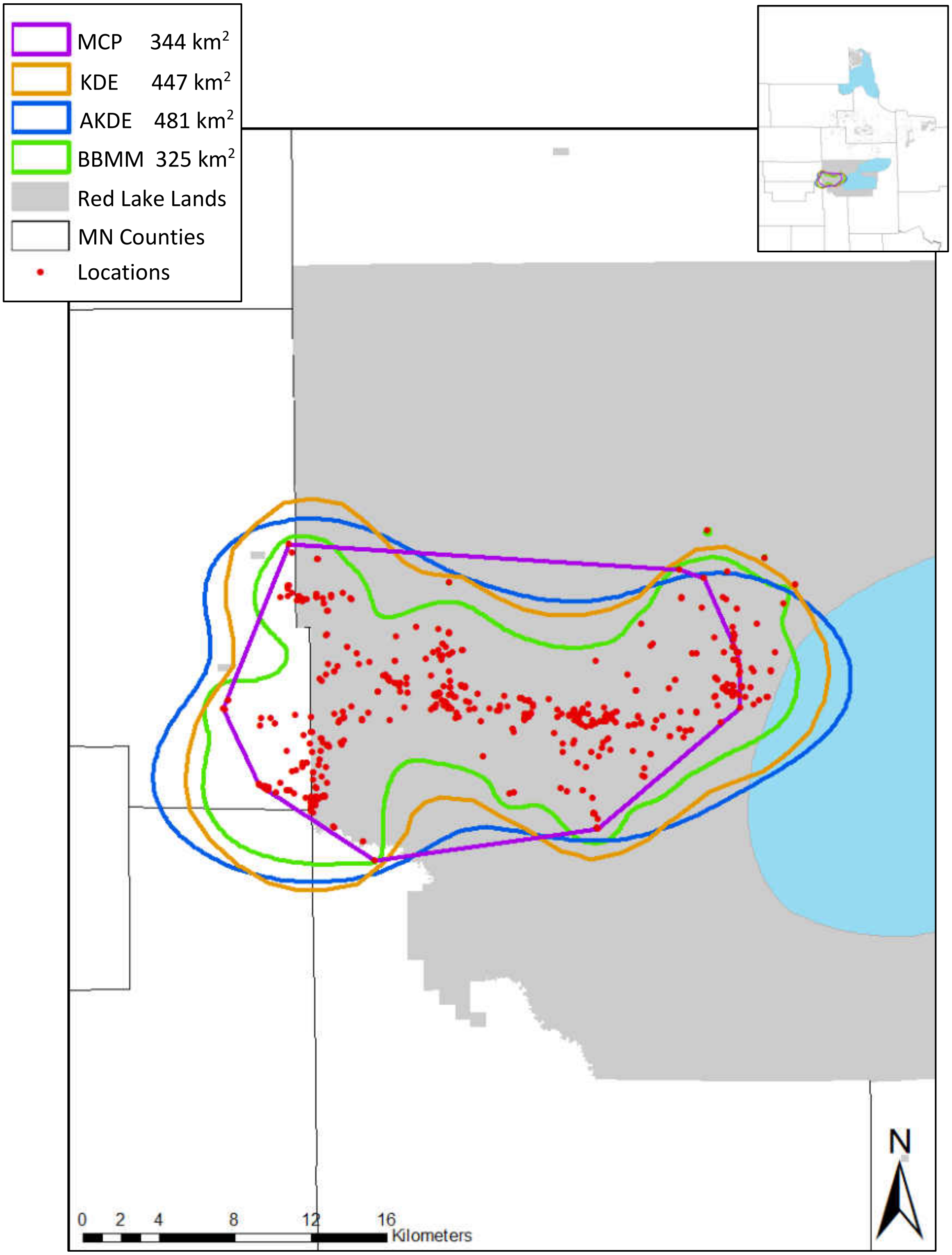

Figure 18h. All applicable 95% home range estimate contours derived from GPS relocation data received from wolf M2013-07 from 8/12/13 to 1/9/14.

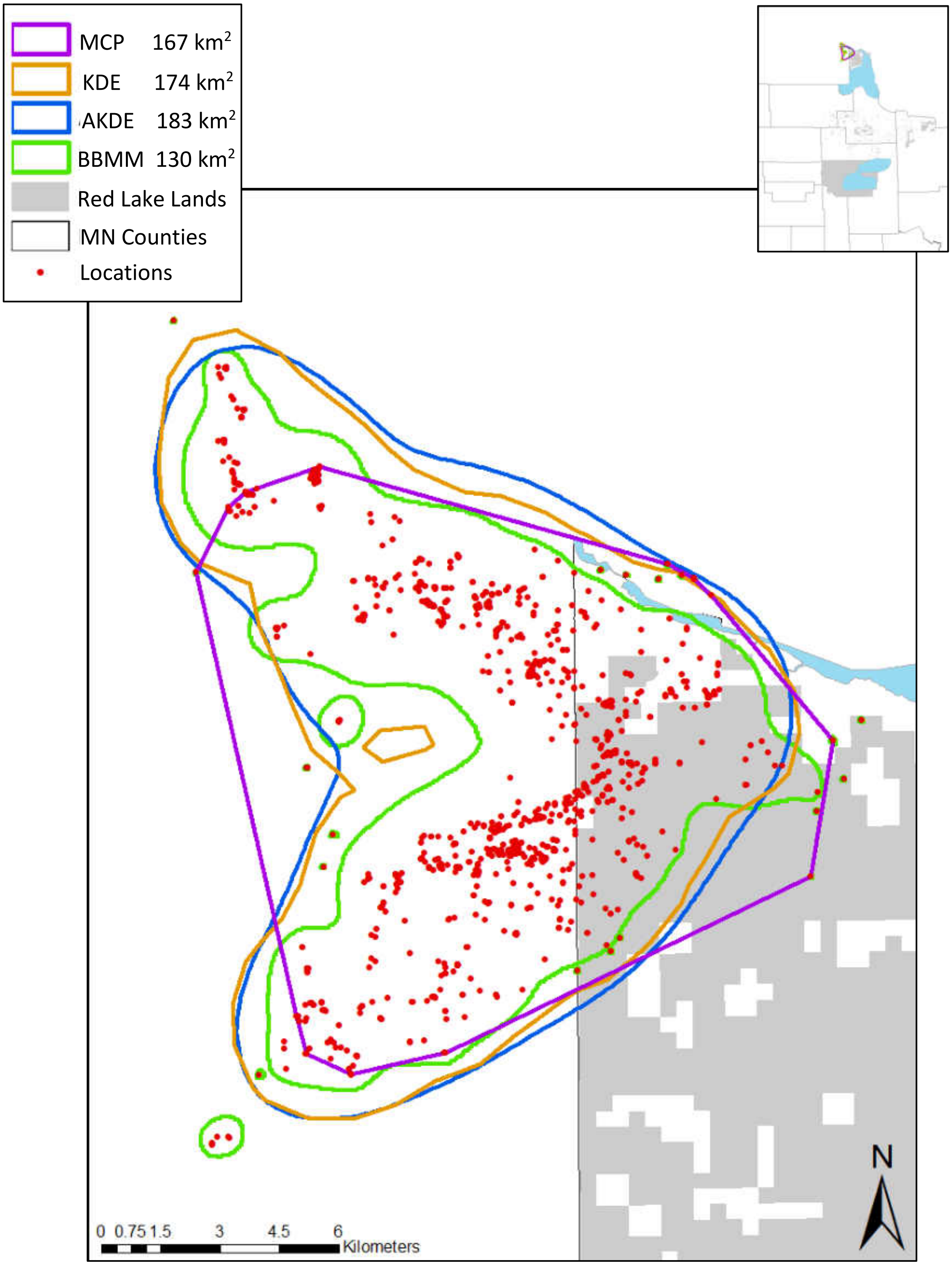

Figure 18i. All applicable 95% home range estimate contours derived from GPS relocation data received from wolf M2013-10 from 9/16/13 to 4/15/14.

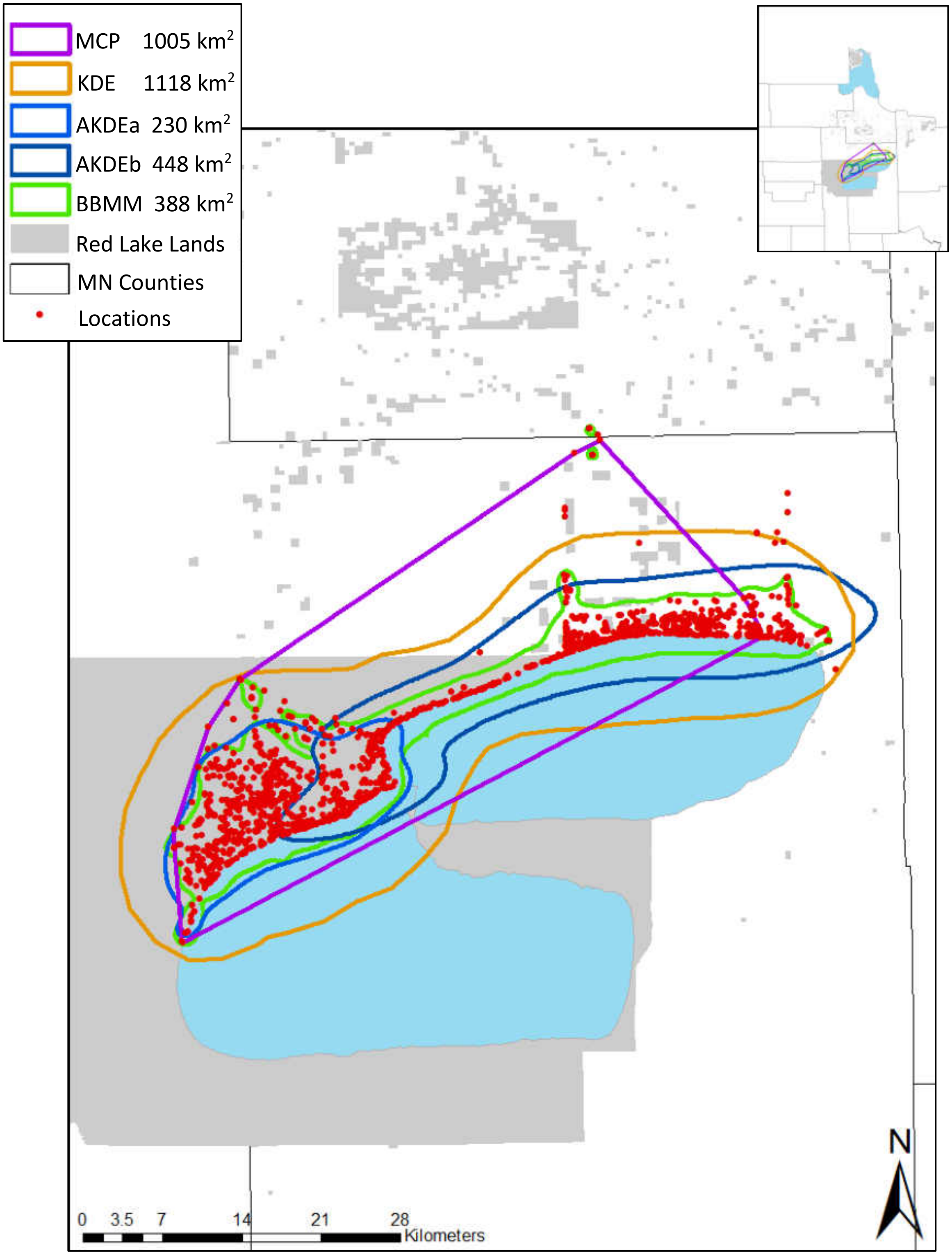

Figure 18j. All applicable 95% home range estimate contours derived from GPS relocation data received from wolf M2014-14 from 9/12/14 to 11/11/15.

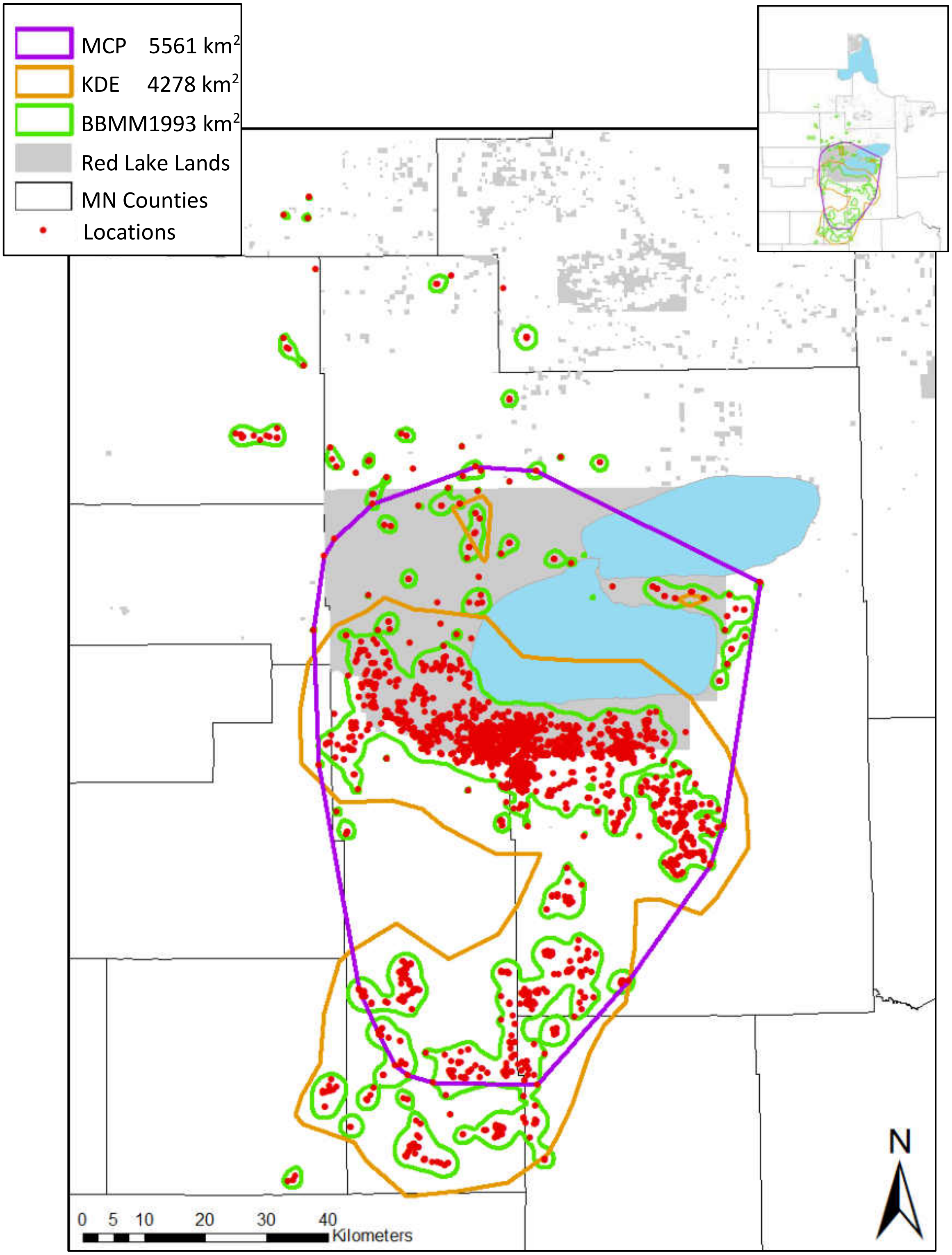

Figure 18k. All applicable 95% home range estimate contours derived from GPS relocation data received from wolf F2015-16 from 8/8/15 to 3/3/17.

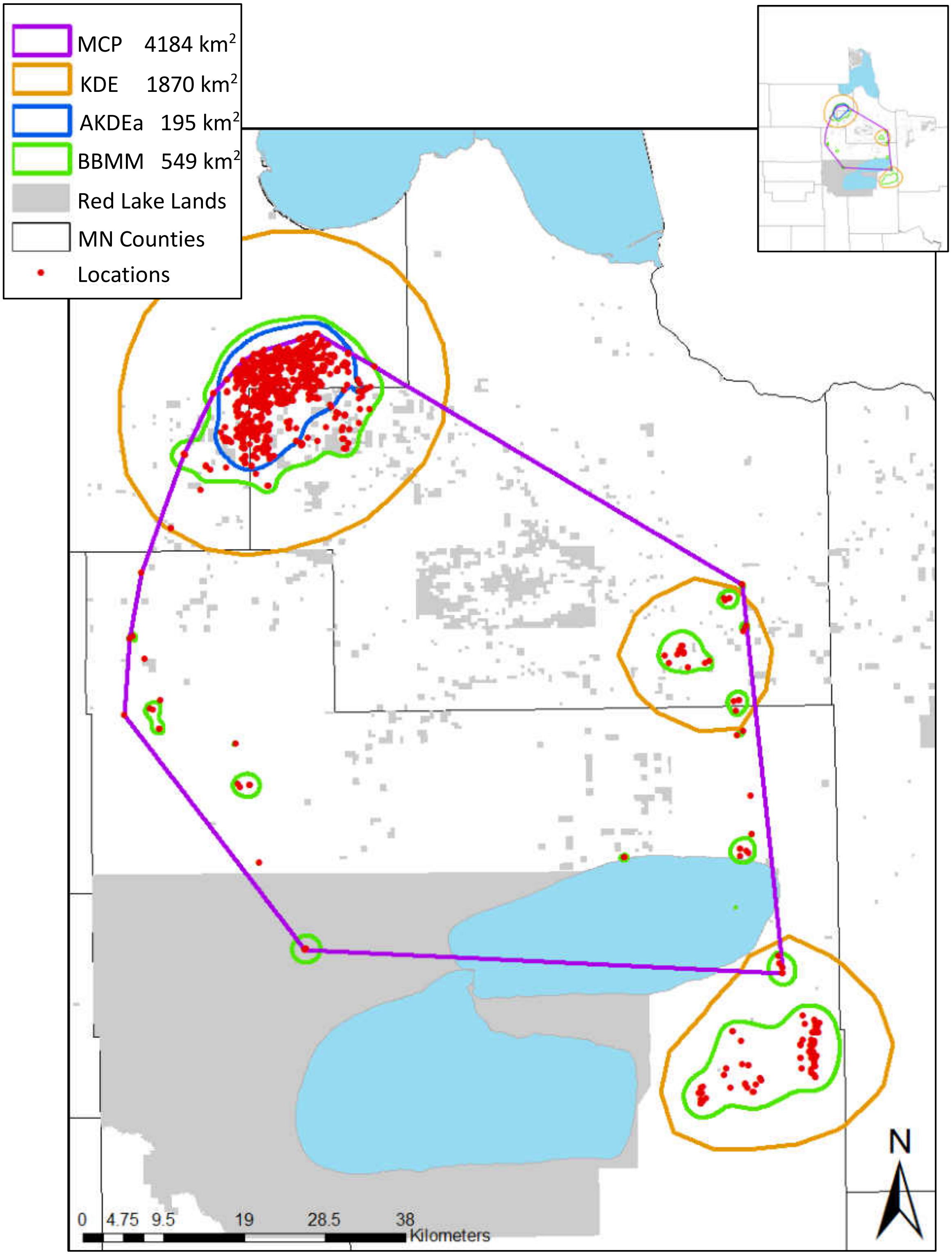

Figure 18l. All applicable 95% home range estimate contours derived from GPS relocation data received from wolf M2016-2710 from 2/8/16 to 5/7/17.

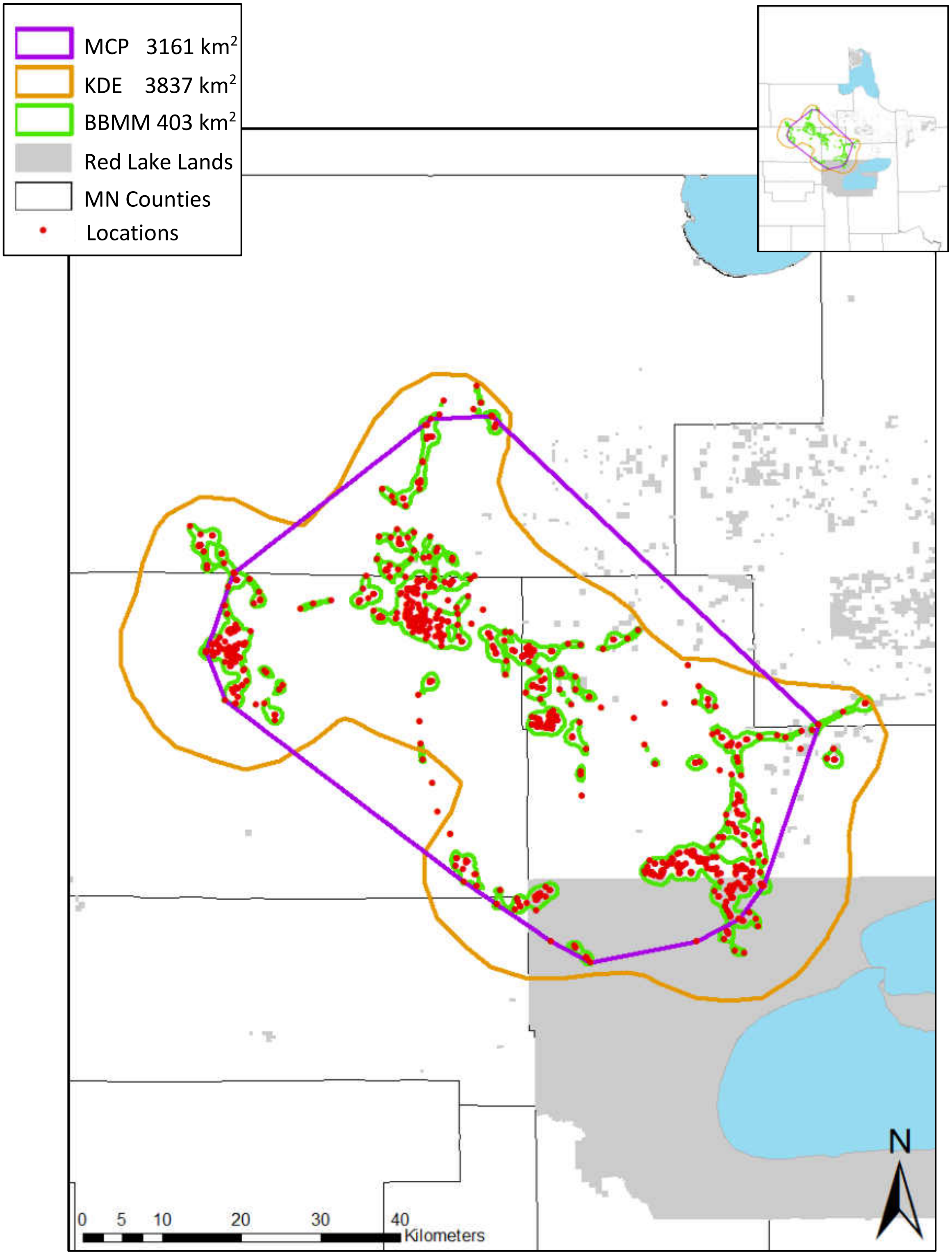

Figure 18m. All applicable 95% home range estimate contours derived from GPS relocation data received from wolf F2016-17 from 8/28/16 to 11/9/16.

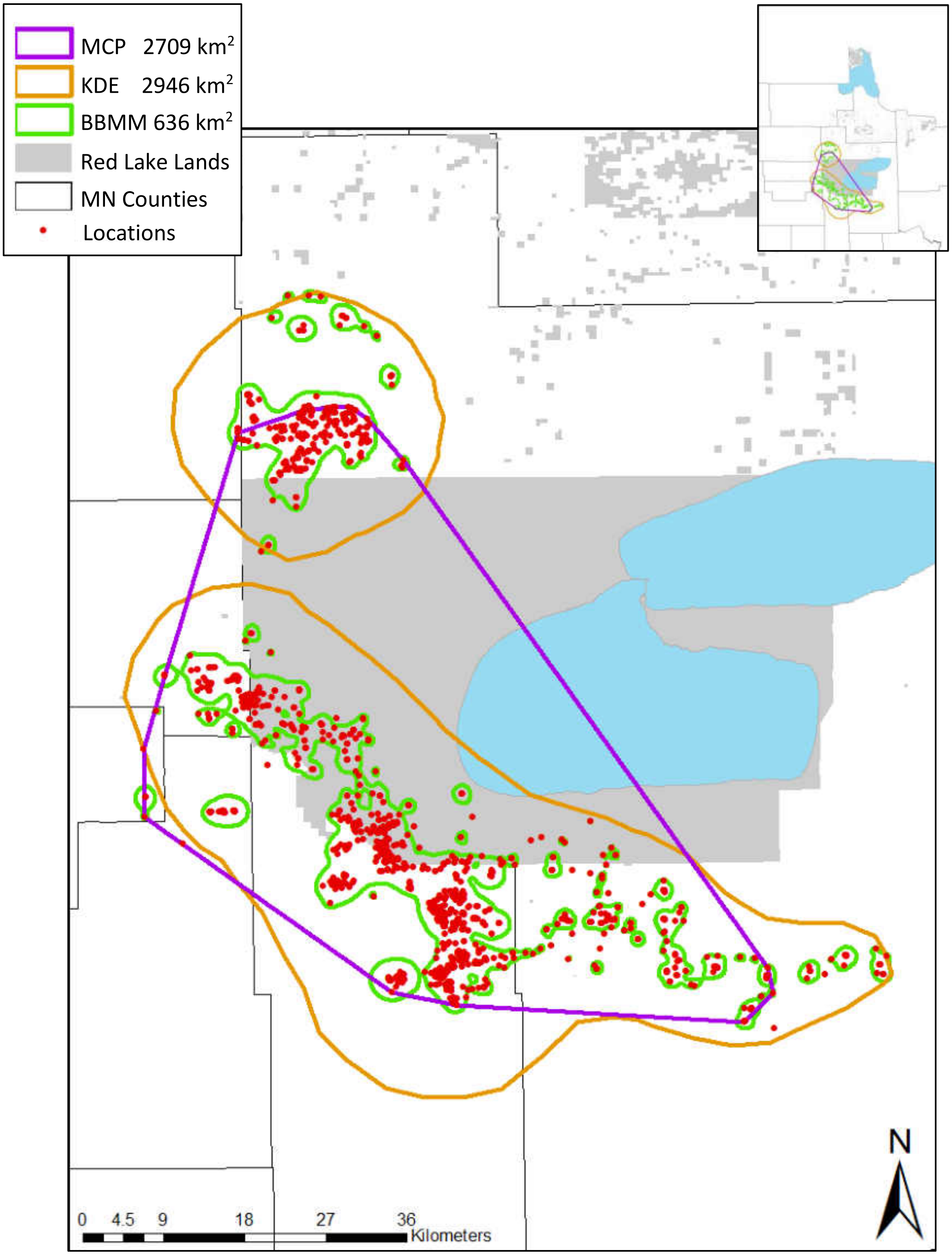

Figure 18n. All applicable 95% home range estimate contours derived from GPS relocation data received from wolf F2017-2723 from 3/2/17 to 11/27/17.

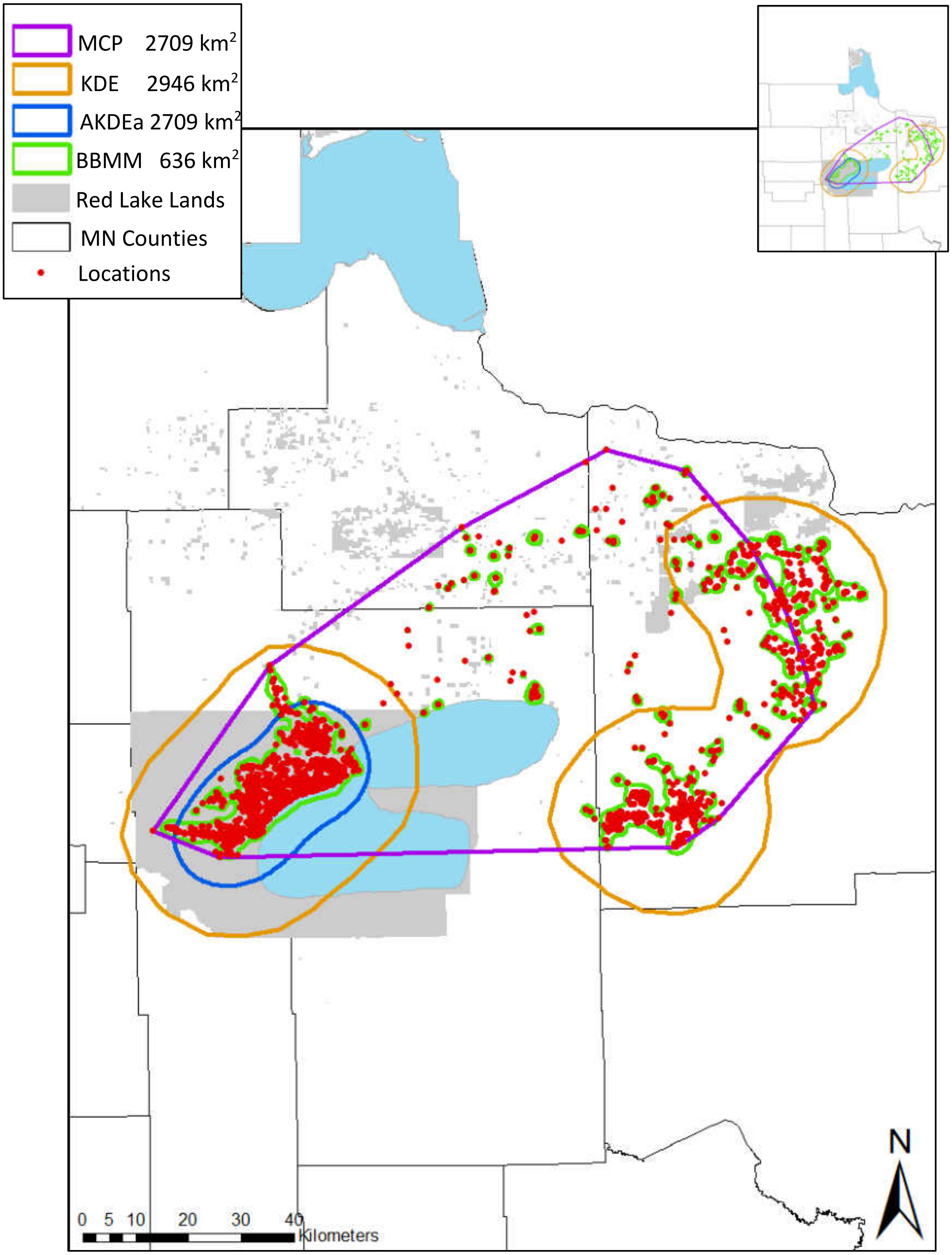

Figure 18o. All applicable 95% home range estimate contours derived from GPS relocation data received from wolf M2017-24 from 8/21/17 to 7/3/19.

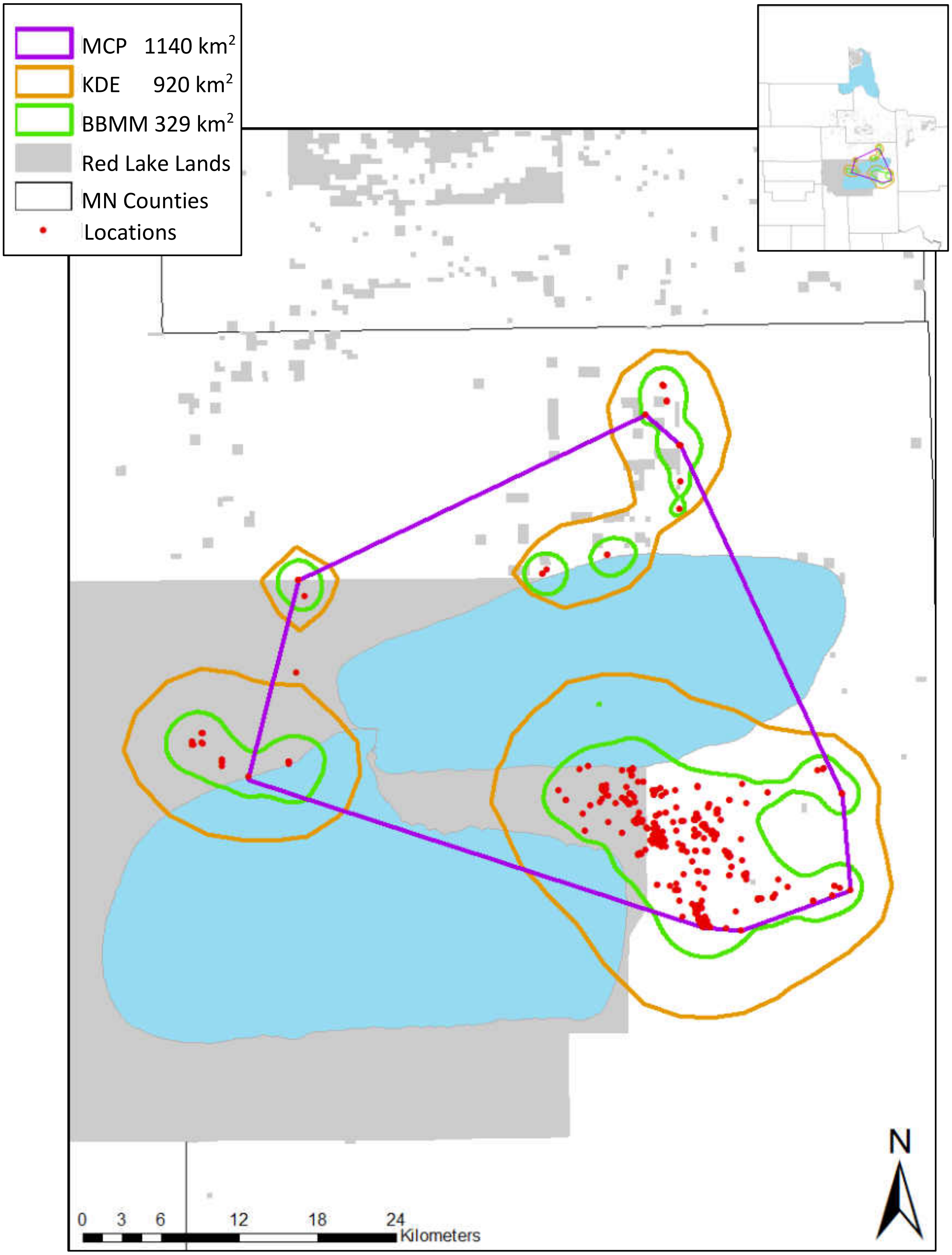

Figure 18p. All applicable 95% home range estimate contours derived from GPS relocation data received from wolf M2018-25 from 2/18/18 to 5/9/18.

CHAPTER III

HABITAT USE AND SELECTION OF RED LAKE GRAY WOLVES (*CANIS LUPUS*)

Abstract

As a recovering endangered species, availability of high quality habitat is essential for survival and recovery of gray wolves (*Canis lupus*). However, today's gray wolves are living on a landscape that has changed drastically since their near eradication by the early 20th century. In northeastern Minnesota, where gray wolves are listed as threatened, much of the land that was once covered in forest has been converted into agriculture, and the wolves live on a human dominated landscape. The Minnesota Department of Natural Resources estimates habitat use of this wolf population; however, a subset of this population lives within the bounds of Red Lake Indian Reservation. The Red Lake Indian Reservation is a sovereign nation where wolves are managed independent of the state and Red Lake lands are declared to be a wolf sanctuary. The Red Lake Department of Natural Resources Wildlife Program has been monitoring wolf population numbers using GPS collars since 2012. Here, I estimated population and individual level habitat use of gray wolves living on Red Lake lands. I also tested for population and individual level habitat selection using multinomial models that allowed us to test for disproportional use of land cover classes in relation to availability. I further

tested for variation in selection in relation to season and sex. Finally, I investigated one aspect of movement behavior by testing if land class, season, or sex predicted movement speed. I found that gray wolves on Red Lake primarily used woody wetlands, regardless of season, time of day, or sex. Furthermore, I detected an overall selection of woody wetlands and an avoidance of developed areas at both the individual and population levels. I found that gray wolves tend to travel slower through forested areas, likely due to foraging, and faster through developed areas, which were used very little, and likely for travel along roads. Red Lake is primarily woody wetlands, and gray wolves use it accordingly. There is currently no limitation of available habitat for wolves on Red Lake, however, because logging is a main industry for the Red Lake Band of Chippewa Indians, monitoring and preservation of wooded areas should continue as wolf populations on Red Lake lands continue to increase.

Introduction

High quality habitat is essential for every species, allowing them to survive and reproduce, and populations to persist (Hall et al. 1997). Although a full characterization of habitat is a large undertaking, landcover data is often readily available and provides a practical way to assess habitat for terrestrial species (Johnson 1980). However, landcover is a dynamic thing, and vast land conversion as a result of human activities has led to altered, fragmented, or entirely lost habitat in (Ellis et al. 2010). For gray wolves (Every animal requires space where they can perform activities to survive and reproduce *lupus*) in particular, the world they live in today is dramatically different from before their near-eradication (Tucker et al. 2018) and understanding what they are using on the new landscape and how they are using it is essential to their continued recovery.

Prior to 1915, gray wolves ranged throughout the contiguous United States (Bacon 2012, Mech 1970, Boitani 2003). By 1930, conflict with early settlers and ranchers resulted in near extinction of the wolf in the lower 48 states, and only small populations of wolves remained in Northern Minnesota and in Isle Royale National Park of Michigan (Mech 1970, Boitani 2003). Today, although wolf populations have increased and expanded across northern Minnesota (Erb et al. 2018), wolves are still listed as threatened in northern Minnesota under the Endangered Species Act (ESA). The ultimate goal for wolves under this act is population recovery resulting in self-sustainability (USFWS 1996), and one very important factor contributing to recovery is available habitat (McDonald et al. 2012, Hagen and Hodges 2006).

The ultimate goal for wildlife management and conservation is understanding how to manage and conserve species in human-dominated landscapes (Hunter 1996), and this is particularly relevant for predators like wolves. Intolerance of wolves is arguably the biggest threat to the persistence of the species (Fuller 1989, Mech, 1989, Wydeven et al, 2001), and wolf-human conflict is likely to continue. Although wolves tend to avoid anthropogenic landscape features such as agricultural land and high-traffic roads (Mladenoff et al. 2009, Oakleaf et al. 2006), lack of non-altered habitat and higher prey densities on agricultural land can draw wolves nearer to people, and consequently their livestock (Mladenoff et al. 1997, Mladenoff et al. 2009). Additionally, much of the landscape that is suitable for wolves is privately owned by people who may or may not be tolerant of wolves (Stricker et al. 2019), creating challenges for managers on access and ability to facilitate necessary population level conservation strategies. The assessment of wolf distribution and habitat selection and the knowledge of how wolves use the landscape provides managers with the ability to manage wolves proactively (Gehring and Potter 2005). This involves the inclusion and cooperation of stakeholders, such as farmers, at the time of wolf recolonization, and could potentially increase the tolerance for wolves on the landscape (Gehring and Potter 2005).

Because gray wolves are habitat generalists (Mech and Boitani 2003*a*), their habitat needs vary geographically, and thus, must be estimated for each population. The Minnesota Department of Natural Resources (MNDNR) estimates gray wolf distribution and habitat use of the northeast Minnesota wolf population every 5 years using data collected from their own GPS collared wolves and from wolves collared by other agencies across the state (e.g. USGS, Voyageurs National Park; Erb et al. 2018). The 2017-2018 Distribution and Abundance of Wolves in Minnesota (Erb et al. 2018) generated from this data reports that gray wolves currently occupy 73,972km^2 of northern Minnesota (Fig 1; Erb et al. 2018).

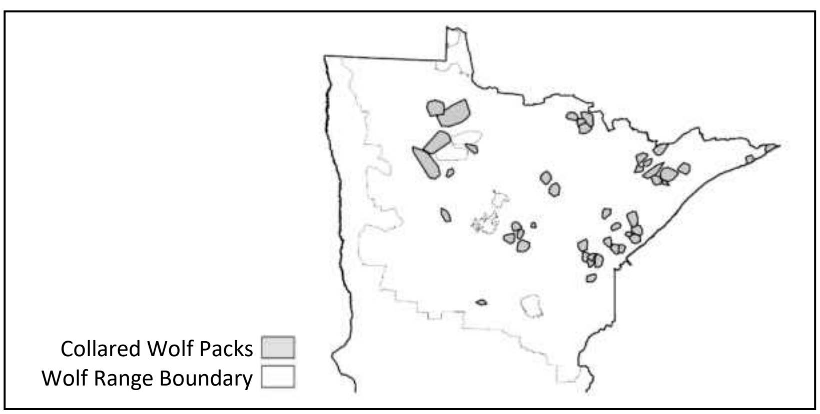

Figure 1. Occupied wolf range in northern Minnesota during the 2017-2018 MNDNR survey (Erb et al. 2018).

The MNDNR uses National Land Cover Data (NLCD) from the United States Geological Survey (USGS) to estimate the land cover within the occupied range in northwestern Minnesota, as well as within individual wolf home ranges. As of their 2017-2018 report, the area in the state currently occupied by wolves consisted of primarily woody wetlands (31.9%) and deciduous forest (23.1%; Erb et al. 2018). Similarly, home ranges of individual wolves consisted of primarily woody wetlands (37.2%) and deciduous forest (18.1%; Erb et al. 2018). Together, these estimates provide valuable information about where wolves currently exist, the type of habitat they are using, and where they are likely to occur in the future based on the available habitat around them.

Red Lake Indian Reservation, as a sovereign nation, manages wolves independently of the state. Because of the historic spiritual connection between gray wolves and Ojibwe people (David 2009), the Red Lake Band of Chippewa Indians' Gray Wolf Management Plan declares all Red Lake Indian Reservation lands to be wolf sanctuary, where wolf harvest is and will likely remain prohibited (RLDNR 2010). If Red Lake lands are to be a long-term wolf sanctuary where wolf populations are afforded greater protection, managers must know the types of habitats that are used by wolves so areas containing these habitat types can be managed to enhance viability of wolf populations. Additionally, knowledge of habitat use will allow managers to assess areas around Red Lake Indian Reservation that are likely to be used by gray wolves. This is important to know because outside of Red Lake Indian Reservation boundaries, wolves are subjected to state management, which will likely include harvest as a means of population control (MNDNR 2001) once wolves no longer meet the requirements for protection under the ESA. Although the MNDNR receives GPS collar information from the Red Lake Department of Natural Resources (RLDNR) for use in its state habitat use assessment, habitat use and selection by wolves found exclusively on Red Lake Indian Reservation had not been estimated.

Objectives

Using GPS collar data from the RLDNR, I estimated habitat use and selection and wolf speed as it relates to habitat for gray wolves on Red Lake Indian Reservation. These estimates provided RLDNR wildlife managers with information about habitat requirements for Red Lake wolves, as well as insight related to the potential of border crossings from Red Lake lands into state management areas. I evaluated Red Lake wolf habitat use and implemented multinomial regression models to test for habitat selection at both the individual and population levels. I tested for effects of habitat, season, diel period, and sex on speed of travel across the landscape. Seasonal estimates were limited to those wolves with sufficient sampling duration. My specific objectives were to:

1. **Assess individual and population level habitat use by Red Lake gray wolves.**
2. **Test for evidence of habitat selectivity by Red Lake wolves at the individual and population level, represented by disproportionate habitat use relative to habitat availability. Further test for evidence of habitat selection during different seasons and diel periods and by male and female wolves; variables known to influence habitat selection.**
3. **Test for effects of variables known to influence wolf speed (season, diel period, sex, and habitat) on Red Lake gray wolf instantaneous speed estimates derived from the Ch. 2 continuous-time movement models.**

Methods

Study Area

Red Lake lands consist of approximately 1,384km^2 of forest or forested wetlands, 1,886km^2 of wetlands, and 971km^2 of lakes. A 2009 GIS analysis of Red Lake lands estimated there to be available wolf habitat on 1,551km^2 within the Diminished Reservation, 151km^2 within the Ceded Lands, and 207km^2 within the Northwest Angle (RLDNR 2010). See Chapter 2 for further details about Red Lake Indian Reservation (Fig 2).

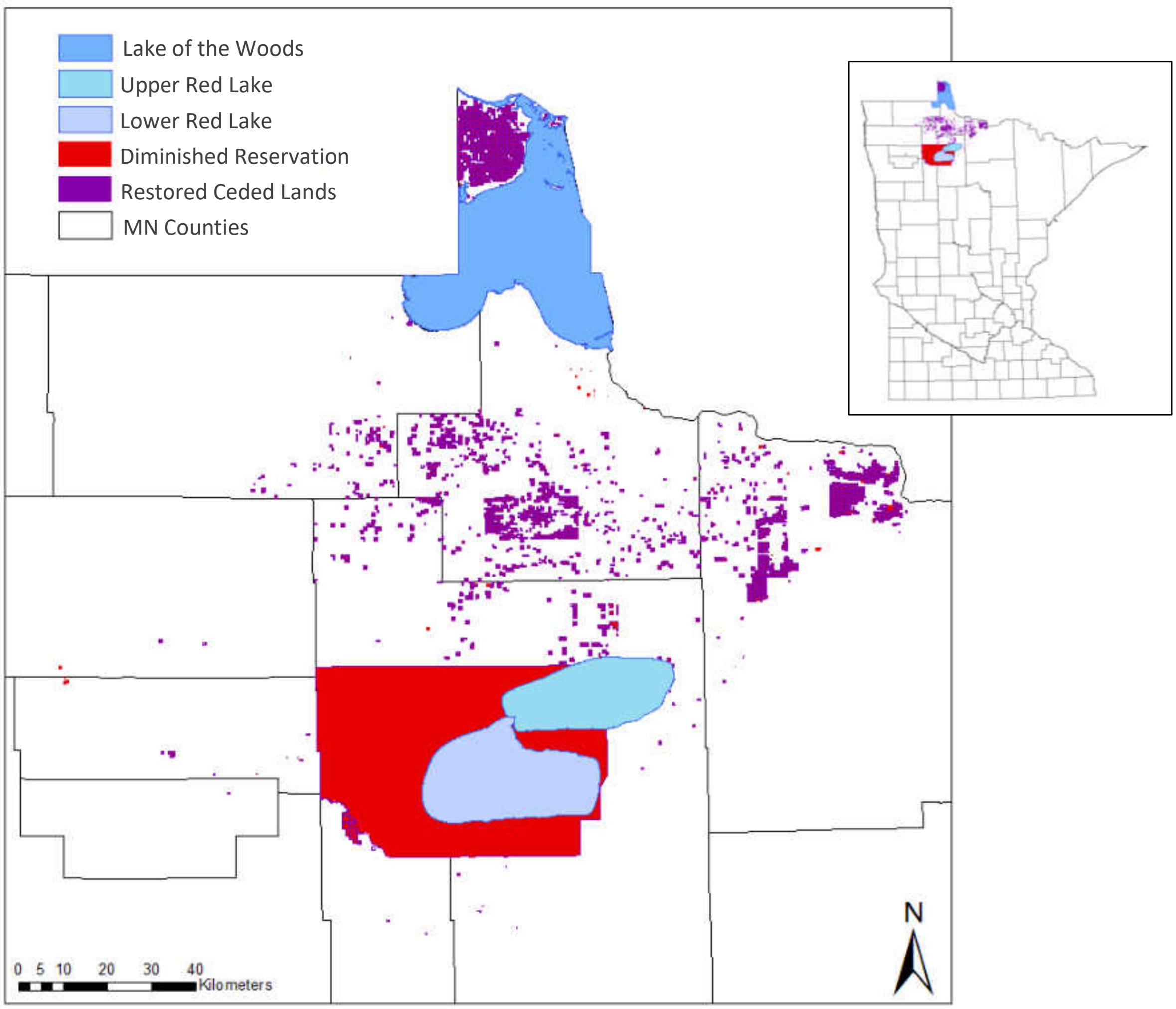

Figure 2. Red Lake Indian Reservation Tribal Lands.

Data Collection

I obtained GPS collar data from 15 Red Lake gray wolves that were captured and collared by RLDNR Wildlife Program (RLDNR-WP) personnel from May 2012 to August 2018. To date, the RLDNR has collected relocation data on 27 gray wolves, but data for 15 of the wolves was sufficient for use in this study (i.e. at least 300 relocations and/or at least 55 days of observation time as well as available land cover data; Table 1). See Chapter 2 for a complete description of field protocols that were used by RLDNR-WP personnel to capture and fit wolves with GPS collar units.

Table 1. Fifteen of the gray wolves collared by the Red Lake Department of Natural Resources Wildlife Program since summer 2012. Wolf ID indicates the sex of the captured animal by beginning with either F (female) or M (male) and year of capture. Capture location occurred within the Diminished Reservation (Dim. Res.), the Restored Ceded Lands (Ced. Lands), or at the Northwest Angle (NW Angle).

Wolf ID	Date Captured	Observation Time Span (days)	Number of Relocations	Capture Location
M2012-01	6.05.2012	291	245	Dim. Res.
F2013-22	5.18.2013	56	310	Ced. Lands
F2013-2459	5.19.2013	418	935	Ced. Lands
F2013-04	6.09.2013	61	307	Dim. Res.
M2013-06	7.14.2013	106	380	Dim. Res.
M2013-15	7.17.2013	190	724	Dim. Res.
F2013-23	7.23.2013	145	767	Ced. Lands
M2013-07	8.12.2013	151	616	Dim. Res.
M2014-14	9.11.2014	426	2679	Dim. Res.
F2015-16	8.08.2015	575	4360	Dim. Res.
M2016-2710	2.07.2016	455	1561	Res. Ced.
F2016-17	8.28.2016	74	1681	Dim. Res.
F2017-2723	3.02.2017	261	2141	Dim. Res.
M2017-24	8.21.2017	682	4936	Dim. Res.
M2018-25	2.18.2018	80	462	Dim. Res.

Data Analysis

Land Classification and Composition

I used National Land Cover Data (NLCD; USGS 2011, USGS 2016) to determine landscape composition on and around Red Lake Indian Reservation. NLCD was derived from 30 m LANDSAT satellite imagery and was available in 2-3 year intervals (Yang et al. 2018); the NLCD applicable for my use were from the years 2011 and 2016. I performed a land classification accuracy assessment on both the 2011 and 2016 NLCD by comparing 900 random points to high resolution (60 cm) 2010 and 2016 National Agriculture Inventory Program (NAIP; USDA 2010, USDA 2016) imagery, respectively. Overall accuracy was 74.9% for 2011 and 79.8% for 2016, indicating good accuracy levels for each of the years (Jensen 2004).

I reclassified both years of NLCD using ArcMap (ESRI 2014, ArcGIS version 10.6) by grouping classes occurring at low frequencies into the classes they were most represented by at the study site (i.e. shrub land class occurred at 1% in the study area and was merged with forest because shrubbery is mixed with forest at the study site). Reclassified land class categories included woody wetlands, forest (primarily deciduous forest), herbaceous wetlands, grass, crops, developed, and water (Table 2).

There appeared to be a slight change in landscape composition from 2011 to 2016, with a 5% increase in woody wetlands and a 4% decrease in forest (Table 2, Figure 3). Although the differences were minimal, both of these habitat types are known to be used by wolves in Minnesota (Erb et al. 2018), and the differences across the years could have altered the results of both the assessment of habitat use and the testing for habitat selectivity. Consequently, I ran analyses on wolves based on their year of capture relative to the year of available NLCD. Wolves captured from 2012-2013 were analyzed using the 2011 NLCD (8 wolves total: here-after referred to as group 2011), and wolves captured from 2014-2018 were analyzed using the 2016 NLCD (7 wolves total: here-after referred to as group 2016).

Table 2. Land class percent occurrence and reclassified land categories for the 2011 and 2016 National Land Cover Data (USGS 2011, USGS 2016).

NLCD			**Reclassified**		
	% Occurrence			**% Occurrence**	
Land Category	**2011**	**2016**	**Land Category**	**2011**	**2016**
Woody Wetlands	28.05	33.23	Woody Wetlands	28.05	33.23
Deciduous Forest	17.98	12.40			
Evergreen Forest	2.70	1.53			
Mixed Forest	0.46	3.08			
Shrub/Scrub	1.00	1.22	Forest	22.14	18.23
Emergent Herbaceous Wetlands	14.87	17.73	Herbaceous Wetlands	14.87	17.73
Grasslands/Herbaceous	1.34	0.82			
Pasture/Hay	6.52	2.72	Grass	7.86	3.54
Barren Land	0.05	0.05			
Cultivated Crops	16.56	18.40	Crops	16.61	18.45
Developed, Open Space	2.38	1.76			
Developed, Low Intensity	0.43	0.44			
Developed, Med Intensity	0.09	0.05			
Developed, High Intensity	0.01	0.01	Developed	2.91	2.26
Open Water	7.37	7.25	Water	7.37	7.25

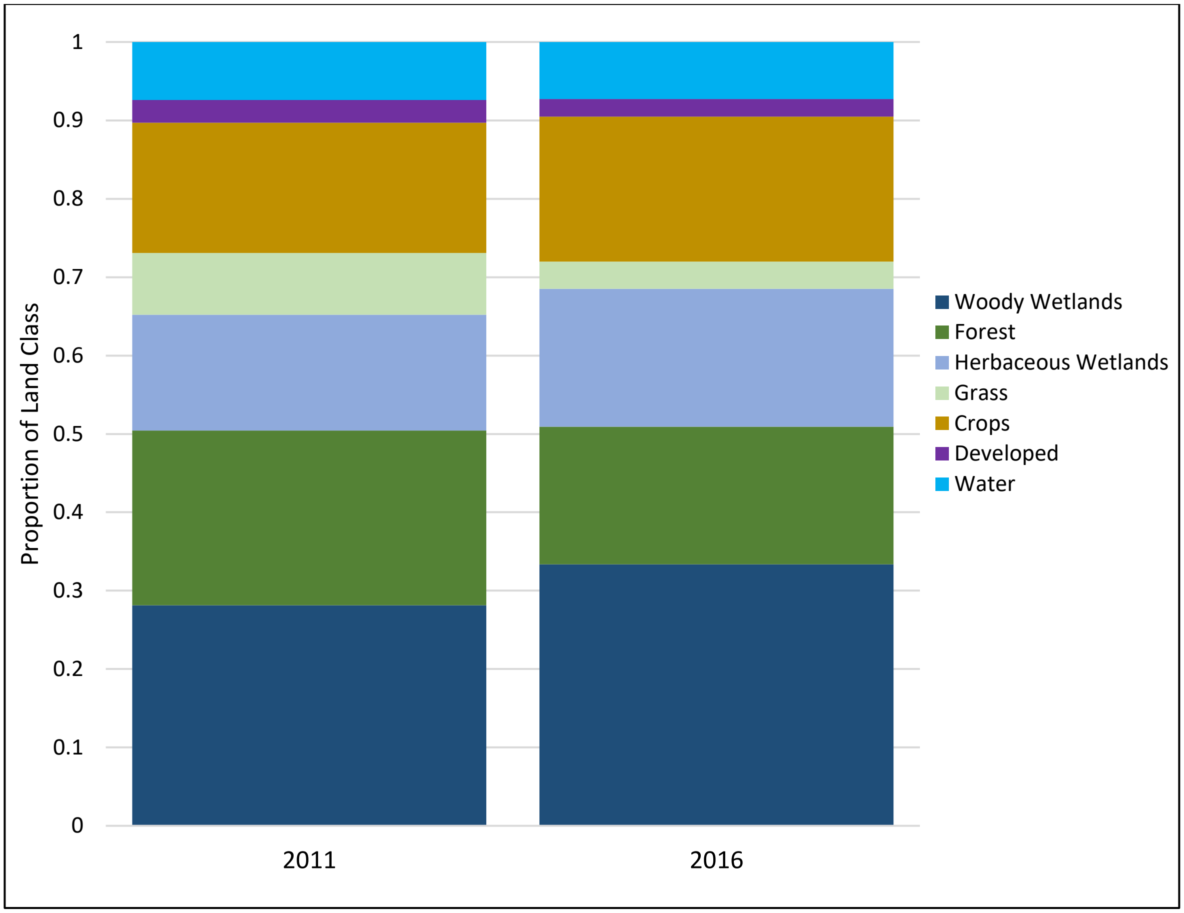

Figure 3. Land class frequencies in 2011 and 2016 based on the reclassified 2011 and 2016 NLCD. There was an increase in woody wetland land cover type and a decrease in forest land cover type over the four year time span.

Habitat Use

I assessed habitat use by extracting the applicable reclassified 2011 and 2016 NLCD land cover data to the GPS relocations of each individual wolf and calculating percent use of each land class. I additionally calculated percent use of each land class at the population level for all wolves in group 2011 and all wolves in group 2016, including assessment of use during each season, during both diel periods, and for each sex for each of the groups.

Habitat Selection

I tested for habitat selection at both the landscape population level (2nd order selection) and the individual home range level (3rd order selection; Johnson 1980) by analyzing landscape composition where the wolves were in relation to what was available to them, as estimated from a large set of randomly selected points. The multi-scale analysis was done to identify differences in habitat preferences among levels (McGarigal et al. 2016).

I limited my analyses to the land classes found within a 30km buffer defined by the observed locations of each wolf for the individual level analysis, and by the observed cumulative locations for each group 2011 and group 2016 for the population level analysis. The 30km buffer was chosen based on an assessment of land cover frequencies at various buffers (10km-60km) around an area defined by the entire set of all wolf observations. Frequency of water was not considered in this assessment or in the following analyses. Landscape composition appeared to not change beyond the 30km buffer. See Appendix A for visualization of reclassified land class frequency assessment and Appendix B for geographic visualization of the reclassified land classes found within each of the 30km buffers.

I drew random points, as a representation of habitat availability, from within each of the 30km buffers, with the total number of random points being equivalent to the total number of relocations within the analysis group of interest (i.e. equivalent to total number of relocations within an individual relocation set, or within either group 2011or group 2016). I extracted the reclassified 2011 and 2016 NLCD land cover data at the appropriate random points and used the points in multinomial regression models to test for significant departures of proportionate land use by individual and grouped wolves compared to randomly sampled points (i.e. disproportionate land use compared to availability of land class; Kneib et al. 2011).

I used the R package nnet (Venables and Ripley 2002, R version 3.6.1 www.r-project.org) with land class as the response variable. Predictor variables for each of the individual level models were all categorical fixed effects. They included wolf points compared to random points, season (breeding: January 15-March 14, denning: March 15-July 31, rendezvous: August 1-October 14, wayfaring: October 15-January 14; seasons expected to be biologically relevant to wolves), and diel period (day or night; calculated using sunrise and sunset times at each GPS location). Predictor variables for each of the population level models included all those from the individual models as well as the categorical fixed effect sex (male or female). For all models, each level of each predictor was compared to the land class at the random samples to determine proportion of land use by wolves (individually or collectively) compared to random points (availability). I used a best subsets approach to model selection (Hosmer and Lemeshow 2000), implemented in the R package MuMin (Barton 2019, R version 3.6.1) using AICc (AIC corrected for small sample size; Burnham and Anderson 2002) as the model comparison criterion. This allowed us to identify which, if any, of the variables were associated with habitat selectivity at the individual and population levels. I determined significance of predictors of top models using a Wald statistic (α=0.05) and compared residual and null deviance to assess model fit.

Effects on Gray Wolf Speed

I estimated the instantaneous speed at each time interval (i.e. displacement rate at the time of each GPS relocation; here-after referred to as speed), which was estimated from the continuous-time movement models developed in Chapter 2 (Calabrese et al. 2016) for 12 of the 15 wolves (I were unable to derive speed estimates for the remaining 3 wolves). I tested for the effects of habitat, season, diel period, and sex (fixed effects) on speed estimates using a general linear mixed effects model with wolf ID, here-after referred to as wolf, as a random effect. I developed a main effects-only model and a model that included main effects and all two-way interactions using the R package nlme (Pinheiro et al. 2019; R version 3.6.1), followed by a best subsets analysis as described above. This allowed us to identify which combination of the variables best predicted wolf speed. I used $\log_{10}$ transformed speed estimates as the response variable to meet the assumptions of normality.

Results

Habitat Use

A majority of the individual wolves used all 6 land classes at least somewhat over the duration of their observation periods. There were 5 of the 15 wolves that had no usage of crops but did use all other habitat types. Crops and developed land were used the least overall, with 11 and 9 of the 15 wolves using <1% of crops and developed land, respectively. Woody wetlands were the most used habitat type for 11 wolves, with herbaceous wetlands being the second most used by 9 of the 11 (Table 3, Fig 4).

Table 3. Individual level percent habitat use by each wolf based on the reclassified 2011 and 2016 NLCD.

Wolf	Woody Wetlands	Forest	Herbaceous Wetlands	Grass	Crops	Developed
M201201	23.05	20.58	44.86	11.11	0	0.41
F201322	68.61	9.71	20.39	0.32	0	0.97
F20132459	54.33	6.52	36.47	0.11	0.21	2.35
F201304	48.18	29.70	13.20	7.59	0.99	0.33
M201306	11.11	50.00	12.17	22.49	2.38	1.85
M201315	33.06	45.56	13.89	3.89	0.28	3.33
F201323	63.61	23.43	9.82	2.62	0.13	0.39
M201307	27.52	30.94	30.94	7.00	0.98	2.61
M201414	62.67	0.27	35.61	0.58	0	0.86
F201516	41.37	40.37	13.91	0.86	2.20	1.30
M20162710	85.97	1.87	11.39	0.19	0	0.58
F201617	56.81	2.68	33.49	0.30	3.81	2.91
F20172723	43.34	29.41	19.00	2.02	5.72	0.52
M201724	77.23	2.12	20.30	0.08	0.02	0.24
M201825	83.22	0.89	11.41	3.80	0	0.67

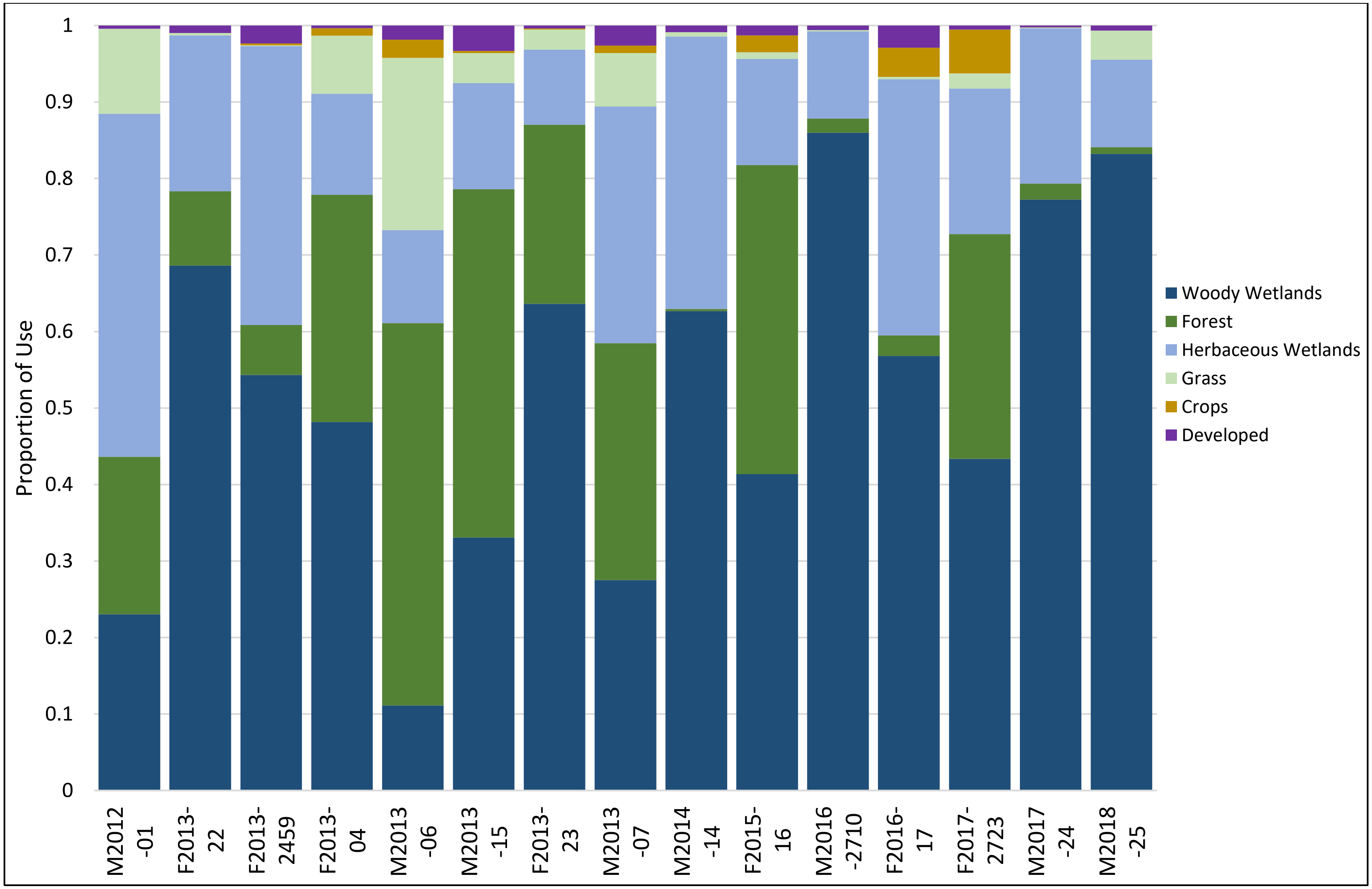

Figure 4. Individual level habitat use by each wolf based on the reclassified 2011 and 2016 NLCD.

When considering population level habitat use, both group 2011 and group 2016 wolves used woody wetlands more than any other habitat type, although there was an overall increase in use of this habitat type between group 2011 and group 2016. This was also the most used habitat type for both groups during all seasons and during both diel periods. However, use of this habitat type was lower during denning season than during other seasons for both groups.

Woody wetlands were the most used habitat type for females in both groups, but males in group 2011 mostly used forest. Group 2011 males only had 26% use of woody wetlands, which nearly tripled to 75% use of woody wetlands by group 2016 males. This not only made it their most used habitat, but also meant that they used it 30% more than group 2016 female wolves.

Grass, crops, and developed land were the least used habitat types for both group 2011 and group 2016. However, wolves from group 2011 had 5% and 2% use of grass and developed land, respectively, whereas group 2016 wolves had <1% use of both habitat types. Conversely, wolves from group 2011 had <1% use of crops, whereas group 2016 wolves had 1.6% use of crops. There was no use of crops or developed land at all by group 2011 wolves during breeding season. Wolves in group 2011 used grass less often during denning season, whereas group 2016 wolves used grass more during denning season. Male wolves from group 2011 used grass, crops, and developed land more than females from group 2011, as well as more than males from group 2016. Females from group 2011 used crops less than females from group 2016 (Table 4, Fig 5).

Table 4. Population level percent habitat use for group 2011 (G11) and group 2016 (G16) based on the reclassified NLCD.

	Woody Wetlands		Forest		Herbaceous Wetlands		Grass		Crops		Developed	
	G11	**G16**	**G11**	**G16**	**G11**	**G16**	**G11**	**G16**	**G11**	**G16**	**G11**	**G16**
All Wolves	43.53	61.18	26.18	14.54	22.60	21.06	5.34	0.70	0.54	1.60	1.80	0.92
Breeding	41.80	65.30	25.41	21.30	24.59	11.04	8.20	0.70	0	0.77	0	0.89
Denning	52.62	61.86	19.20	12.02	24.43	22.04	2.01	1.32	0.44	1.91	1.31	0.85
Rendezvous	37.68	59.27	29.23	12.41	22.30	24.53	8.22	0.57	0.88	2.39	1.70	0.82
Wayfaring	43.35	60.49	28.44	15.87	21.17	21.45	4.25	0.25	0.23	0.82	2.55	1.12
Day	45.75	61.36	25.06	14.55	23.38	21.72	4.13	0.54	0.58	1.24	1.10	0.58
Night	41.41	61.03	27.26	14.54	21.85	20.53	6.50	0.84	0.50	1.88	2.47	1.19
Female	58.50	45.08	15.58	29.71	22.46	19.29	1.95	1.04	0.26	3.45	1.25	1.43
Male	25.83	75	38.72	1.52	22.76	22.58	9.36	0.41	0.87	0.01	2.46	0.49

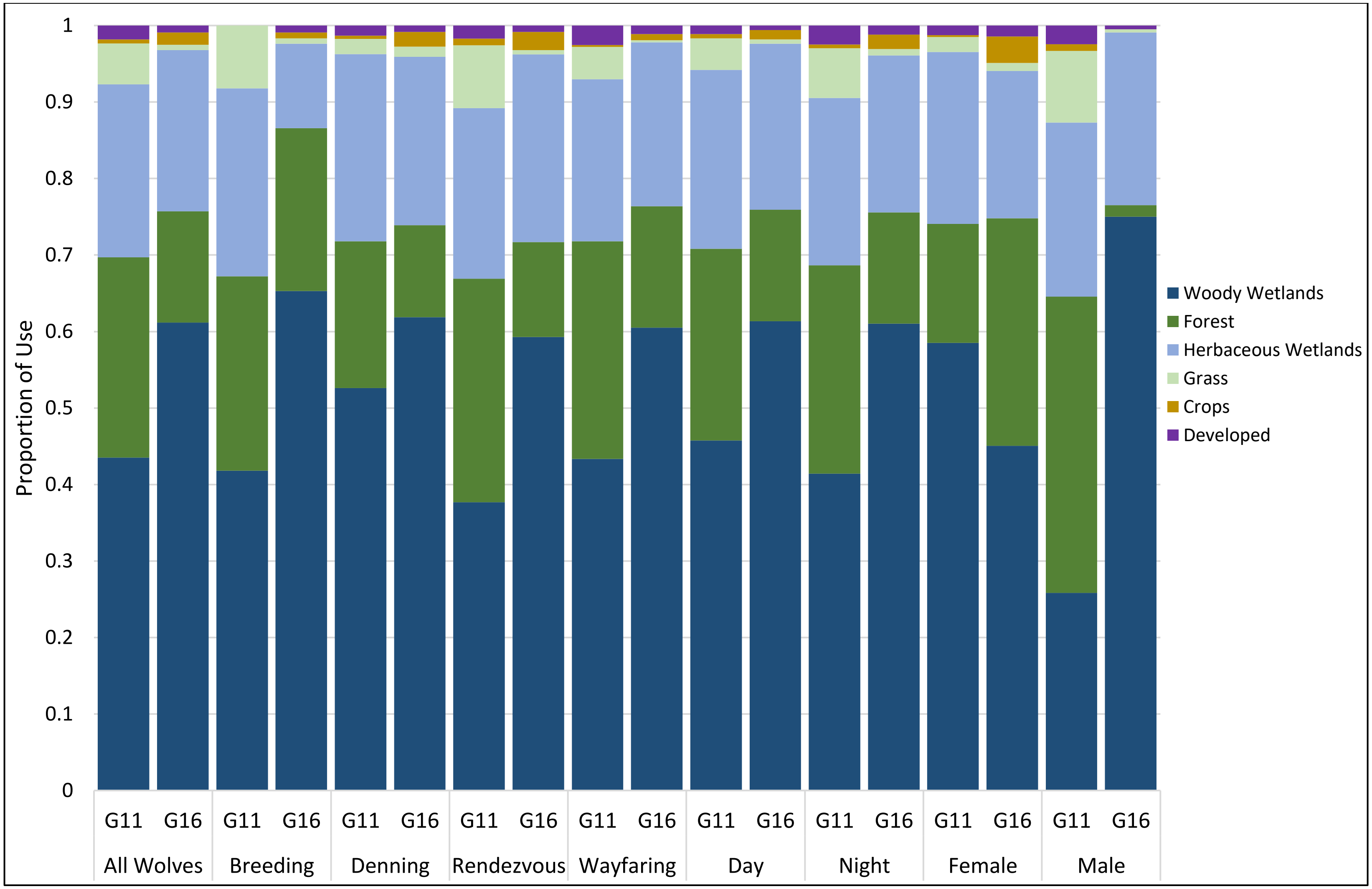

Figure 5. Population level habitat use for group 2011 (G11) and group 2016 (G16) based on the reclassified NLCD.

Habitat Selection

I assigned woody wetlands as the reference category for the land class response in the multinomial models due to the consistent use by individual wolves as well as the high frequency of availability within the individual and population level 30km buffers (Fig 6-7). See Appendix C for visualization of additional individual and population level habitat use compared to availability.

There were several top ranked individual level multinomial models with ΔAICc<2 for all but 1 of the 8 wolves in group 2011 and for all 7 of the wolves in group 2016. Considering residual deviance, most of these models were nearly indistinguishable in terms of model likelihood. Therefore, the log odds coefficients were averaged for these models to synthesize the information content. The model for wolf F2013-22 was not averaged due to selection of a clear top model. There were two top ranked population multinomial models with ΔAICc<2 for group 2011. The model for group 2016 was not averaged due to selection of a clear top model. See Appendix D for habitat selection model selection details.

At the individual level, 4 of 8 wolves from group 2011 used forest more than expected by chance (Fig 6, Table 5), whereas 6 of 7 wolves from group 2016 used forest less than expected by chance (Fig 7, Table 6). Herbaceous wetlands were used less than expected by 3 wolves in group 2011, but by all 7 wolves in group 2016. Grass was used consistently less than expected across both groups. Nearly every wolf with significant association with crops and/or developed were using those land covers less than would be expected by chance, with higher occurrence of negative association in group 2011.

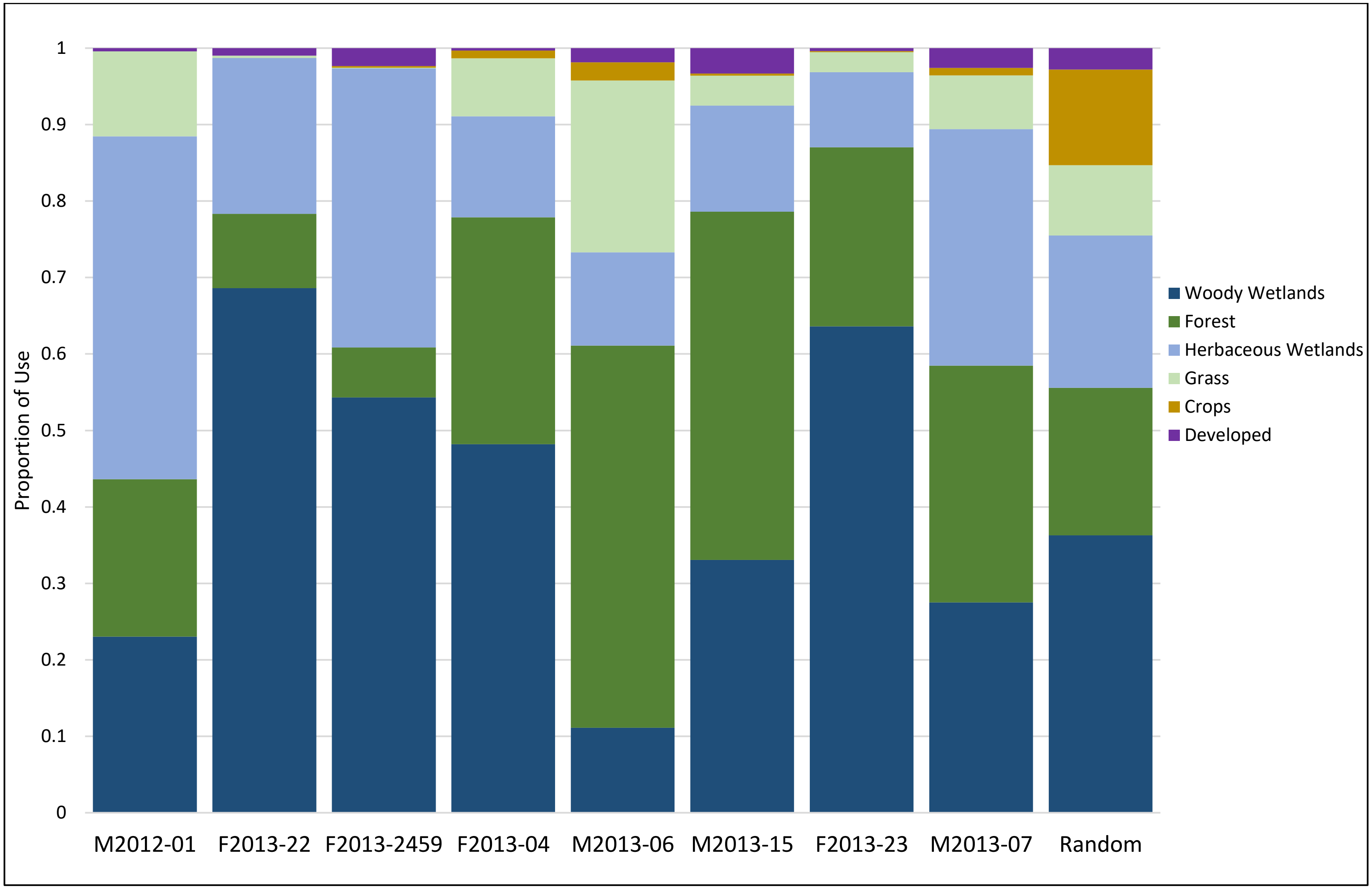

Figure 6. Habitat use of each wolf within group 2011 compared to the availability of habitat (Random) within the 30km buffer based on the reclassified 2011 NLCD.

Table 5. Individual level log odds ($\hat{\beta}$) and standard errors (SE) of significant explanatory variables averaged across the top models (ΔAICc<2) for each of the group 2011 Red Lake Indian Reservation gray wolf based on Wald's Chi Square (α = 0.05). *F201322 had only one top model and therefore the model is the not the result of model averaging.

		Forest		Herb Wetlands		Grass		Crop		Developed	
Wolf	**Variable**	$\hat{\beta}$	**SE**	$\hat{\beta}$	**SE**	$\hat{\beta}$	**SE**	$\hat{\beta}$	**SE**	$\hat{\beta}$	**SE**
M201201	Wolf			0.77	0.25						
	Day					-0.97	0.40				
F201322*	Wolf			-0.69	0.19	-3.09	1.04			-1.51	0.65
F20132459	Wolf					-6.35	2.45				
F201304	Wolf	0.43	0.13			0.69	0.20	-2.71	0.38		
	Denning					-0.82	0.34	4.24	0.77		
	Rendezvous	1.03	0.32			1.86	0.41	-8.52	1.00		
	Day	0.19	0.19					-2.26	1.00		
	Night	0.46	0.23			1.55	0.34			-12.24	3.07
M201306	Wolf	0.30	0.14	0.46	0.18			0.82	0.38		
	Denning	1.20	0.39	1.15	0.45						
	Rendezvous					1.42	0.34				
	Wayfaring	-1.16	0.36								
	Night							1.11	0.54		
M201315	Wolf					-2.93	0.18			-4.70	0.21
	Breeding					-9.65	0.43			-6.07	0.75
	Denning					2.79	0.65	-10.48	1.62	-10.16	0.19
	Rendezvous					1.36	0.57			3.29	1.07
	Wayfaring	-0.92	0.20	-1.07	0.27					5.43	0.98
	Day					-3.45	1.04			-4.00	1.44
	Night									-3.51	1.43

Continued

F201323	Wolf	0.59	0.17	-0.58	0.13			-9.50	0.50	-7.31	0.32
	Denning									-10.09	4.51
	Rendezvous			-1.01	0.34						
	Wayfaring	1.24	0.34	-0.95	0.36			-17.05	7.68	-15.74	7.96
M201307	Wolf	0.23	0.10			-0.51	0.15	-2.32	0.47	-0.50	0.24
	Rendezvous					-0.89	0.35				
	Wayfaring	0.38	0.19								
	Day	0.29	0.14							-1.19	0.54
	Night							-1.61	0.67		

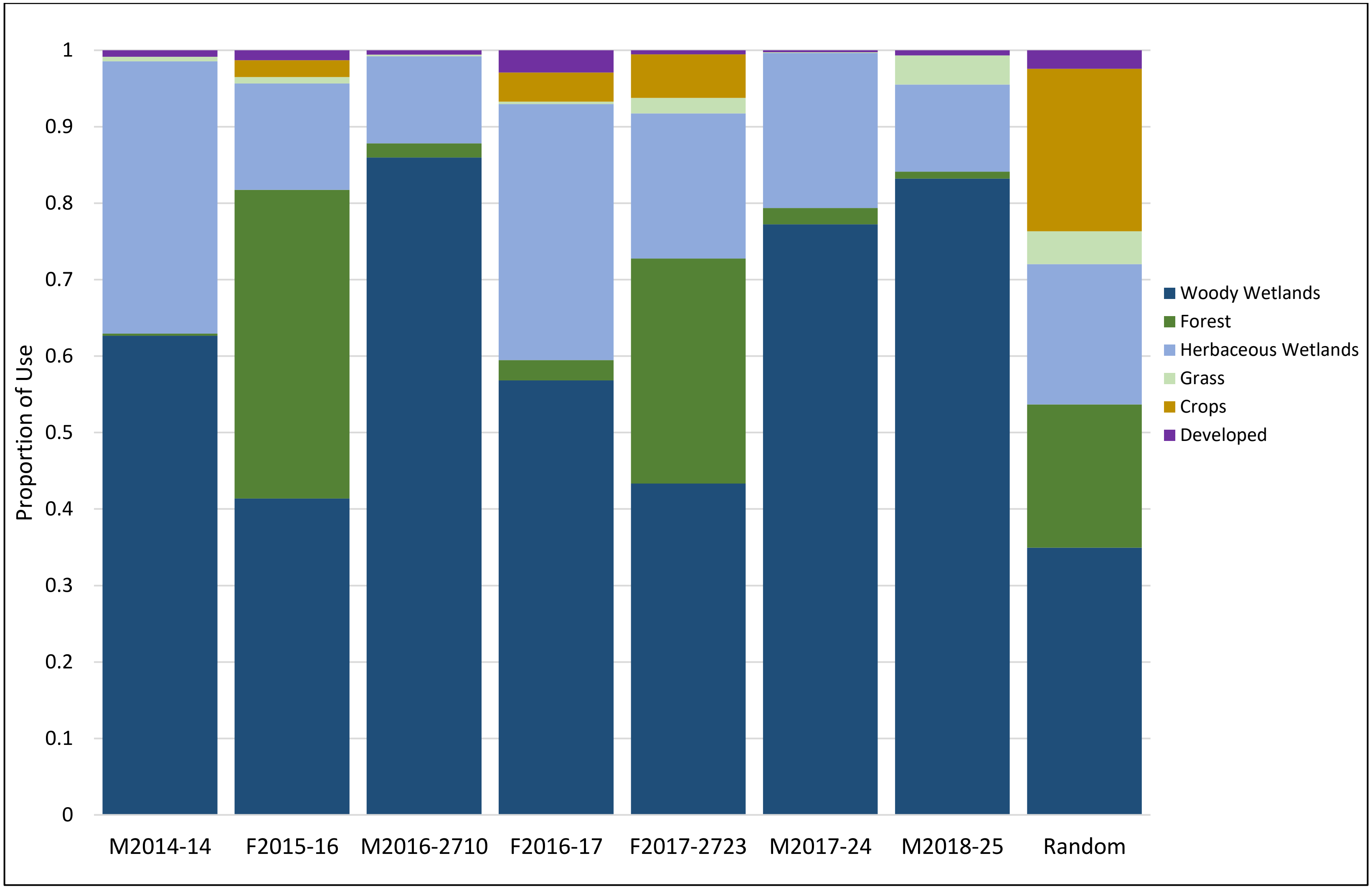

Figure 7. Habitat use of each wolf within group 2016 compared to the availability of habitat (Random) within the 30km buffer based on the reclassified 2016 NLCD.

Table 6. Individual level log odds ($\hat{\beta}$) and standard errors (SE) of significant explanatory variables averaged across the top models (ΔAICc<2) for each of the group 2016 Red Lake Indian Reservation gray wolf based on Wald's Chi Square ($\alpha = 0.05$).

		Forest		**Herb Wetlands**		**Grass**		**Crop**		**Developed**	
Wolf	**Variable**	$\hat{\beta}$	**SE**	$\hat{\beta}$	**SE**	$\hat{\beta}$	**SE**	$\hat{\beta}$	**SE**	$\hat{\beta}$	**SE**
M201414	Wolf	-7.37	0.25			-8.83	0.16			-1.08	0.32
	Breeding	-21.16	9.53	-0.82	0.11	-16.54	2.05				
	Denning			0.52	0.07	9.50	3.31				
	Rendezvous			0.66	0.07	9.50	3.31				
	Wayfaring			-0.32	0.07	-13.51	2.33			-1.72	0.64
	Day	-4.01	0.55			-5.80	1.16			-2.32	0.84
	Night	-3.97	0.51			-5.25	1.15				
F201516	Wolf	0.13	0.03	-0.34	0.04	-1.63	0.21	-1.94	0.12	-0.66	0.10
	Breeding	0.41	0.08								
	Denning	-0.17	0.09	0.68	0.10						
	Rendezvous			-0.24	0.09	-1.10	0.40			-0.79	0.26
	Wayfaring			-1.10	0.11	-1.76	0.45	-2.76	0.49	-0.88	0.26
	Day			-0.34	0.13	-2.83	0.76	-2.88	0.70	-1.07	0.30
	Night	0.17	0.06								
M20162710	Wolf	-1.36	0.21	-0.82	0.09						
	Breeding			-0.44	0.19	-16.91	5.47				
	Denning					13.38	2.36				
	Rendezvous	-1.37	0.63								
	Wayfaring			-0.38	0.19	-21.84	9.36				
	Day	-2.21	0.75	-0.89	0.39						

Continued

F201617	Wolf	-1.36	0.21	-0.82	0.09						
	Breeding			-0.44	0.19	-16.91	5.47				
	Rendezvous	-1.37	0.63			13.38	2.36				
	Wayfaring			-0.38	0.19	-21.84	9.36				
	Day	-2.21	0.75	-0.89	0.39						
F20172723	Wolf					-1.46	0.15	-1.01	0.10		
	Breeding	0.91	0.09					-0.82	0.32		
	Denning	-0.13	0.06	-0.37	0.06			-0.80	0.19		
	Rendezvous			0.26	0.08						
	Wayfaring	-0.59	0.16					0.51	0.19		
	Night							-1.24	0.34		
	Breeding:Day							-0.98	0.45		
	Breeding:Night	0.73	0.14								
	Denning:Night	-0.24	0.09	-0.39	0.09			-0.88	0.24		
	Rendezvous:Day			0.40	0.14						
	Rendezvous:Night	-0.30	0.13								
	Wayfaring:Night							-0.88	0.43		
M201724	Wolf	-1.64	0.10	-0.61	0.06	-4.96	0.40			-1.91	0.32
	Breeding			-2.22	0.38	-15.91	6.61				
	Denning	-1.70	0.85								
	Rendezvous	-2.36	0.87								
M201825	Wolf	-2.15	0.58	-0.96	0.23			-20.99	2.05		
	Day							-12.21	2.87		
	Night			-1.11	0.47	0.81	0.37	-13.40	3.15		

At the population level, there was only significant association with forest and herbaceous land covers for group 2011 (Table 7), whereas there was significant association with every land class for group 2016 (Table 8). There were 3 of 8 wolves from group 2011 that used forest more than expected by chance, whereas 3 of 8 wolves from group 2016 used forest less than expected by chance. There were 2 wolves from group 2011 that used herbaceous wetlands less than expected by chance, however only 3 wolves from that group had significant association with herbaceous wetlands. Conversely, group 2016 had 6 wolves with significant association with herbaceous wetlands, but half used it less and half used it more than expected by chance.

There were 10 different wolves at the individual and population level with significant association with forest, and although the wolves were different, half of the wolves at each level used forest less than expected by chance. The same equal use of herbaceous wetlands occurred at the population level, but there was overall less use than expected by chance at the individual level. Although fewer wolves had significant associations with grass, crops, and developed land at the population level, the trend for all 3 land classes was overall less use than expected by chance at both levels (Table 9).

Forest was used more often than expected by chance during breeding season and less often than expected during denning and rendezvous seasons at both the individual and population level. Conversely, herbaceous wetlands were used less often than expected during breeding season and wayfaring season, and more often than expected during denning season at both levels. For both of these classes, there were more instances of seasonal significance at the population level. Grass was used less often than expected by chance during breeding and wayfaring seasons and more often during denning and rendezvous seasons. Notably, there were 23 instances of seasonal significance at the individual level, and only 3 instances at the population level. Although crops and developed land were used less than expected by chance for all seasons at both levels, these land classes were particularly avoided during denning and rendezvous seasons (Table 10).

Use of grass, crops, and developed land was less than expected by chance during the day at both the individual and population level; however, at the population level, use of crops and developed land was more than would be expected by chance (Table 11).

Table 7. Population level log odds ($\hat{\beta}$) and standard errors (SE) of significant explanatory variables averaged across the top models (ΔAICc<2) for group 2011 Red Lake Indian Reservation gray wolves based on Wald's Chi Square (α = 0.05).

	Forest		**Herb Wetlands**	
Variable	$\hat{\beta}$	**SE**	$\hat{\beta}$	**SE**
M201201			0.78	0.23
F201322	-0.57	0.19	-0.38	0.14
F20132459	-1.20	0.31		
F201304	0.54	0.26		
M201306	1.05	0.29		
M201315	0.62	0.30		
F201323			-0.58	0.22
M201307			0.33	0.17
Denning			0.34	0.11
Wayfaring			-0.27	0.11
Night	0.21	0.07		
Female	-0.60	0.07	-0.46	0.07
Male	0.77	0.06	0.50	0.07
M201201:Rendezvous			0.76	0.29
F20132459:Denning			-0.41	0.15
F20132459:Rendezvous			0.35	0.16
F20132459:Wayfaring			0.52	0.16
F201304:Rendezvous	0.88	0.29		
M201306:Denning	1.41	0.35		
M201306:Rendezvous	0.50	0.22		
M201306:Wayfaring	-0.86	0.31		
M201315:Wayfaring	-0.58	0.19	-0.70	0.24
F201323:Denning			0.53	0.26
F201323:Rendezvous	-0.77	0.19	-0.79	0.18
F201323:Wayfaring	0.74	0.19		
M201307:Rendezvous				
M201307:Wayfaring	0.33	0.16	0.35	0.15

Table 8. Population level log odds ($\hat{\beta}$) and standard errors (SE) of significant explanatory variables for group 2016 Red Lake Indian Reservation gray wolves based on Wald's Chi Square ($\alpha = 0.05$).

	Forest		**Herb Wetlands**		**Grass**		**Crops**		**Developed**	
Variable	$\hat{\beta}$	**SE**	$\hat{\beta}$	**SE**	$\hat{\beta}$	**SE**	$\hat{\beta}$	**SE**	$\hat{\beta}$	**SE**
M201414	-2.90	0.17	0.21	0.03			-1.75	0.49		
F201516	2.02	0.05							0.62	0.18
M20162710	-0.54	0.17	-0.55	0.04	-1.68	0.66	-1.79	0.54	-1.61	0.76
F201617			0.28	0.03			0.53	0.18	0.93	0.22
F20172723	1.85	0.06	0.28	0.04	0.77	0.19	1.18	0.16		
M201724			-0.40	0.04	-1.44	0.37	-1.89	0.38	-0.73	0.24
M201825	-3.97	0.21	-0.41	0.07						
Breeding	-3.47	0.09	-0.53	0.06	-1.27	0.58	-1.31	0.51		
Denning	0.31	0.11					-1.23	0.46		
Rendezvous	-0.70	0.13	0.09	0.03			-0.81	0.38		
Wayfaring	-0.09	0.04			-1.28	0.44	-1.42	0.40	-1.15	0.55
Day	-2.06	0.11	-0.24	0.03	-2.06	0.26	-2.56	0.33	-1.61	0.31
Night	-1.84	0.11	-0.33	0.03	-1.11	0.16	-2.21	0.29	-0.87	0.21
M201414:Breeding	-9.16	0.00	-0.39	0.11						
M201414:Denning	1.78	0.41	0.46	0.07						
M201414:Rendezvous	3.19	0.39	0.46	0.07	1.68	0.84				
M201414:Wayfaring	1.28	0.47	-0.32	0.07						
M201414:Day	-1.41	0.34							-1.11	0.54
M201414:Night	-1.49	0.31	0.16	0.05					0.69	0.34
F201516:Breeding	3.37	0.10	0.64	0.10						
F201516:Denning	-1.02	0.13	0.71	0.08			1.43	0.49		
F201516:Rendezvous			-0.32	0.07						
F201516:Wayfaring	-0.47	0.11	-1.01	0.09			-1.61	0.49		

Continued

F201516:Day	1.06	0.10			-0.88	0.40	-0.89	0.35		
F201516:Night	0.96	0.10	0.11	0.05	0.89	0.26	1.15	0.30	0.46	0.21
M20162710:Breeding	2.22	0.31								
M20162710:Denning	-1.34	0.32	-0.27	0.12						
M20162710:Rendezvous	-1.30	0.51								
M20162710:Wayfaring			-0.30	0.12						
M20162710:Day	-1.11	0.33	-0.47	0.08						
M20162710:Night	0.56	0.23								
F201617:Rendezvous	-1.40	0.26	-0.52	0.05	-1.62	0.54				
F201617:Wayfaring	1.19	0.19	0.80	0.06	1.38	0.48	0.91	0.34	1.51	0.45
F201617:Day			0.18	0.06						
F201617:Night							0.92	0.30	0.57	0.23
F20172723:Breeding	4.26	0.13	0.49	0.15						
F20172723:Denning	-1.11	0.13	-0.57	0.09	-0.82	0.34				
F20172723:Rendezvous			0.23	0.11			1.09	0.41		
F20172723:Wayfaring	-1.34	0.19								
F20172723:Day	1.15	0.11	0.31	0.07	1.55	0.25	1.35	0.30	1.51	0.46
F20172723:Night	0.70	0.11			-0.78	0.23			-1.86	0.58
M201724:Breeding	3.64	0.15	-1.40	0.17						
M201724:Denning	-1.84	0.22							-1.63	0.70
M201724:Rendezvous	-1.36	0.25	0.35	0.07						
M201724:Wayfaring	-0.59	0.17	0.60	0.07						
M201724:Day			-0.26	0.05						
M201724:Night			-0.14	0.04			-1.39	0.64	-0.85	0.30
M201825:Breeding	-7.81	0.00								
M201825:Denning	3.84	0.21	-0.41	0.13						
M201825:Day	-1.40	0.49								
M201825:Night	-2.57	0.57	-0.44	0.14						

Table 9. Individual (Ind) and Population (Pop) level log odds for wolves with significant land class use based on Wald's Chi Square (α = 0.05). N_{neg} is the count of estimates with disproportionately lower use of the land class versus woody wetlands than would be expected at random (selection for woody wetlands) and N_{pos} is the count of estimates with disproportionately higher use of the land class versus woody wetlands than would be expected at random (selection for that land class).

	Forest		**Herb Wetlands**		**Grass**		**Crops**		**Developed**	
Variable	**Ind**	**Pop**	**Ind**	**Pop**	**Ind**	**Pop**	**Ind**	**Pop**	**Ind**	**Pop**
M201201			0.77	0.78						
F201322		-0.57	-0.69	-0.38	-3.09				-1.51	
F20132459		-1.20			-6.35					
F201304	0.43	0.54			0.69		-2.71			
M201306	0.30	1.05	0.46				0.82			
M201315		0.62			-2.93				-4.70	
F201323	0.59		-0.58	-0.58			-9.50		-7.31	
M201307	0.23			0.33	-0.51		-2.32		-0.50	
M201414	-7.37	-2.90		0.21	-8.83				-1.08	
F201516	0.13	2.02	-0.34		-1.63		-1.94	-1.75	-0.66	0.62
M20162710	-1.36	-0.54	-0.82	-0.55		-1.68				-1.61
F201617	-1.36		-0.82	0.28				-1.79		0.93
F20172723		1.85		0.28	-1.46	0.77	-1.01	0.53		
M201724	-1.64		-0.61	-0.40	-4.96	-1.44		1.18	-1.91	-0.73
M201825	-2.15	-3.97	-0.96	-0.41			-20.99	-1.89		
N	10	10	9	10	9	3	7	5	7	4
N_{neg}	5	5	7	5	8	2	6	3	7	2
N_{pos}	5	5	2	5	1	1	1	2	0	2

Table 10. Individual (Ind) and Population (Pop) level log odds of significant wolf by season interactions based on Wald's Chi Square ($\alpha = 0.05$). N_{neg} is the count of estimates with disproportionately lower use of the land class versus woody wetlands than would be expected at random (selection for woody wetlands) and N_{pos} is the count of estimates with disproportionately higher use of the land class versus woody wetlands than would be expected at random (selection for that land class).

	Forest		Herb Wetlands		Grass		Crops		Developed	
Variable	**Ind**	**Pop**	**Ind**	**Pop**	**Ind**	**Pop**	**Ind**	**Pop**	**Ind**	**Pop**
M201315:Breeding					-9.65				-6.07	
M201414:Breeding	-21.16	-9.16	-0.82	-0.39	-16.54					
F201516:Breeding	0.41	3.37		0.64						
M20162710:Breeding		2.22	-0.44		-16.91					
F201617:Breeding			-0.44		-16.91					
F20172723:Breeding	0.91	4.26			0.49				-0.82	
M201724:Breeding		3.64	-2.22	-1.40	-15.91					
M201825:Breeding		-7.81								
F20132459:Denning				-0.41						
F201304:Denning					-0.82		4.24			
M201306:Denning	1.20	1.41	1.15							
M201315:Denning					2.79		-10.48		-10.16	
F201323:Denning				0.53					-10.09	
M201414:Denning		1.78	0.52	0.46	9.50					
F201516:Denning	-0.17	-1.02	0.68	0.71						1.43
M20162710:Denning		-1.34		-0.27	13.38					
F20172723:Denning	-0.13	-1.11	-0.37		-0.57			-0.82	-0.80	
M201724:Denning	-1.70	-1.84								-1.63
M201825:Denning		3.84		-0.41						
M201201:Rendezvous				0.76						
F20132459:Rendezvous				0.35						

Continued										
F201304:Rendezvous	1.03	0.88			1.86		-8.52			
M201306:Rendezvous		0.50			1.42					
M201315:Rendezvous					1.36				3.29	
F201323:Rendezvous		-0.77	-1.01	-0.79						
M201307:Rendezvous					-0.89					
M201414:Rendezvous		3.19	0.66	0.46	9.50	1.68				
F201516:Rendezvous			-0.24	-0.32	-1.10				-0.79	
M20162710:Rendezvous	-1.37	-1.30								
F201617:Rendezvous	-1.37	-1.40		-0.52	13.38	-1.62				
F20172723:Rendezvous			0.26		0.23					1.09
M201724:Rendezvous	-2.36	-1.36		0.35						
F20132459:Wayfaring				0.52						
M201306:Wayfaring	-1.16	-0.86								
M201315:Wayfaring	-0.92	-0.58	-1.07	-0.70					5.43	
F201323:Wayfaring	1.24	0.74	-0.95				-17.05		-15.74	
M201307:Wayfaring	0.38	0.33		0.35						
M201414:Wayfaring		1.28	-0.32	-0.32	-13.51				-1.72	
F201516:Wayfaring		-0.47	-1.10	-1.01	-1.76		-2.76	-1.61	-0.88	
M20162710:Wayfaring			-0.38	-0.30	-21.84					
F201617:Wayfaring		1.19	-0.38	0.80	-21.84	1.38		0.91		1.51
F20172723:Wayfaring	-0.59	-1.34							0.51	
M201724:Wayfaring		-0.59		0.60						
N	16	29	18	24	23	3	5	3	12	4
N_{neg}	10	15	13	12	13	1	4	2	9	1
N_{pos}	6	14	5	12	10	2	1	1	3	3

Table 11. Individual (Ind) and Population (Pop) level log odds of significant wolf by diel period interactions based on Wald's Chi Square ($\alpha = 0.05$). N_{neg} is the count of estimates with disproportionately lower use of the land class versus woody wetlands than would be expected at random (selection for woody wetlands).and N_{pos} is the count of estimates with disproportionately higher use of the land class versus woody wetlands than would be expected at random (selection for that land class).

	Forest		Herb Wetlands		Grass		Crops		Developed	
Variable	**Ind**	**Pop**	**Ind**	**Pop**	**Ind**	**Pop**	**Ind**	**Pop**	**Ind**	**Pop**
M201201:Day					-0.97					
F201304:Day	0.19						-2.26			
M201315:Day					-3.45				-4.00	
M201307:Day	0.29								-1.19	
M201414:Day	-4.01	-1.41			-5.80				-2.32	-1.11
F201516:Day		1.06	-0.34		-2.83	-0.88	-2.88	-0.89	-1.07	
M20162710:Day	-2.21	-1.11	-0.89	-0.47						
F201617:Day	-2.21		-0.89	0.18						
F20172723:Day		1.15		0.31		1.55		1.35		1.51
M201724:Day				-0.26						
M201825:Day		-1.40							-12.21	
F201304:Night	0.46				1.55				-12.24	
M201306:Night							1.11			
M201315:Night									-3.51	
M201307:Night							-1.61			
M201414:Night	-3.97	-1.49		0.16	-5.25					0.69
F201516:Night	0.17	0.96		0.11		0.89		1.15		0.46
M20162710:Night		0.56								
F201617:Night								0.92		0.57
F20172723:Night		0.70				-0.78	-1.24			-1.86

Continued

M201724:Night				-0.14				-1.39		-0.85
M201825:Night		-2.57	-1.11	-0.44			0.81		-13.40	
N	8	10	4	8	6	4	6	5	8	7
N_{neg}	4	5	4	4	5	2	4	2	8	3
N_{pos}	4	5	0	4	1	3	2	3	8	4

Effects on Gray Wolf Speed

Wolves moved faster on average through developed land class (0.319m/s) and slowest through woody wetlands (0.240m/s) and fastest on average during rendezvous season (0.261m/s) and slowest during breeding season (0.239m/s). Wolf speed was the same on average during the day (0.250m/s) as it was during the night (0.251m/s). Male wolves moved slightly slower on average (0.24m/s) than female wolves (0.271m/s; Table 12). See Appendix E for visualization of variation of gray wolf speed across categories.

When considering only main effects (land class, season, diel period, sex), gray wolf speed was slower through forest than through woody wetlands and faster through developed lands, grass, and herbaceous wetlands than through woody wetlands. Speed was faster speed during denning and rendezvous seasons than during breeding season (Table 13).

When two way interactions between main effects were included, the top model included land class, season, sex, and a season by sex interaction as the best predictors of wolf speed, although the second ranked model had ΔAICc<2. Land class effects followed those of the main effects model with wolves moving slower through forest than woody wetlands. However, the trend for the seasonal effect was reversed, with wolves moving slower during denning, rendezvous, and wayfaring seasons than during breeding season. When considering sex, males moved faster during denning, rendezvous, and wayfaring seasons than females did during breeding season, which is contradictory to the mean speeds where males moved slower than females during breeding and denning season (Table 14, Fig 8).

Table 12. Mean speed estimates (m/s) derived from continuous-time movement models for gray wolves on Red Lake Indian Reservation.

				95% CI	
Variable	**N**	**Mean**	**SD**	**Lower**	**Upper**
Woody Wetlands	7089	0.24	0.078	0.238	0.242
Herbaceous Wetlands	2553	0.275	0.094	0.271	0.278
Forest	1690	0.25	0.064	0.247	0.253
Grass	182	0.248	0.079	0.237	0.26
Crops	140	0.294	0.051	0.285	0.302
Developed	121	0.319	0.129	0.296	0.342
M2012-01	75	0.13	0.031	0.123	0.137
F2013-2459	601	0.383	0.057	0.378	0.388
F2013-04	260	0.191	0.05	0.185	0.197
M2013-15	541	0.271	0.026	0.269	0.273
F2013-23	681	0.148	0.025	0.146	0.15
M2013-07	462	0.269	0.049	0.264	0.273
M2014-14	2177	0.29	0.093	0.286	0.294
F2015-16	1775	0.275	0.071	0.272	0.278
M2016-2710	1074	0.239	0.038	0.237	0.242
F2017-2723	769	0.308	0.031	0.305	0.31
M2017-24	2926	0.198	0.048	0.196	0.2
M2018-25	434	0.22	0.07	0.213	0.226
Breeding	1788	0.239	0.08	0.234	0.242
Denning	3761	0.252	0.082	0.249	0.254
Rendezvous	2824	0.261	0.086	0.258	0.265
Wayfaring	3402	0.247	0.078	0.244	0.25
Day	5269	0.25	0.076	0.248	0.252
Night	6506	0.251	0.089	0.249	0.253
Female	4086	0.271	0.09	0.268	0.273
Male	7689	0.24	0.075	0.238	0.241
2011	2620	0.252	0.097	0.249	0.256
2016	9155	0.25	0.077	0.248	0.251

Table 13. Linear mixed main effects model for $\log_{10}$ transformed speed estimates derived from continuous-time movement models for Red Lake Indian Reservation gray wolves.

	Estimate	$\log_{10}$ Estimate	SE	p-value
(Intercept)	0.238	-1.436	0.144	0
Crops	1.022	0.022	0.016	0.168
Developed	1.133	0.125	0.017	0
Forest	0.986	-0.014	0.006	0.014
Grass	1.028	0.027	0.014	0.048
Herbaceous Wetlands	1.026	0.025	0.004	0
Denning	1.024	0.024	0.005	0
Rendezvous	1.018	0.017	0.006	0.003
Wayfaring	1.009	0.009	0.005	0.101
Night	1.003	0.003	0.003	0.424
Male	0.905	-0.100	0.188	0.606

Table 14. Top linear mixed model for $\log_{10}$ transformed speed estimates derived from continuous-time movement models for Red Lake Indian Reservation gray wolves.

	Estimate	$\log_{10}$ Estimate	SE	p-value
(Intercept)	0.249	-1.390	0.143	0
Crops	1.021	0.021	0.016	0.196
Developed	1.131	0.123	0.017	0
Forest	0.987	-0.013	0.006	0.025
Grass	1.026	0.026	0.014	0.060
Herbaceous Wetlands	1.025	0.024	0.004	0
Denning	0.977	-0.023	0.010	0.021
Rendezvous	0.976	-0.024	0.011	0.024
Wayfaring	0.956	-0.045	0.010	0
Male	0.854	-0.158	0.187	0.418
Denning:Male	1.067	0.065	0.012	0
Rendezvous:Male	1.057	0.055	0.013	0
Wayfaring:Male	1.078	0.075	0.012	0

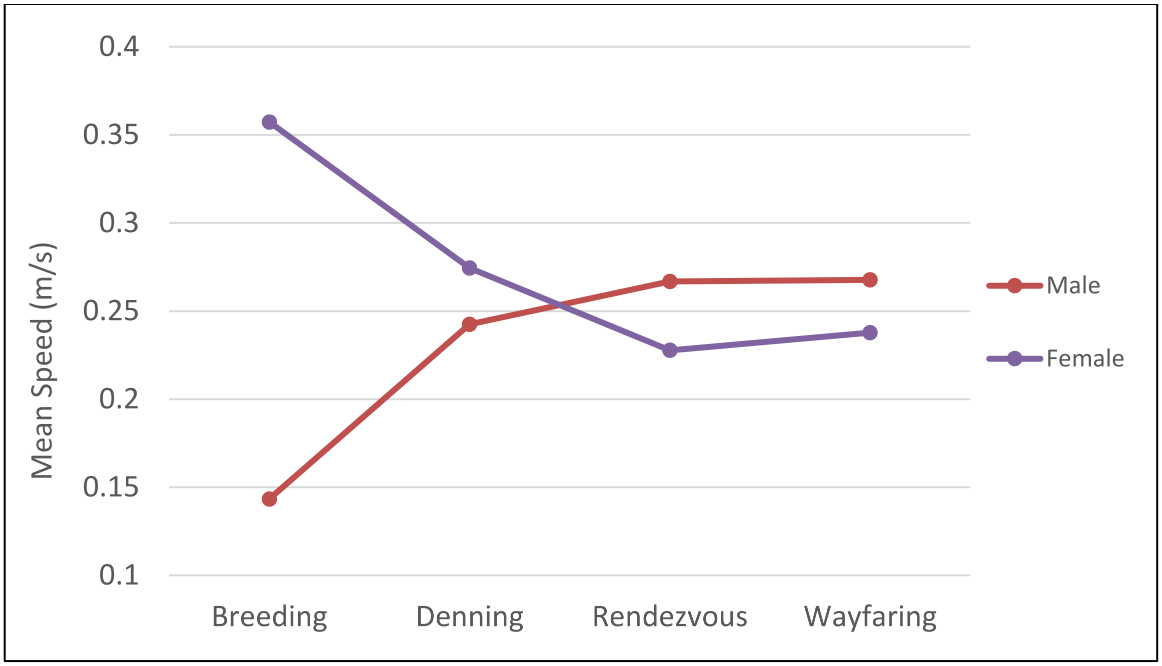

Figure 8. Interaction between season and sex for speed of gray wolves on Red Lake Indian Reservation. Speed is similar between sexes except for during breeding season.

Discussion

Habitat Use

Red Lake gray wolves consistently used woody wetlands more than any other habitat type, regardless of season, diel period, or sex, and at both the individual and population levels. This is similar to wolves in northeastern Minnesota, whose territories were comprised of primarily woody wetlands (Erb et al. 2018). These results are not surprising considering that the majority of the habitat within the total occupied wolf range in Minnesota, which includes Red Lake Indian Reservation, is woody wetlands (Erb et al. 2018). However, next to woody wetlands, northeastern wolves are using forest the most, whereas Red Lake wolves are using herbaceous wetlands. This is likely representative of the local availability of each habitat type in northeast Minnesota versus Red Lake. Land cover consists greatly of a mixture of woody and herbaceous wetlands around Red Lake, particularly north of the Diminished Reservation, which is where a majority of Red Lake wolves are living. Conversely, land cover in northeast Minnesota consists less of herbaceous wetlands, and more of forest (USGS 2016).

Although woody wetlands were used most often for both group 2011 and group 2016, there was more intense use of woody wetlands by group 2016, particularly for males. This, again, is likely representative of the availability of this habitat type in earlier years versus later years. Although the increase in woody wetlands was minimal (5%), the increased availability is likely the reason behind the increased use of this habitat type by gray wolves in later years.

There was consistent, minimal use of grass, crops, and developed land by Red Lake gray wolves. This was also similar to northeastern wolves, with these combined habitat types making up only 7% of the land cover within their territories. As shown in previous studies of wolves in the Great Lakes Region, which includes Minnesota, there was not much use of these anthropogenic classes at either the individual or population level scale (Mladenoff et al. 2009, Oakleaf et al. 2006).

Habitat Selection

I saw an aversion to grass at both the individual and population levels. This could be because in northern Minnesota, grassy areas are often intermittently used as pasture for cattle (Hoch 2013), essentially making them functionally the same as anthropogenic features. Although cattle depredation is a prevalent concern among ranchers (Olson et al. 2015), and depredation still does occur (Benson et al. 2017), it appears that on and around Red Lake, the presence of humans is more of a deterrent than the potential attraction of cattle as prey.

Although the avoidance of anthropogenic features was consistent in all seasons and during both day and night, I did detect other seasonal effects at both levels of selection. In general, I saw selection for woody wetlands over both herbaceous wetlands and forest during breeding and wayfaring seasons and over forest during denning and rendezvous seasons. However, there was selection for herbaceous wetlands over woody wetlands during denning season, which was surprising because it has been documented that wooded areas are often the preferred habitat types during pup-rearing seasons (Norris et al. 2002, Trapp et al. 2008). The shift towards selection for herbaceous wetlands can potentially be explained by the logging activities that occur across Red Lakes Reservation Lands. Logging is an industry that has been a source of income for the Red Lake Tribe throughout its history, with logging occurring each year from late spring to early summer (Red Lake Nation 2019). Gray wolves tend to avoid exposure to human activities when selecting den sites (Sazatornil et al. 2016, Llaneza et al. 2018), and because the logging time span overlaps with both denning and rendezvous season, it is possible that these activities have caused wolves to den away from some wooded areas. Previous research has shown that Minnesota wolves appear more tolerant of human activities, even during pup-rearing seasons when I would expect them to be less tolerant (Thiel et al. 1998); however, more recent studies show that wolves will move pups away from areas of human disturbance (Argue et al. 2008, Sidorovich et al. 2017).

At the population level, I detected significant differences in selection between males and females. Furthermore, the differences between the sexes were not consistent between group 2011and group 2016. For group 2011, I saw selection for woody wetlands for females and for herbaceous wetlands and forest for males. The role of male wolves is primarily foraging and hunting, whereas the role of females is primarily pup-rearing (Mech 1999). This means that male wolves are leaving their territories more often or moving within their home ranges more often, resulting in more travel across the landscape, which could explain why they display selection differently for more land classes than females. For group 2016, I did not detect a difference in selection between sexes. The fact that males no longer select forest could be due to the shift of available land cover from forest in 2011 to woody wetlands in 2016.

Effects on Gray Wolf Speed

I saw a significant increase in gray wolf speed over developed areas. Use of developed areas was generally minimal; however, it is known that wolves use developed roads for ease of travel (Zimmerman 2014). I am unsure if use of developed areas by wolves within my data set was specific to roads, but this could explain why I saw faster speeds across this land class.

I saw a significant increase in speed through grass, which supports the idea that grass is functionally anthropogenic due to its intermittent use as cattle pasture. There was a significant decrease in speed through forest, most likely due to foraging behavior. The primary prey for wolves is deer (*Odocoileus virginianus*; Mech and Boitani 2003*b)*, which are found primarily in forest in Minnesota (Mooty 1987).

There was a significant decrease in speed during both denning and rendezvous seasons compared to breeding for the top model. This reflects the ecology of wolves during pup-rearing season when wolves spend most of their time around the den site (Mech 1970, Ruprecht 2012). Counter intuitively, speed during wayfaring season when wolves are moving about their territories (Mech 1970) was also significantly slower than during breeding season. This could be due to wolves dispersing from their natal packs during breeding season, and possibly traveling long distances (Jimenez et al. 21017) in search of mates and new territory (Mech and Boitani 2003*b*).

There were no significant overall effects of sex; however, there was a significant interaction between season and sex with males moving faster than females during both breeding, denning, and rendezvous seasons. Although females had faster speeds on average overall and during every season, the small sample size of females (N=4086 locations versus N=7689 locations for males) may not make the average speed representative of the true mean speed of females. Because males tend to do the foraging during these seasons (Mech 1999), it would be reasonable to expect that pup-rearing females, which remain around the den site, would move around more slowly. Additionally, foraging males may need to travel farther distances in search of prey when densities are low (Johnson et al. 2017), which can be the case for deer in Minnesota during these cold seasons (DeLgiudice et al. 2002). Although wolves are traveling farther to reach prey, Johnson et al. 2017 found that the time between hunting events was similar to when prey density was high and wolves were not traveling as far, suggesting that wolves are traveling faster to reach prey located greater distances away.

Management Implications

This study provided the RLDNR with site-specific estimates of habitat selection and movement patterns for Red Lake gray wolves. From this study, predictions can be made about wolf occurrence on and around Red Lake lands, and habitats in those areas can be managed accordingly. Although logging on Red Lake lands has potentially shifted denning and rendezvous sites from some wooded areas, wooded habitat is widely available on Red Lake lands. Furthermore, the Red Lake DNR Forestry Program has an ongoing Forest Development plan to restore and maintain wooded areas, which are still primarily used by wolves. However, gray wolves in other areas have shown a preference for old growth forests that are usually found further from high density roads and human activity, particularly during denning season (Roffler et al. 2018). Because pup-rearing plays a crucial role in the stability and perseverance of gray wolf populations (Fuller 1989, Fuller et al. 2003), maintenance of areas containing old growth forest on Red Lake lands should be a priority. Additionally, pup survival at den sites located near logging activities should be monitored and relocation of den sites to areas farther away from logging activities should be particularly noted, as movement of pups during denning may increase pup mortality (Frame et al. 2007, Argue et al. 2008),

Red Lake Indian Reservation lands consist primarily of woody wetlands and herbaceous wetlands, both of which are consistently used by Red Lake gray wolves. Because these habitat types are widely available across Red Lake lands, and are not likely to be converted to agriculture, the primary concern for wolves on Red Lake Indian Reservation is less about habitat availability, and more about range availability and location, as seen in Chapter 2. As the gray wolf population on Red Lake lands continues to grow, wolf population numbers should continue to be studied and used in combination with current and future home range estimates to monitor the quantity of space available to gray wolves.

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Appendix A

Frequencies of Land Classes Across Buffers for Land Composition Assessment

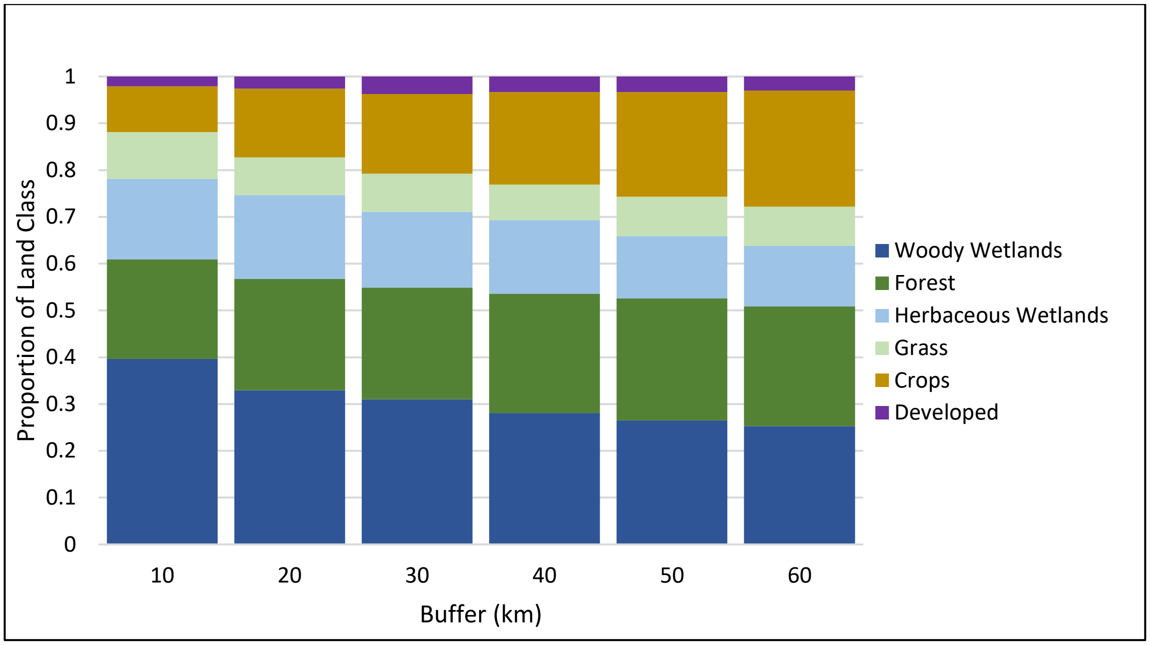


Figure 9a. Land class frequencies within various buffers around the collective relocations from Red Lake Indian Reservation gray wolves in group 2011.

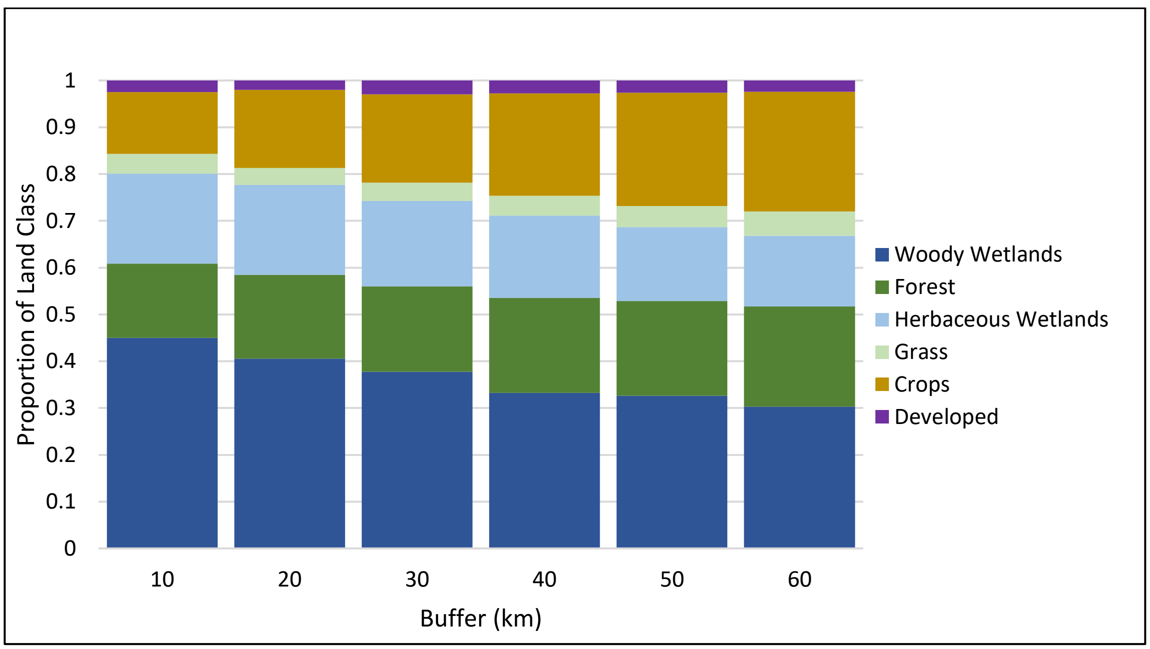


Figure 9b. Land class frequencies within various buffers around the collective relocations from Red Lake Indian Reservation gray wolves in group 2016.

Appendix B

Maps Depicting Geographic Land Class Distribution Within Each 30km Buffer for Both Individual and Population Levels

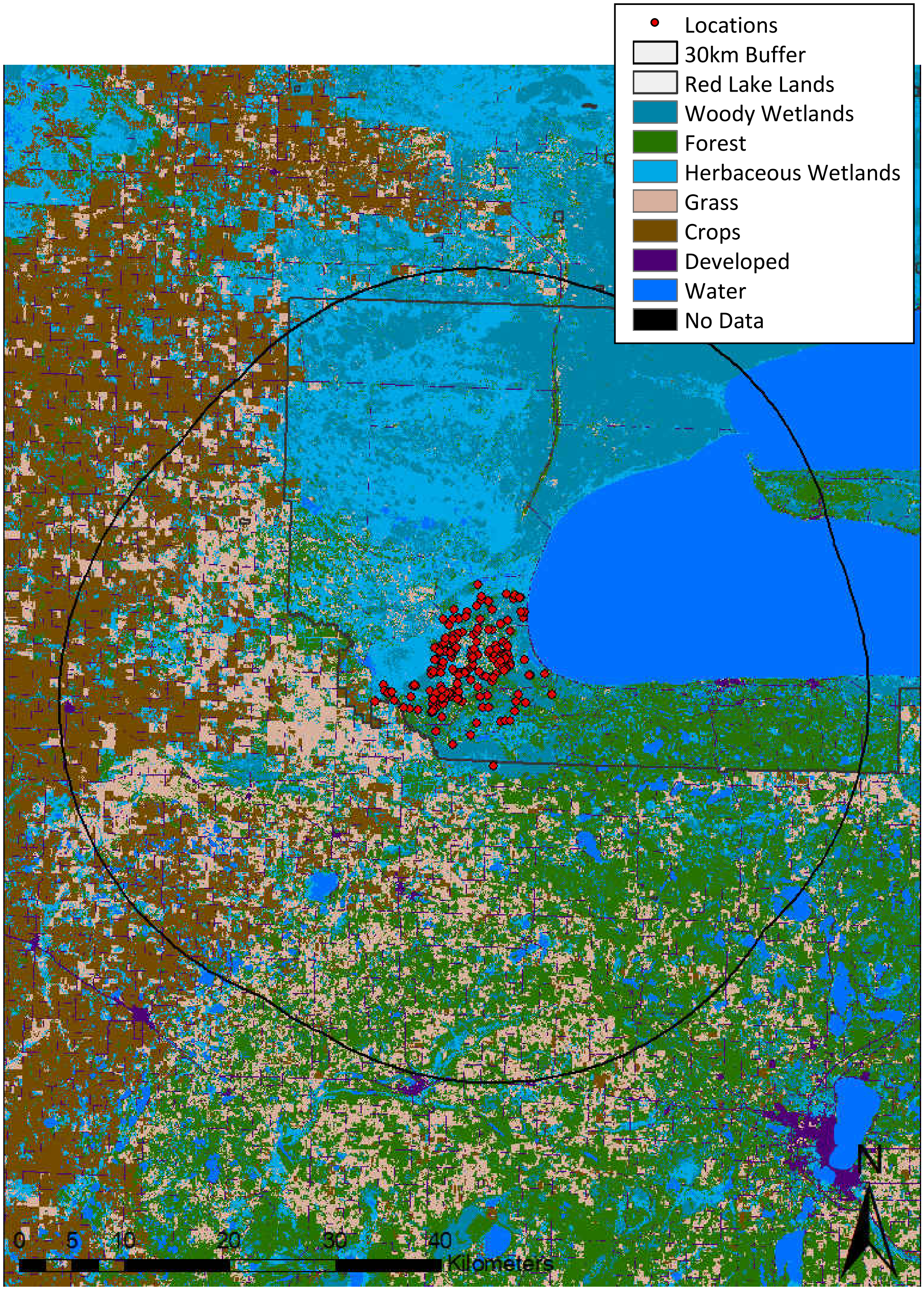


Figure 10a. Land class distribution within the 30km buffer for wolf M2012-01.

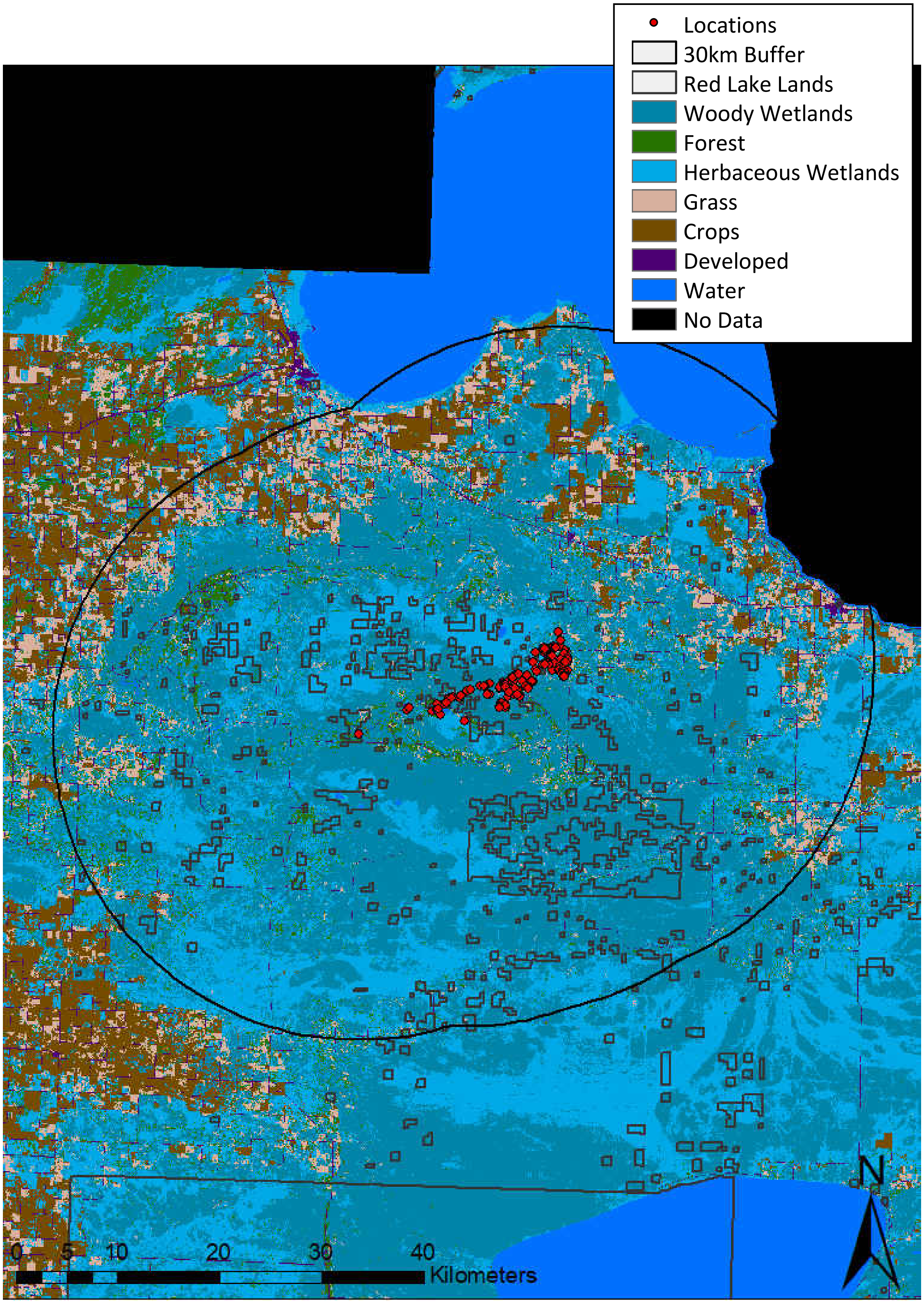


Figure 10b. Land class distribution within the 30km buffer for wolf F2013-22.

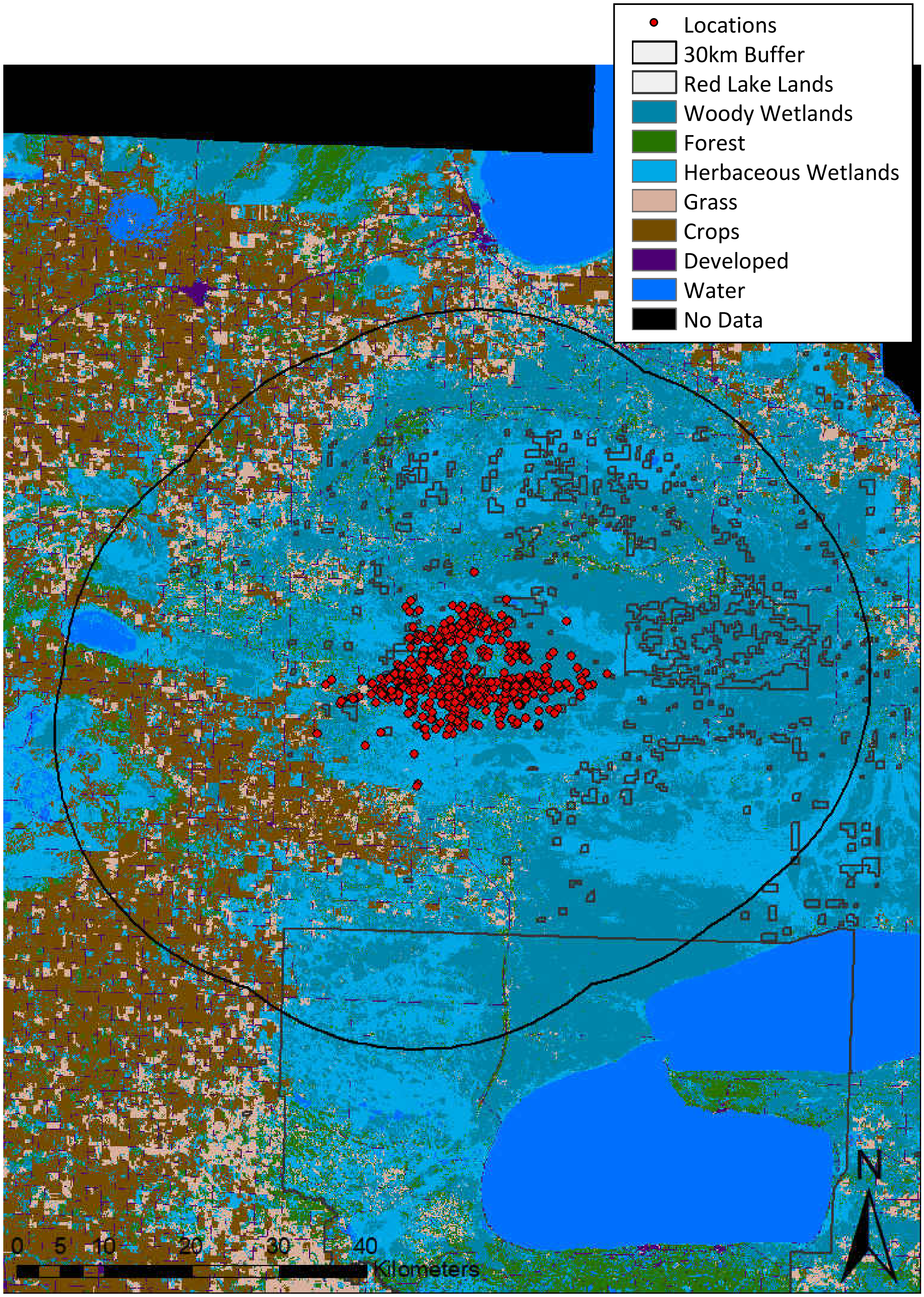


Figure 10c. Land class distribution within the 30km buffer for wolf F2013-2359.

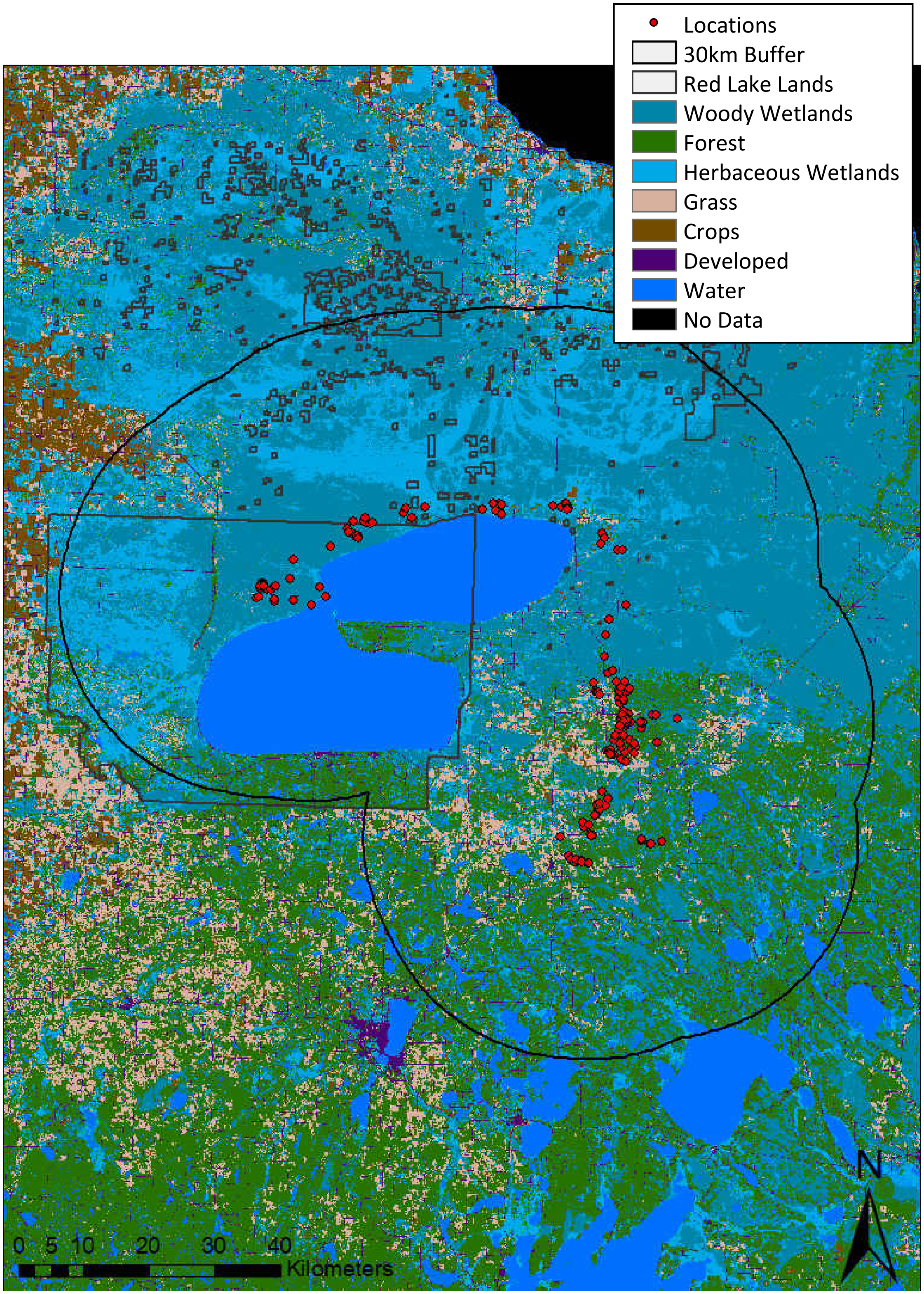


Figure 10d. Land class distribution within the 30km buffer for wolf F2013-04.

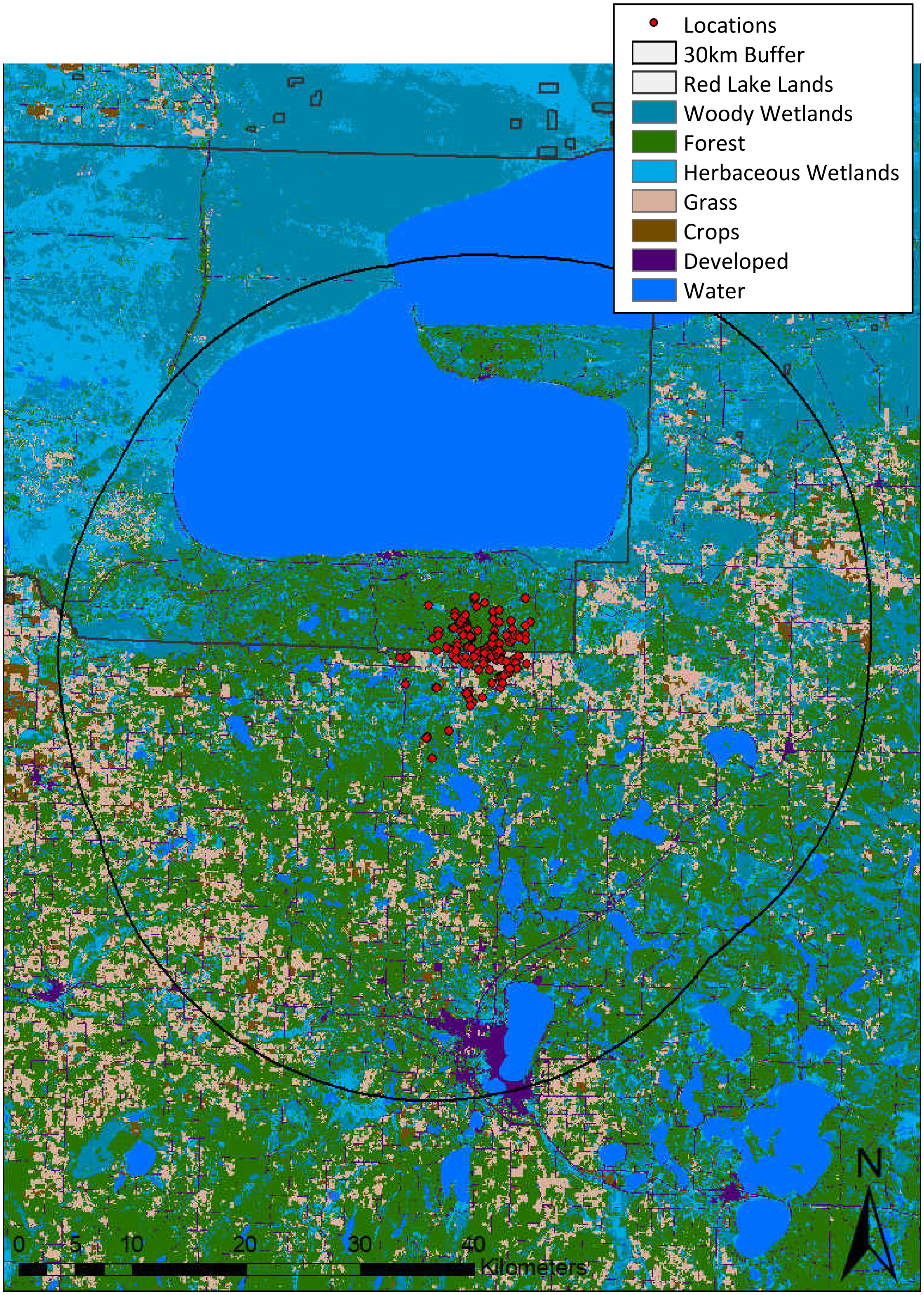


Figure 10e. Land class distribution within the 30km buffer for wolf M2013-06.

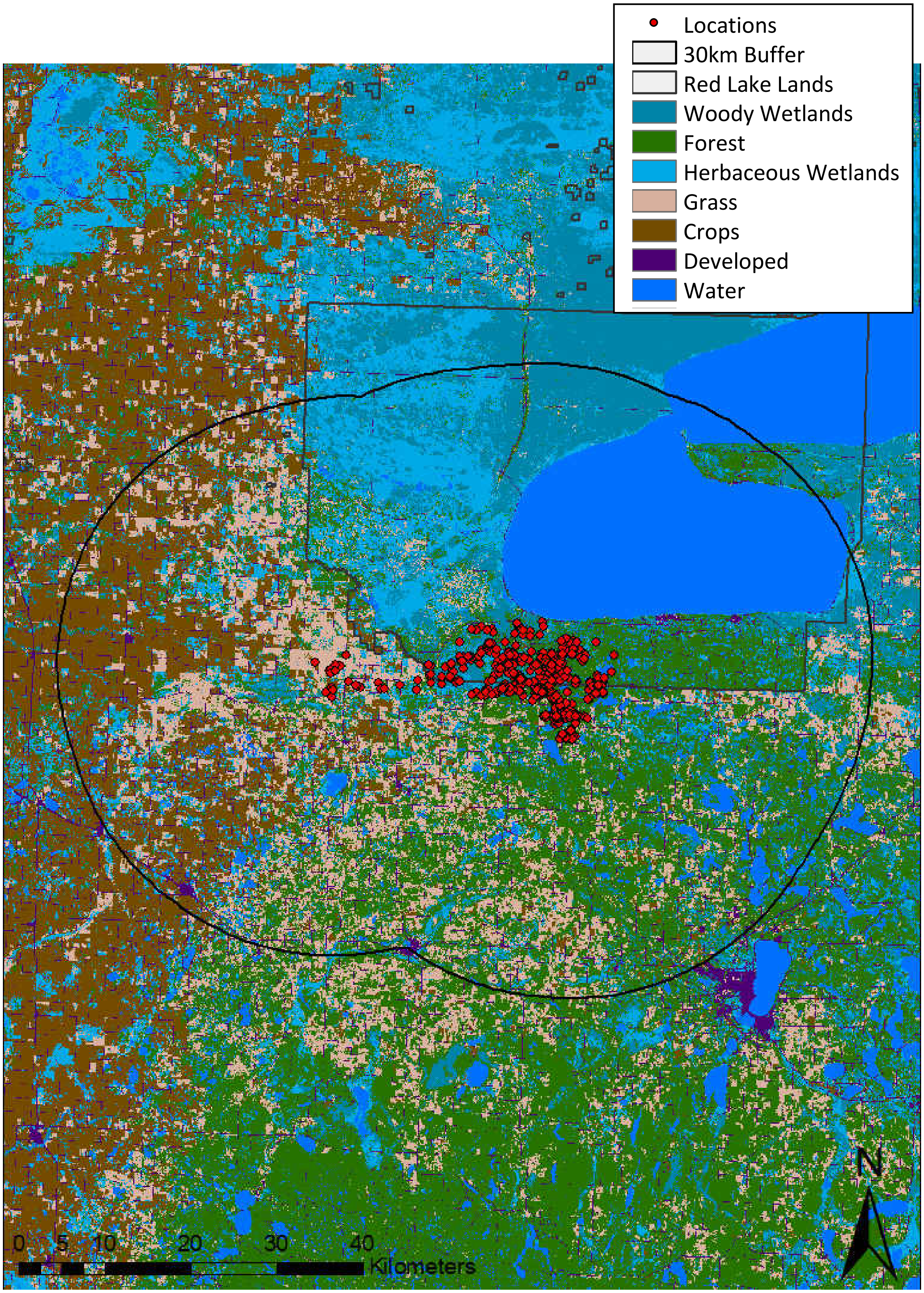


Figure 10f. Land class distribution within the 30km buffer for wolf M2013-15.

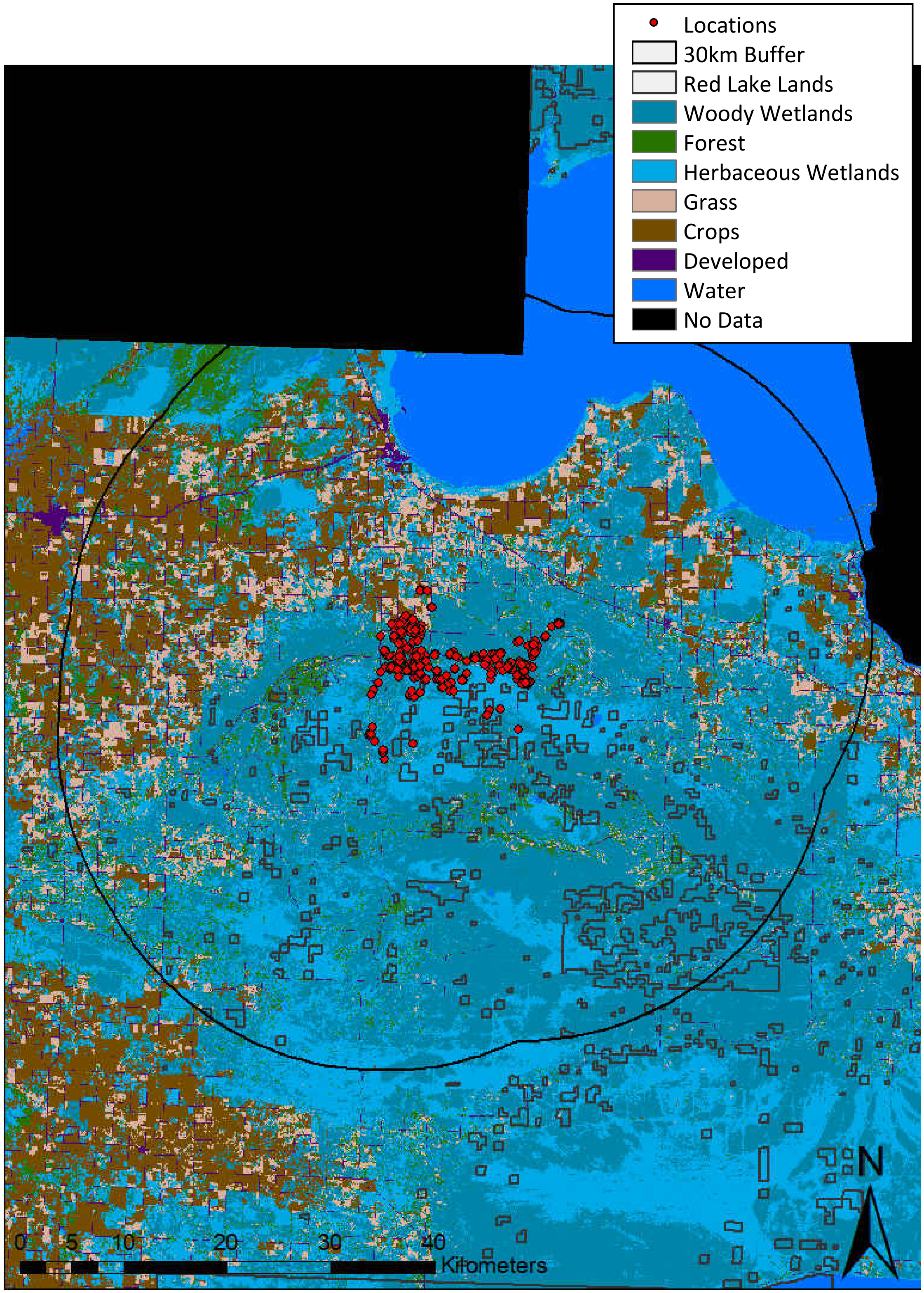


Figure 10g. Land class distribution within the 30km buffer for wolf F2013-23.

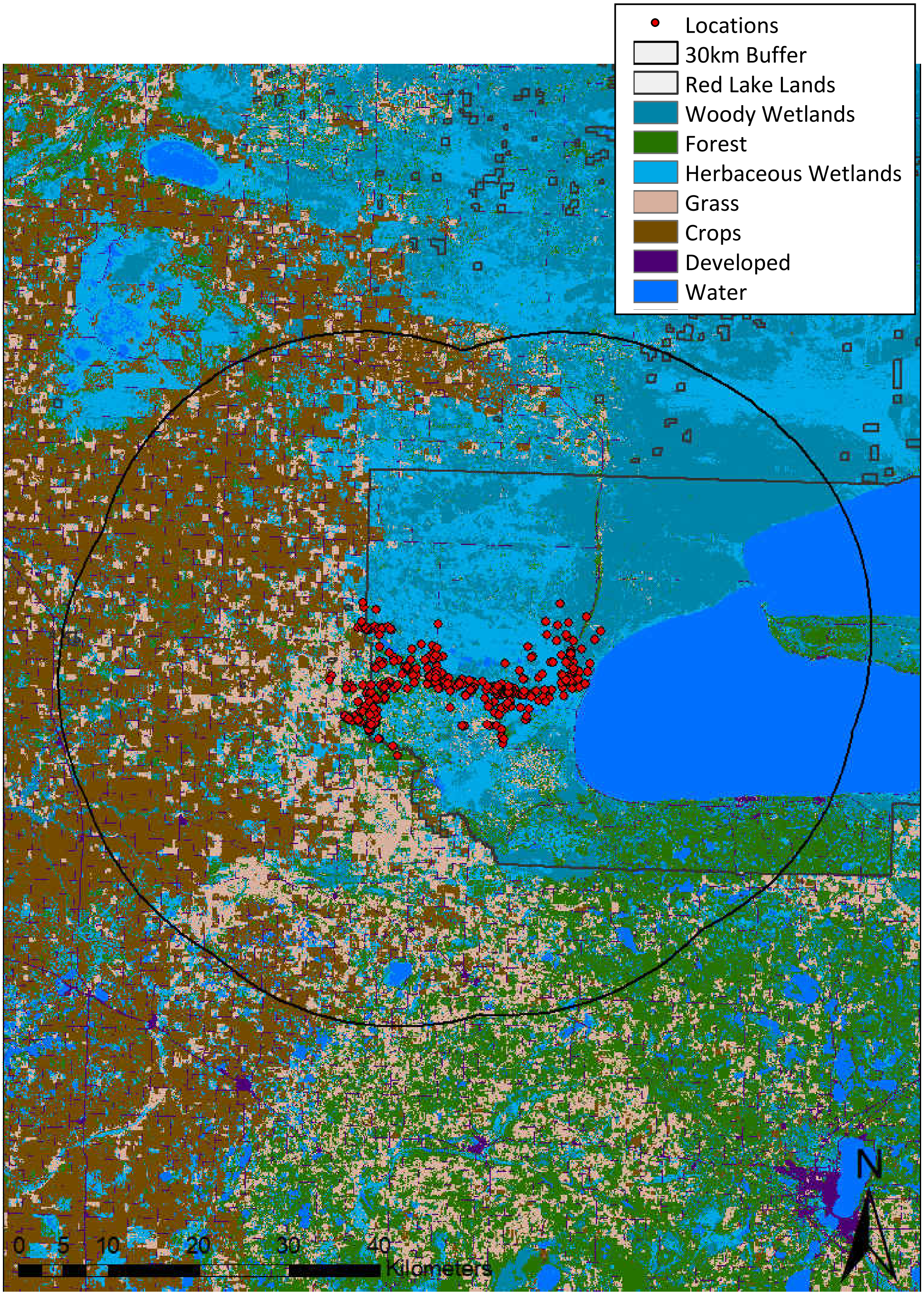


Figure 10h. Land class distribution within the 30km buffer for wolf M2013-07.

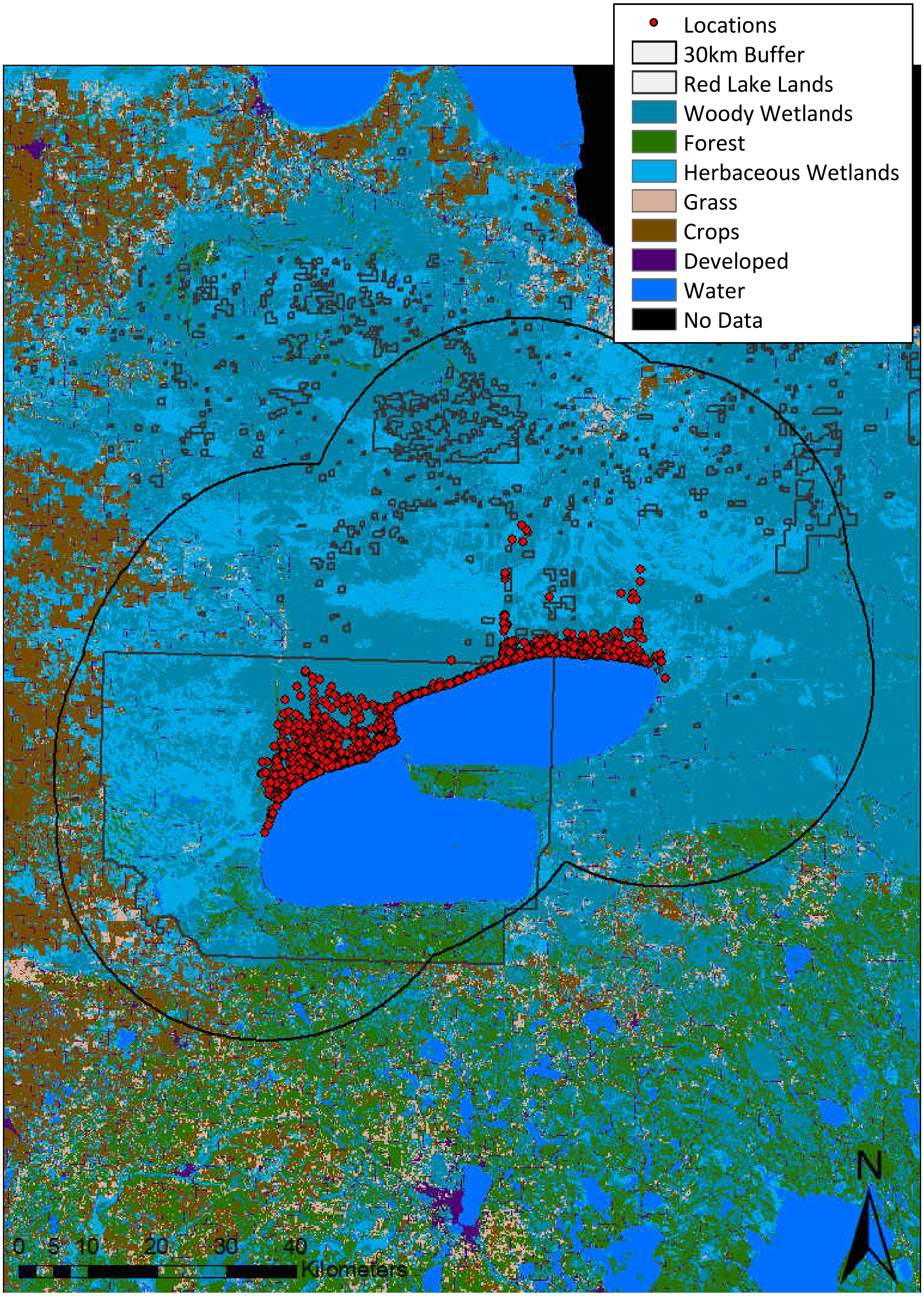


Figure 10i. Land class distribution within the 30km buffer for wolf M2014-14.

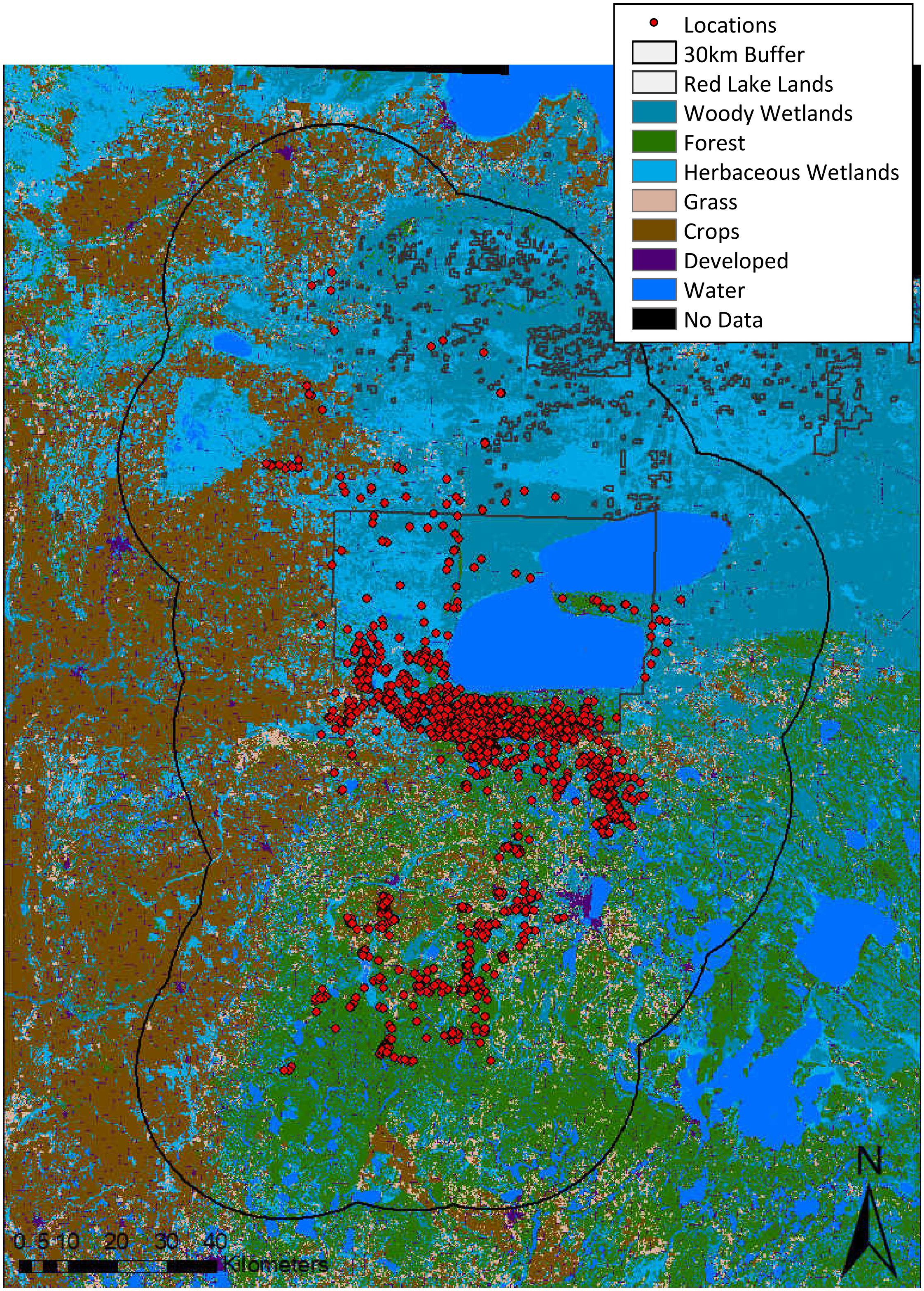


Figure 10j. Land class distribution within the 30km buffer for wolf F2015-16.

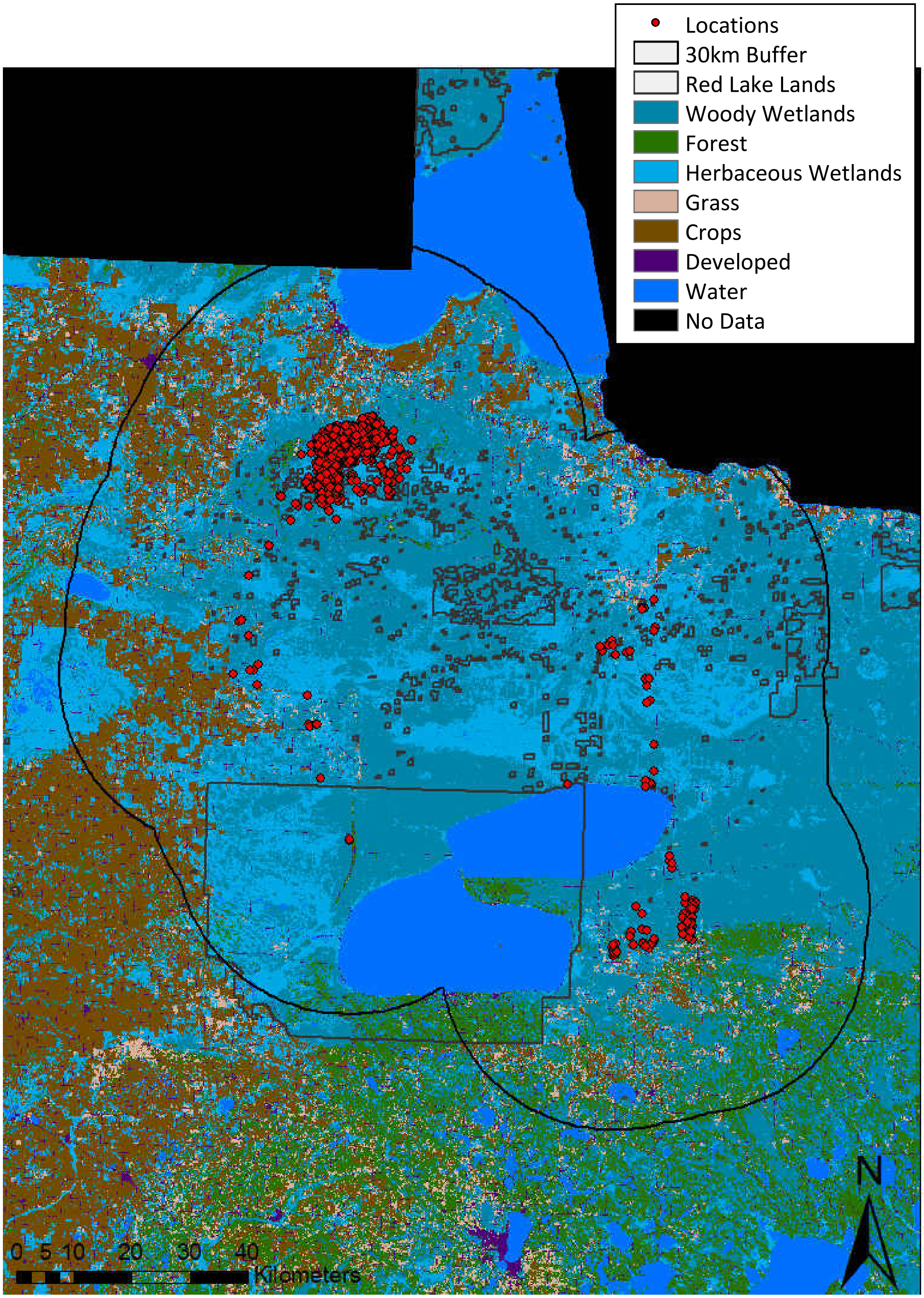


Figure 10k. Land class distribution within the 30km buffer for wolf M2016-2710.

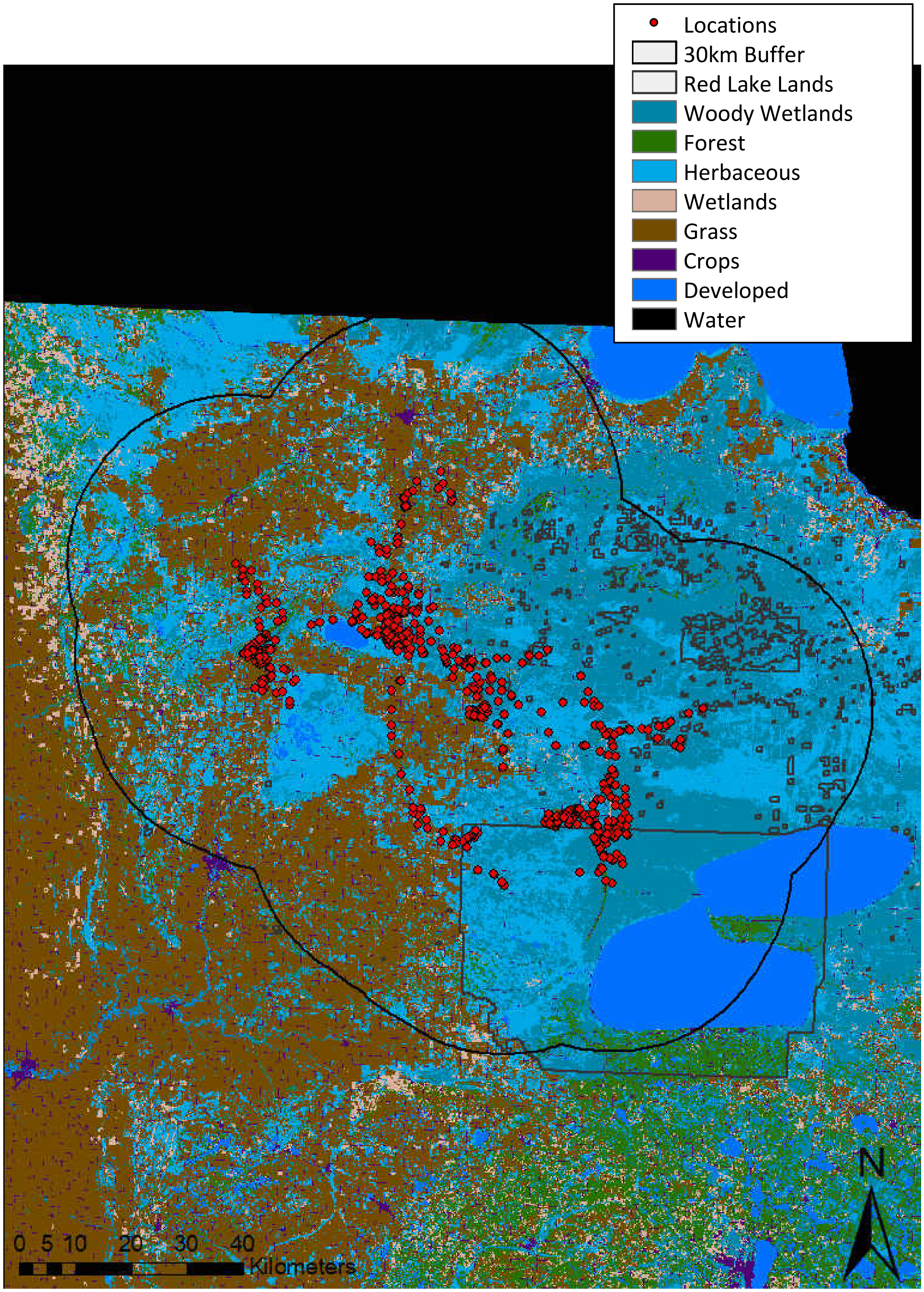


Figure 10l. Land class distribution within the 30km buffer for wolf F2016-17.

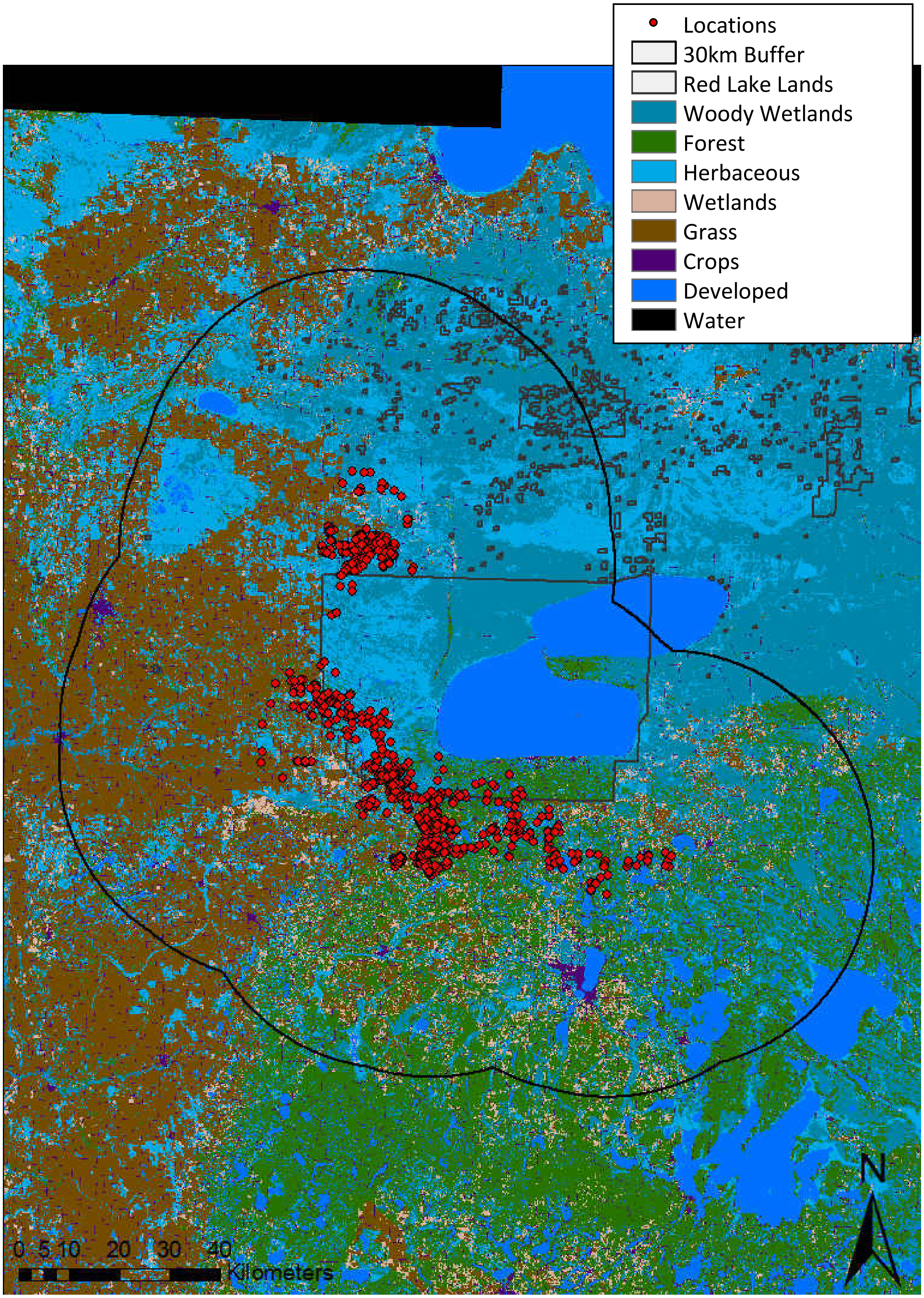


Figure 10m. Land class distribution within the 30km buffer for wolf F2017-2723.

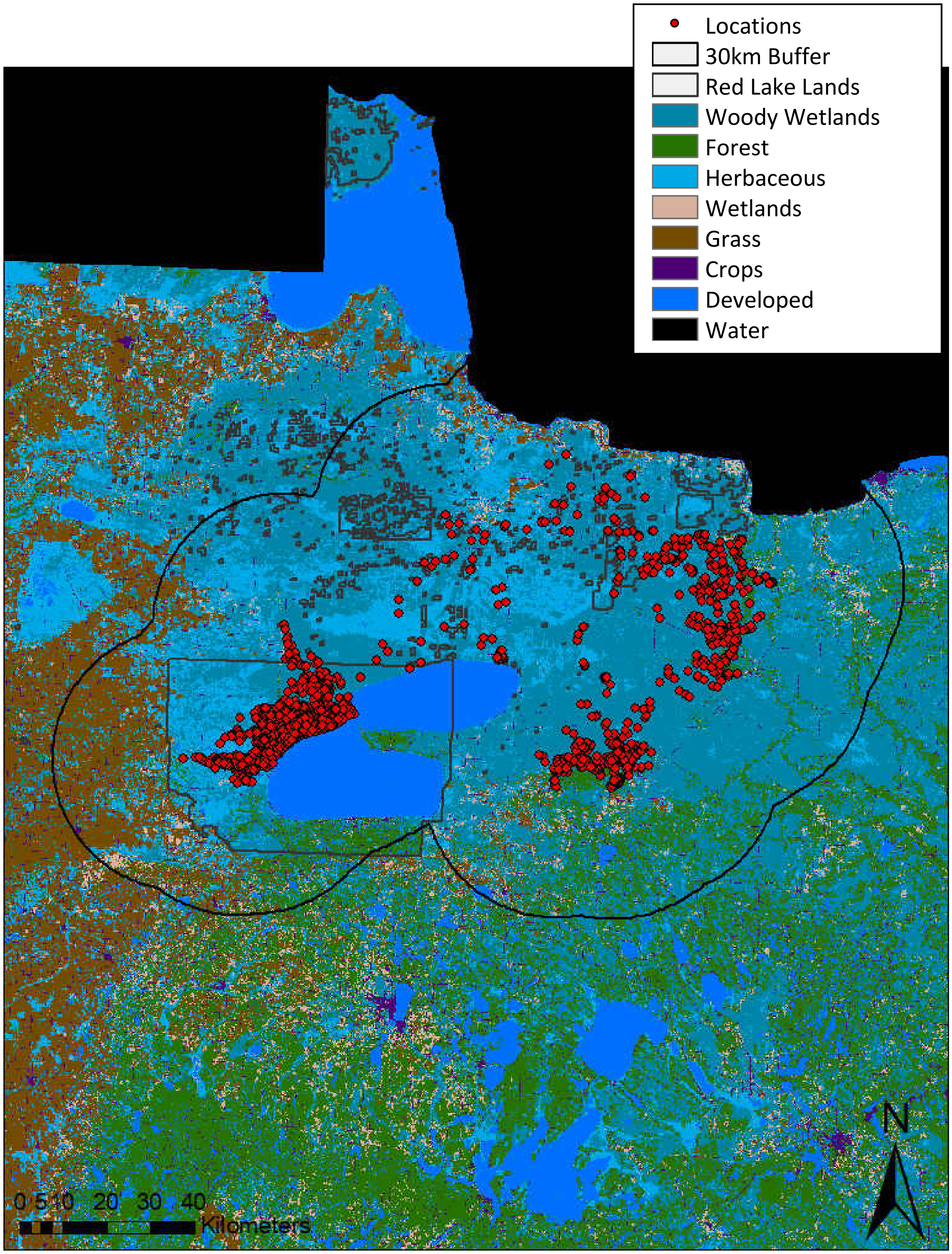


Figure 10n. Land class distribution within the 30km buffer for wolf M2017-24.

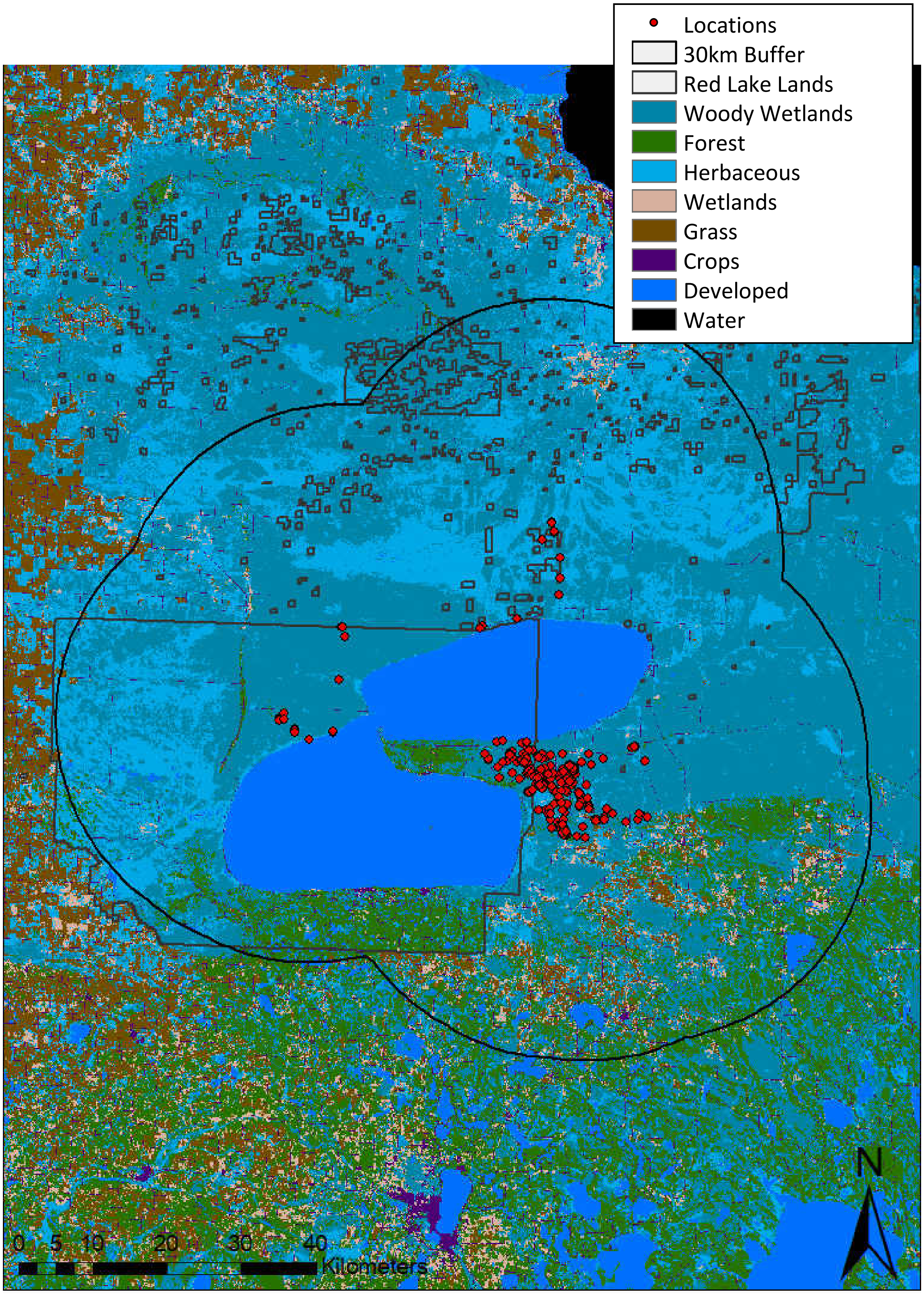


Figure 10o. Land class distribution within the 30km buffer for wolf M2018-25.

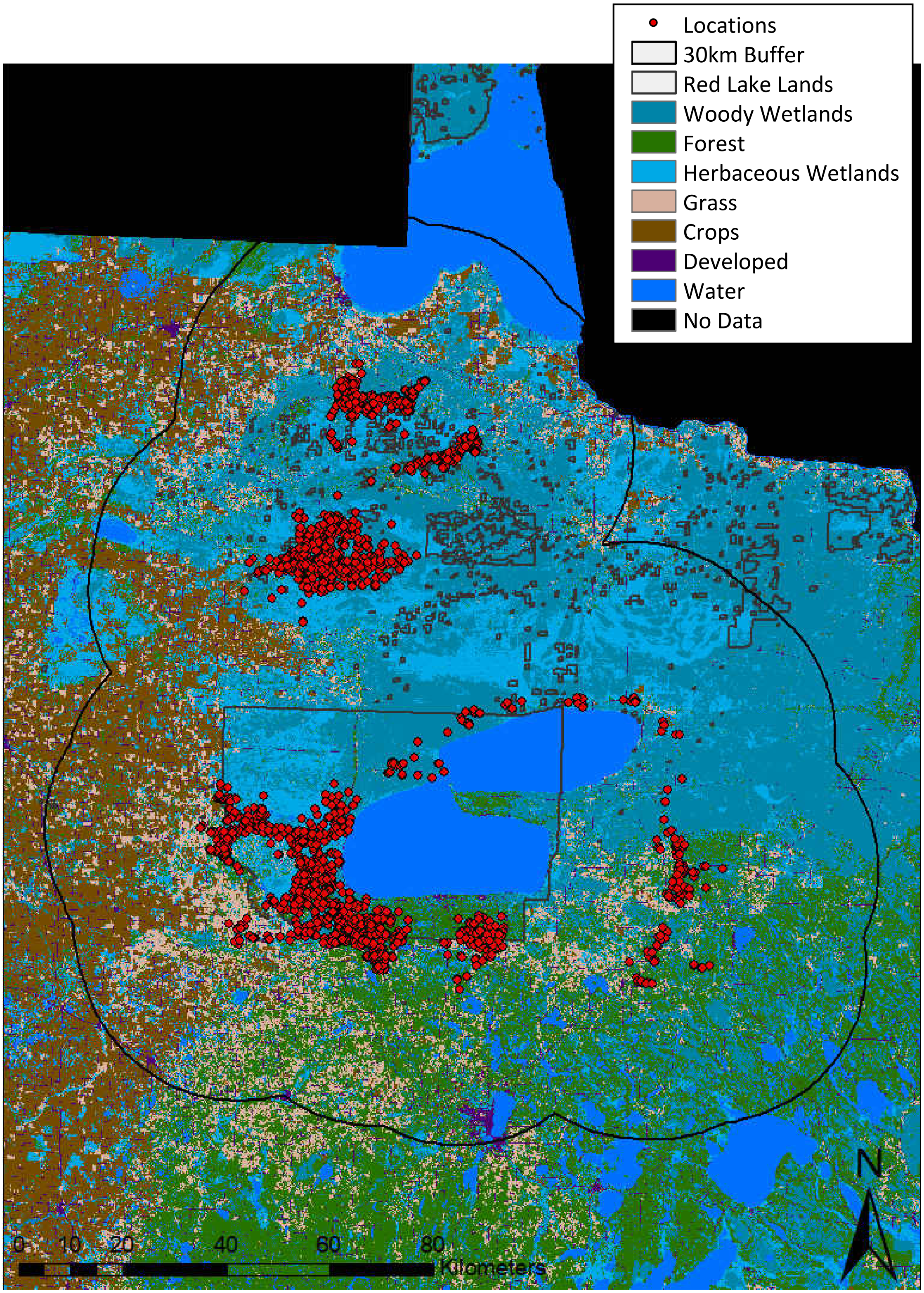


Figure 11a. Land class distribution within the 30km buffer for group 2011.

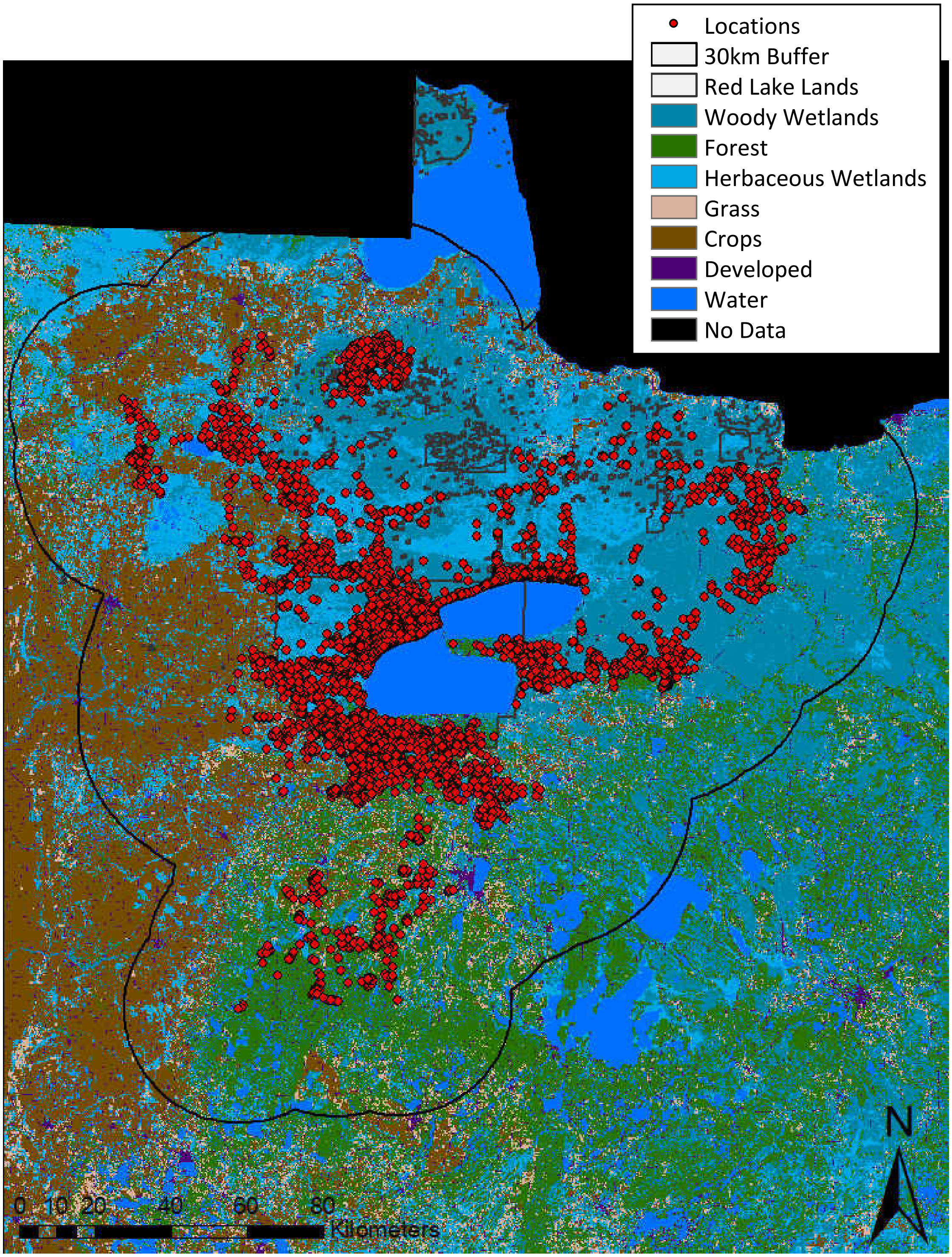


Figure 11b. Land class distribution within the 30km buffer for group 2016.

Appendix C

Habitat Use by Gray Wolves Compared to Habitat Availability

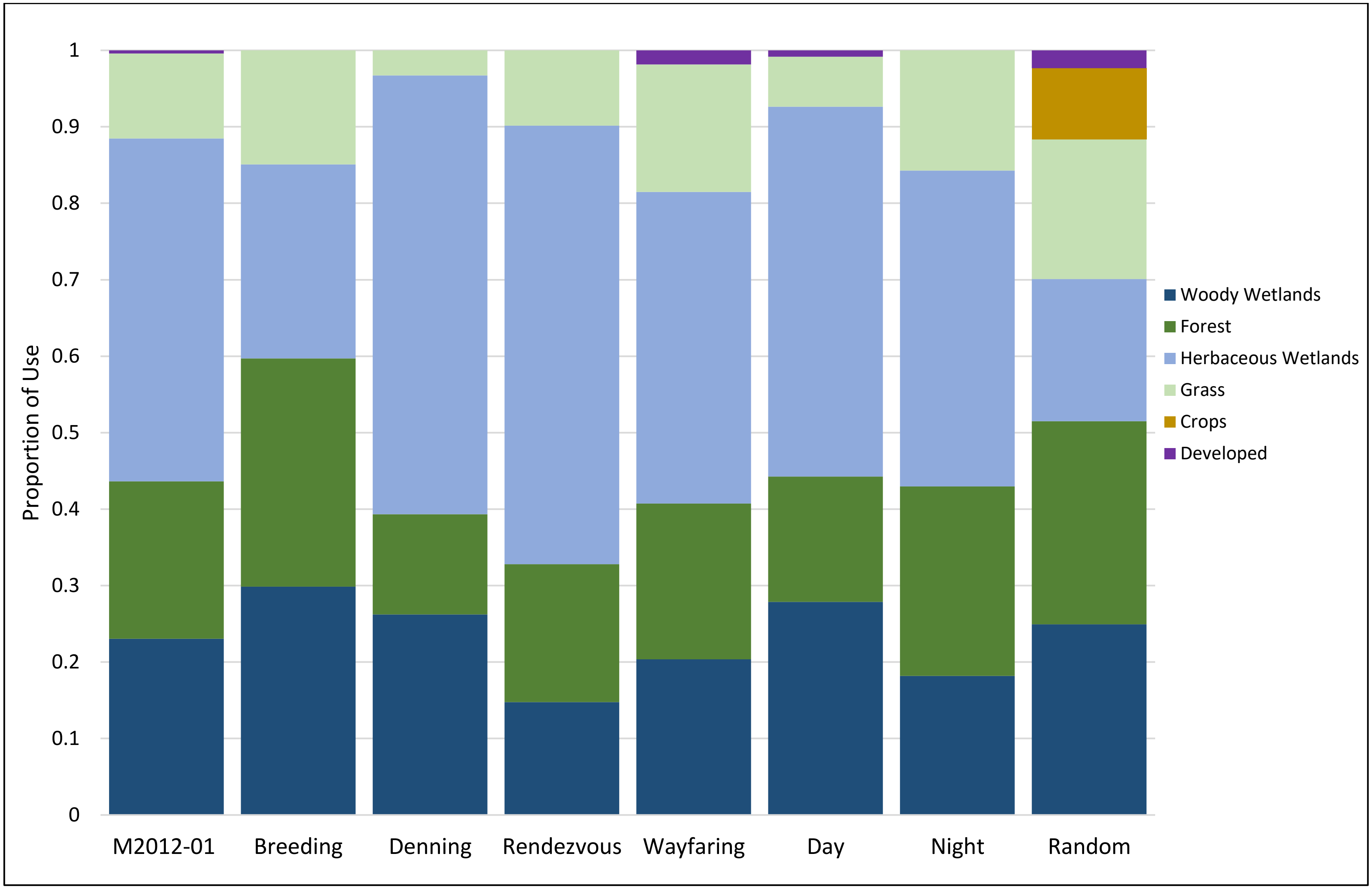


Figure 12a. Habitat use of wolf M2012-01 during each applicable season and each diel period compared to the availability of habitat (Random) within the individual 30km buffer based on the reclassified 2011 NLCD.

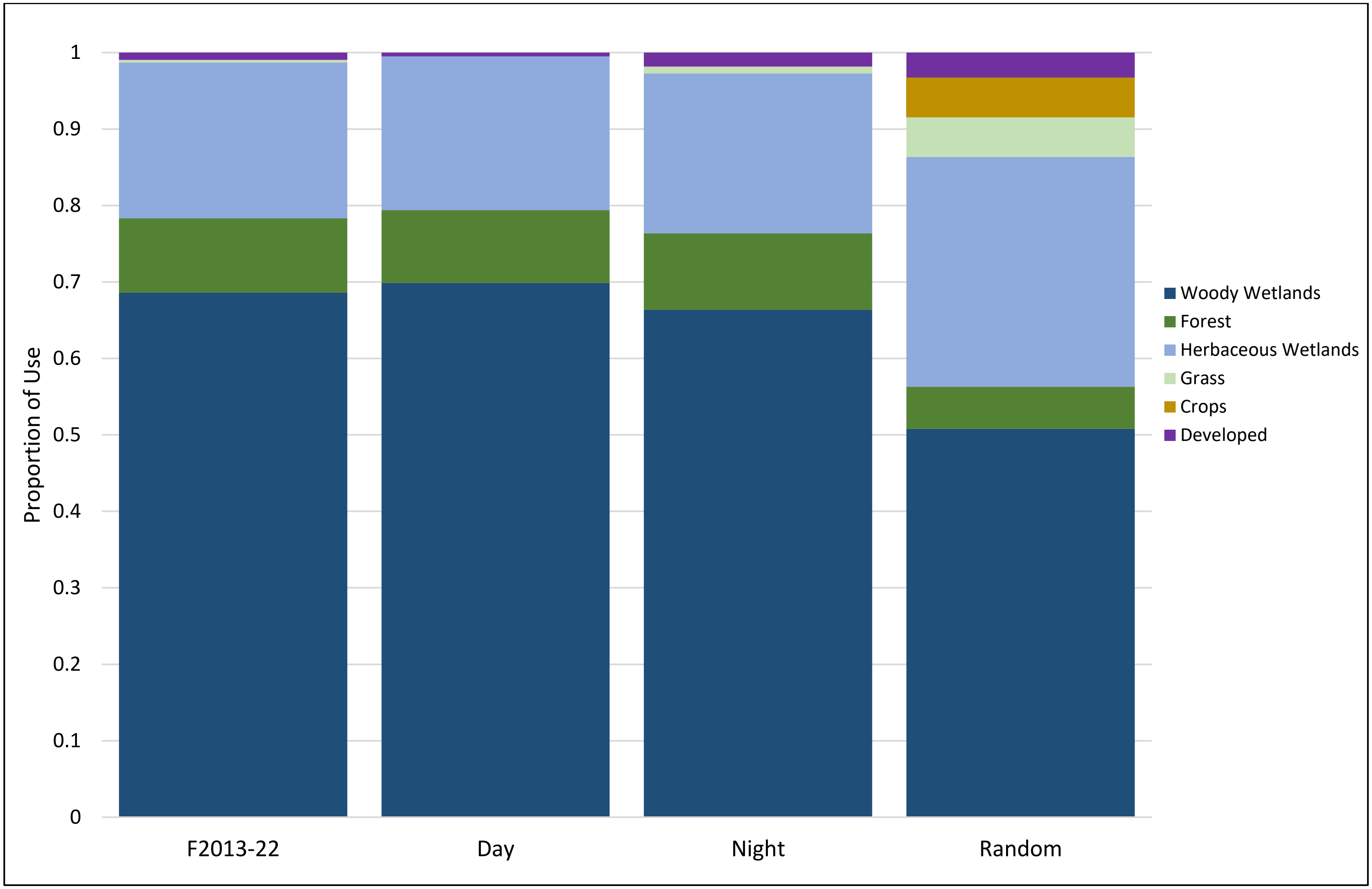


Figure 12b. Habitat use of wolf F2013-22 during each diel period compared to the availability of habitat (Random) within the individual 30km buffer based on the reclassified 2011 NLCD. All use occurred during denning season.

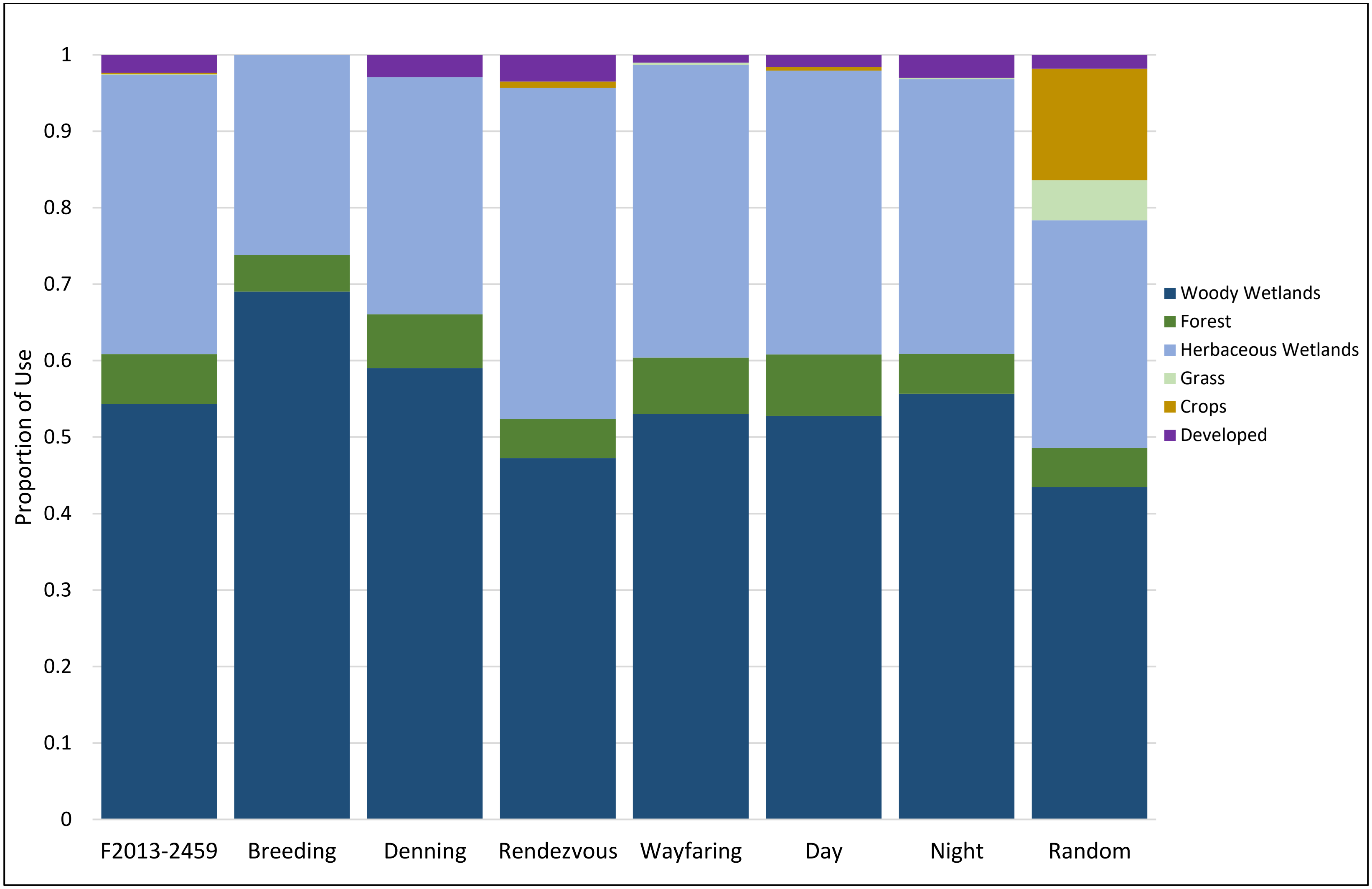


Figure 12c. Habitat use of wolf F2013-2459 during each applicable season and each diel period compared to the availability of habitat (Random) within the individual 30km buffer based on the reclassified 2011 NLCD.

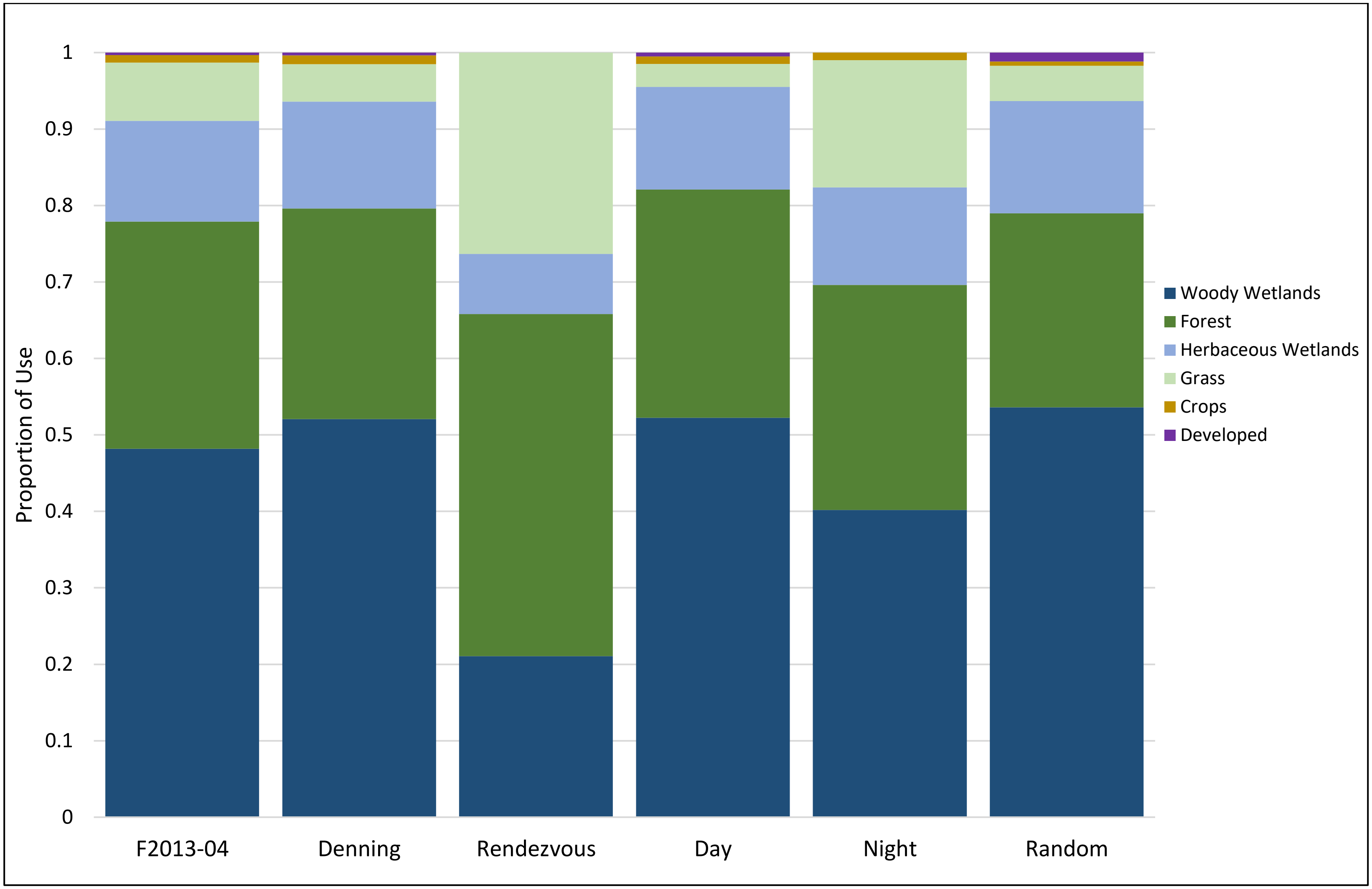


Figure 12d. Habitat use of wolf F2013-04 during each applicable season and each diel period compared to the availability of habitat (Random) within the individual 30km buffer based on the reclassified 2011 NLCD.

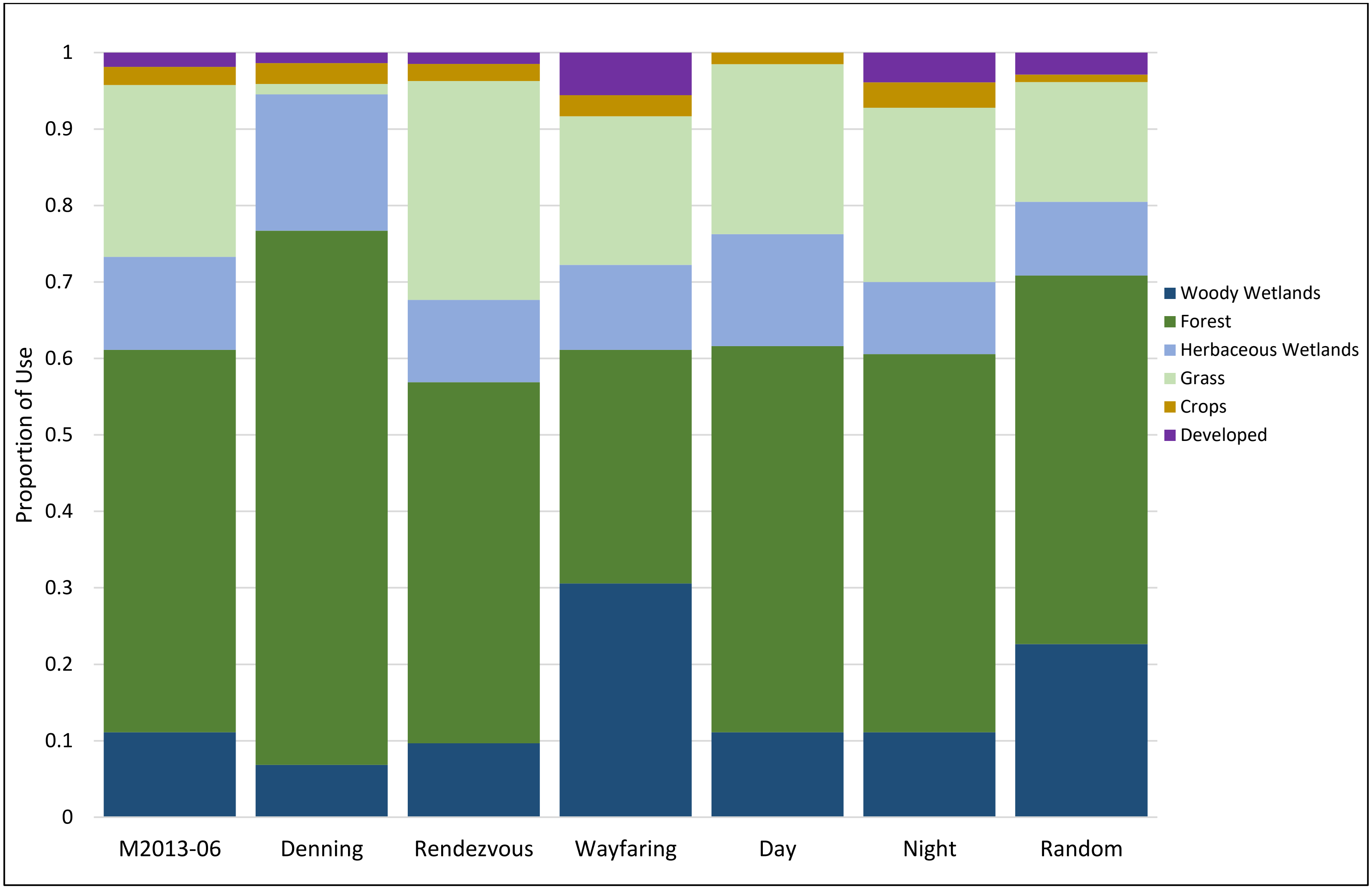


Figure 12e. Land class use frequency of wolf M2013-06 during each applicable season and each diel period compared to the availability of land classes (Random) within the individual 30km buffer based on the reclassified 2011 NLCD.

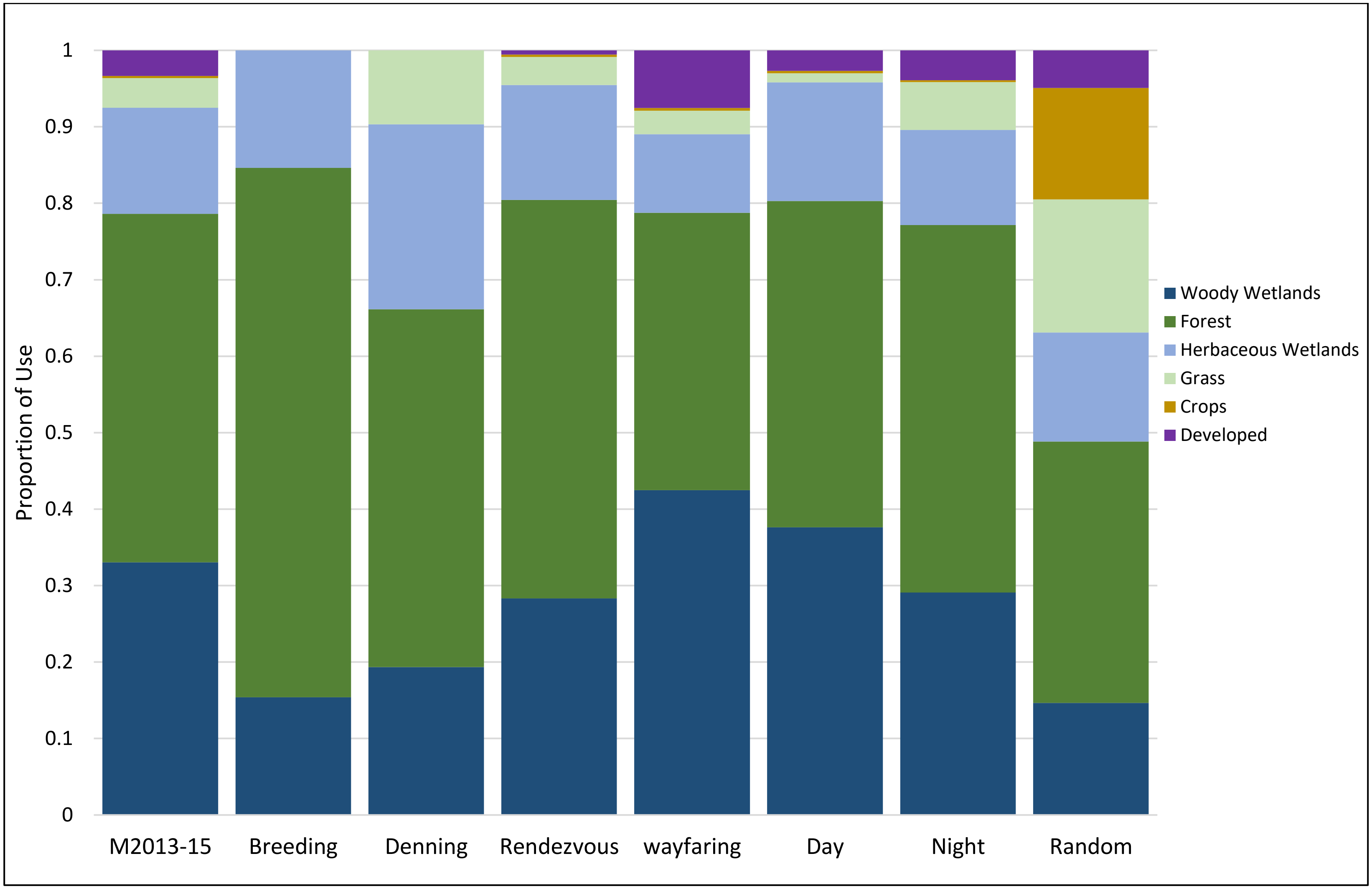


Figure 12f. Habitat use of wolf M2013-15 during each applicable season and each diel period compared to the availability of habitat (Random) within the individual 30km buffer based on the reclassified 2011 NLCD.

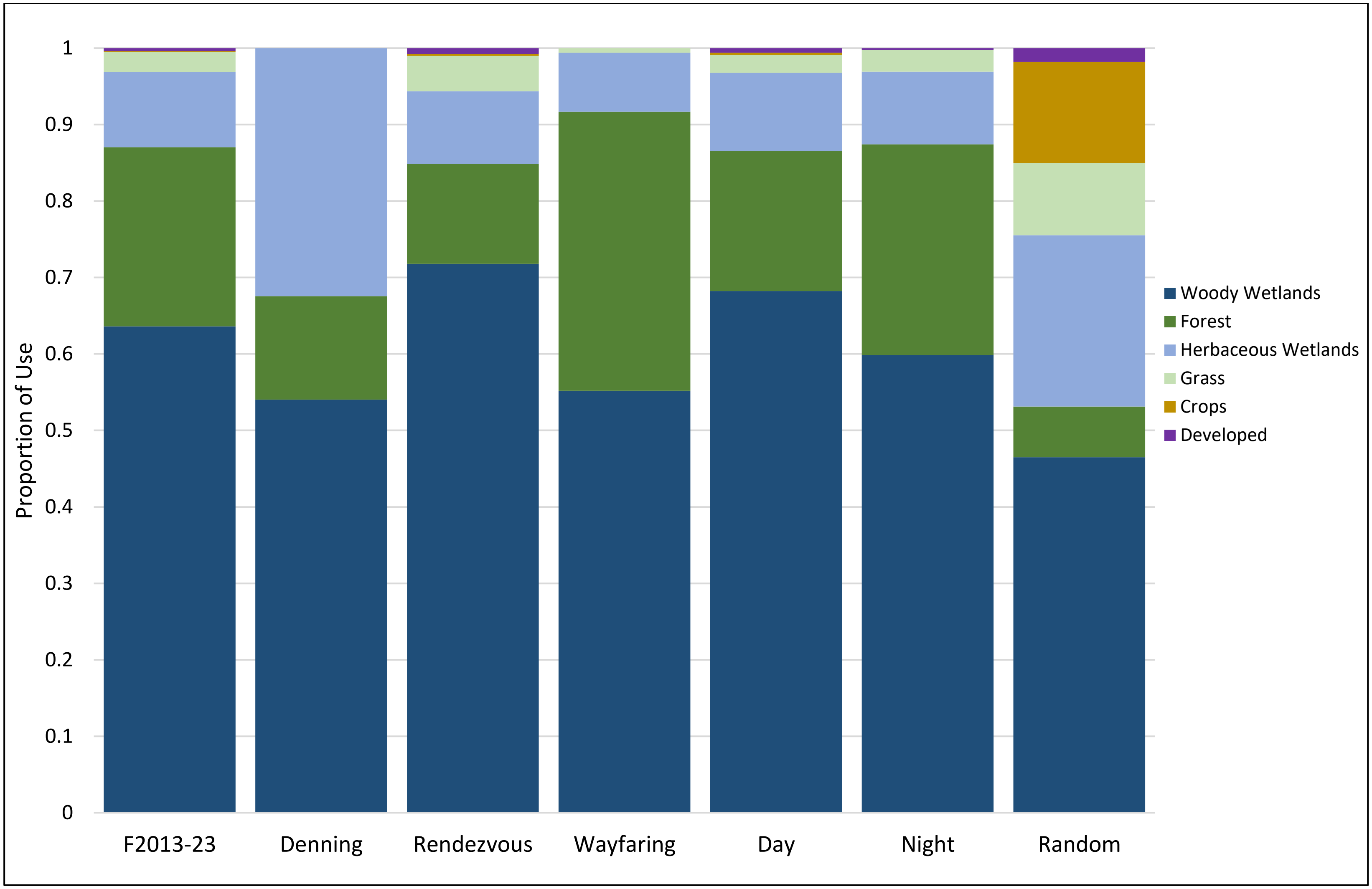


Figure 12g. Habitat use of wolf F2013-23 during each applicable season and each diel period compared to the availability of habitat (Random) within the individual 30km buffer based on the reclassified 2011 NLCD.

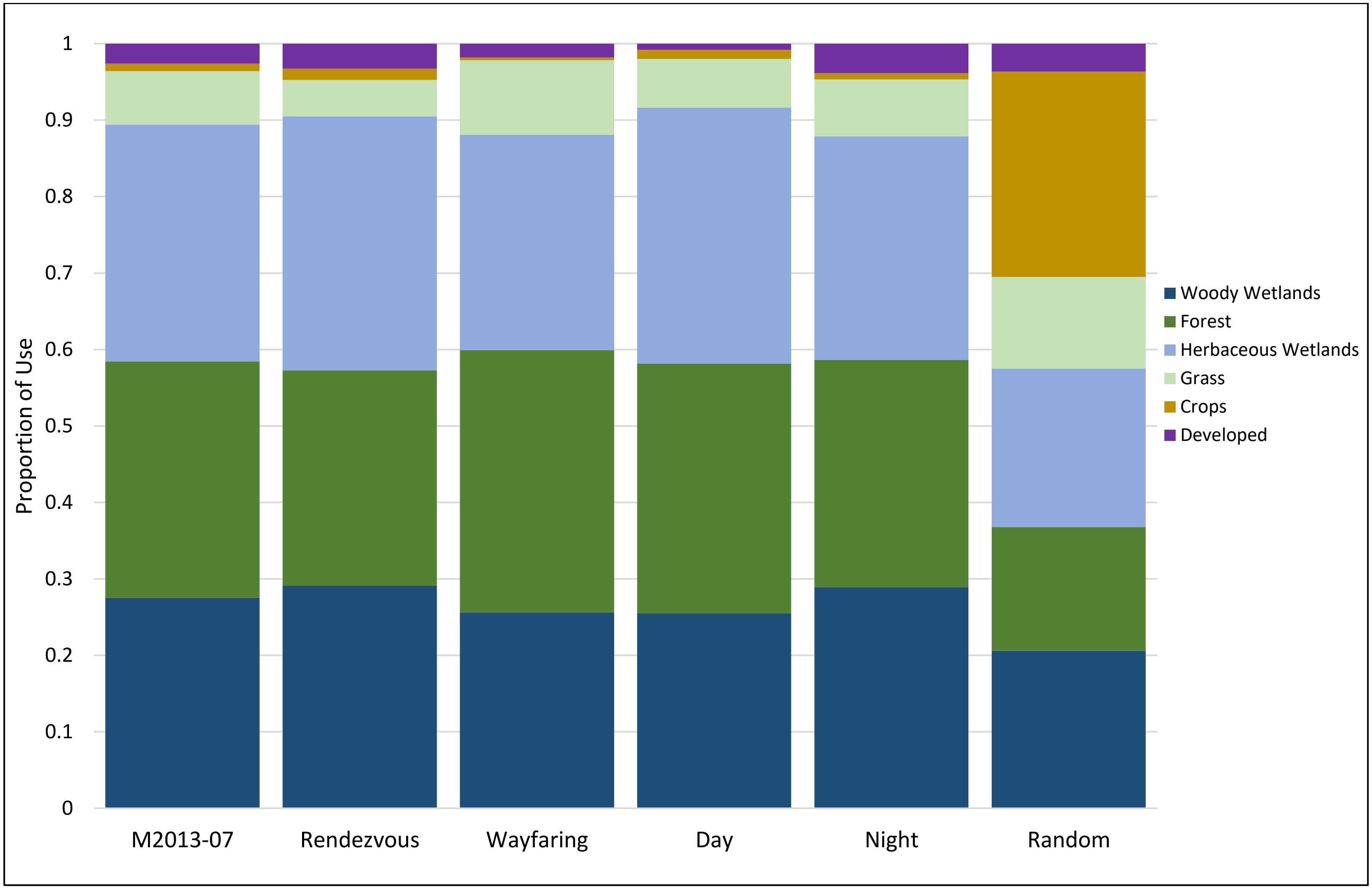


Figure 12h. Habitat use of wolf M2013-07 during each applicable season and each diel period compared to the availability of habitat (Random) within the individual 30km buffer based on the reclassified 2011 NLCD.

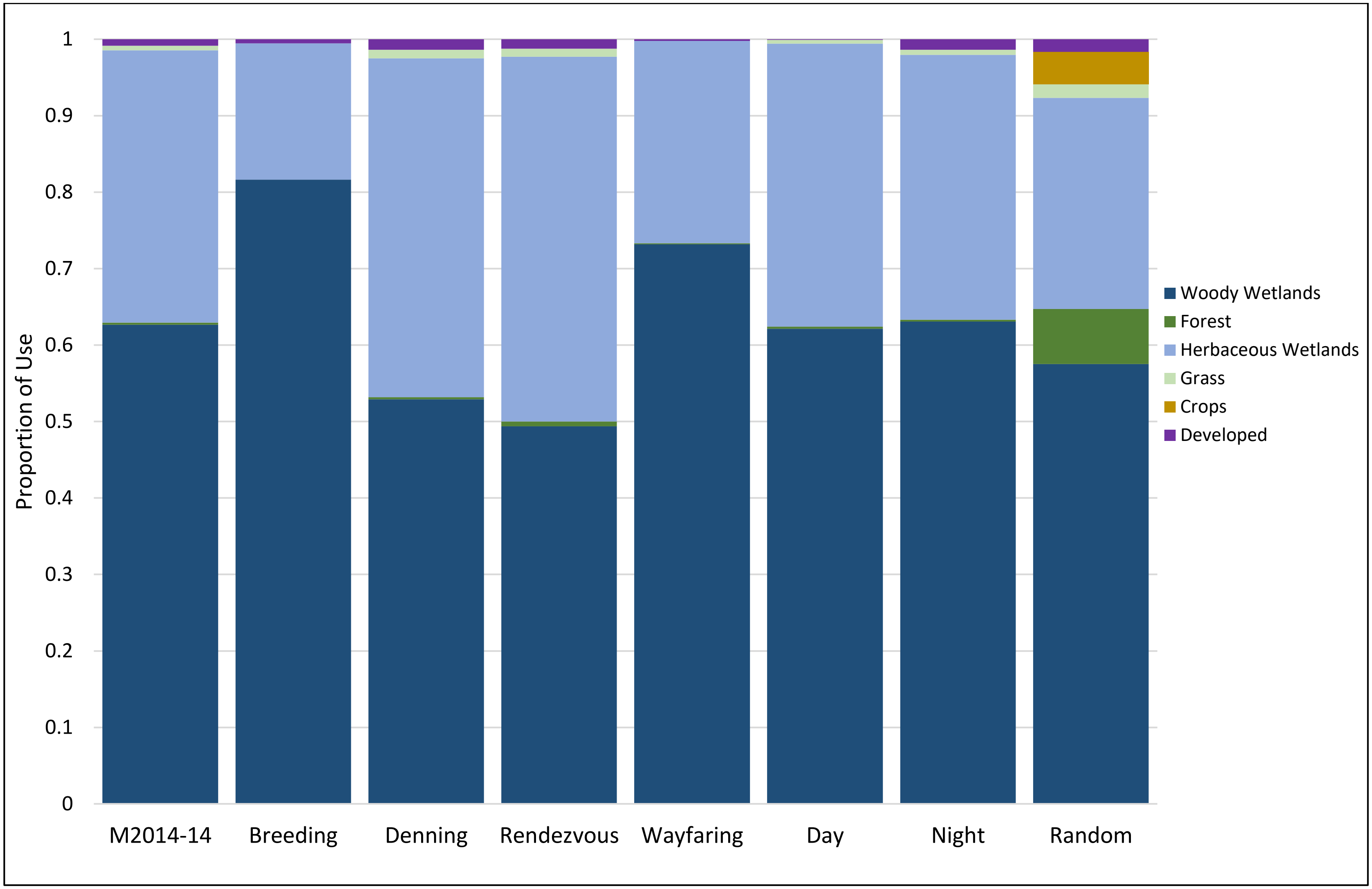


Figure 12i. Habitat use of wolf M2014-14 during each applicable season and each diel period compared to the availability of habitat (Random) within the individual 30km buffer based on the reclassified 2016 NLCD.

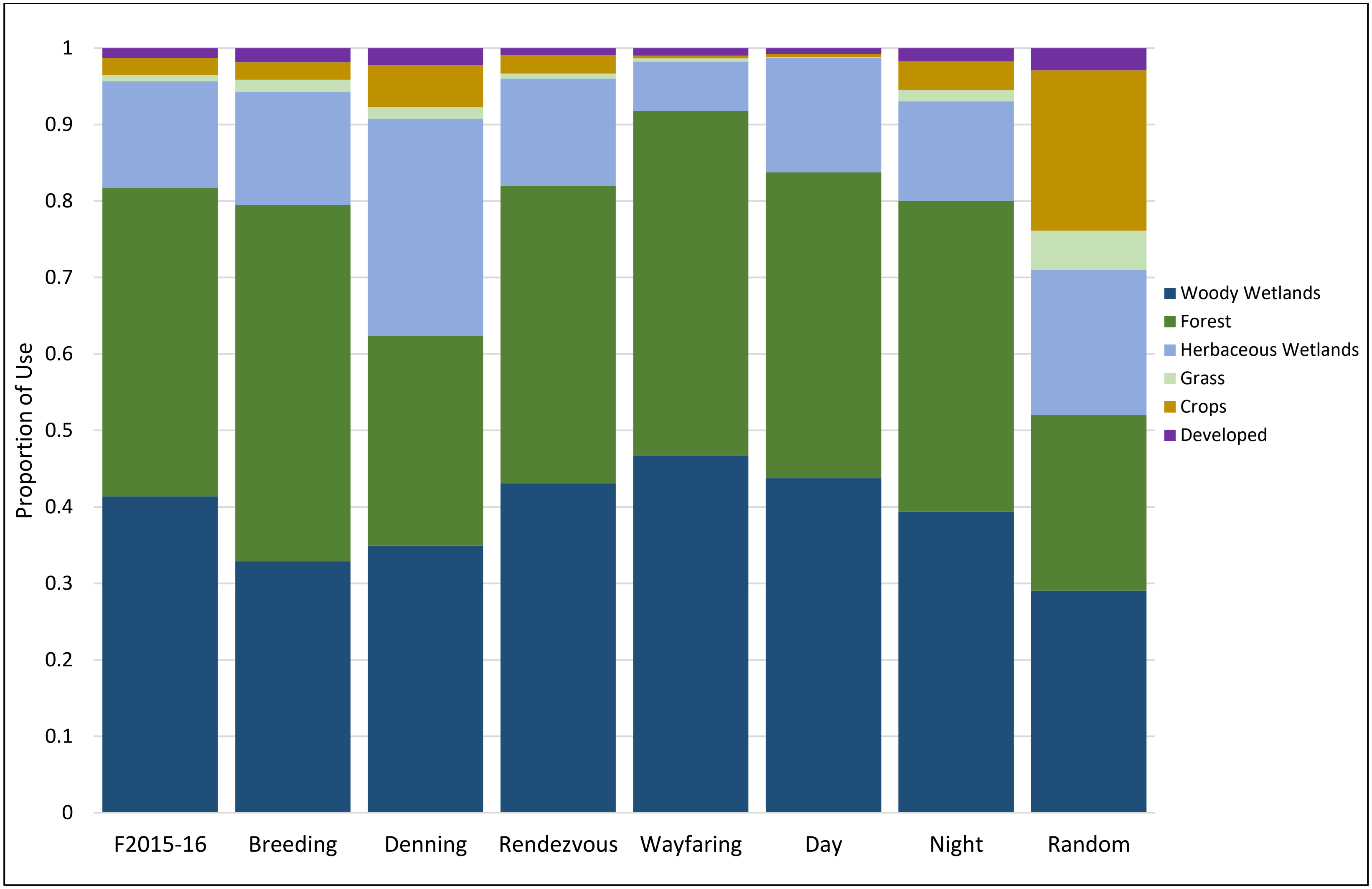


Figure 12j. Habitat use of wolf F2015-16 during each applicable season and each diel period compared to the availability of habitat (Random) within the individual 30km buffer based on the reclassified 2016 NLCD

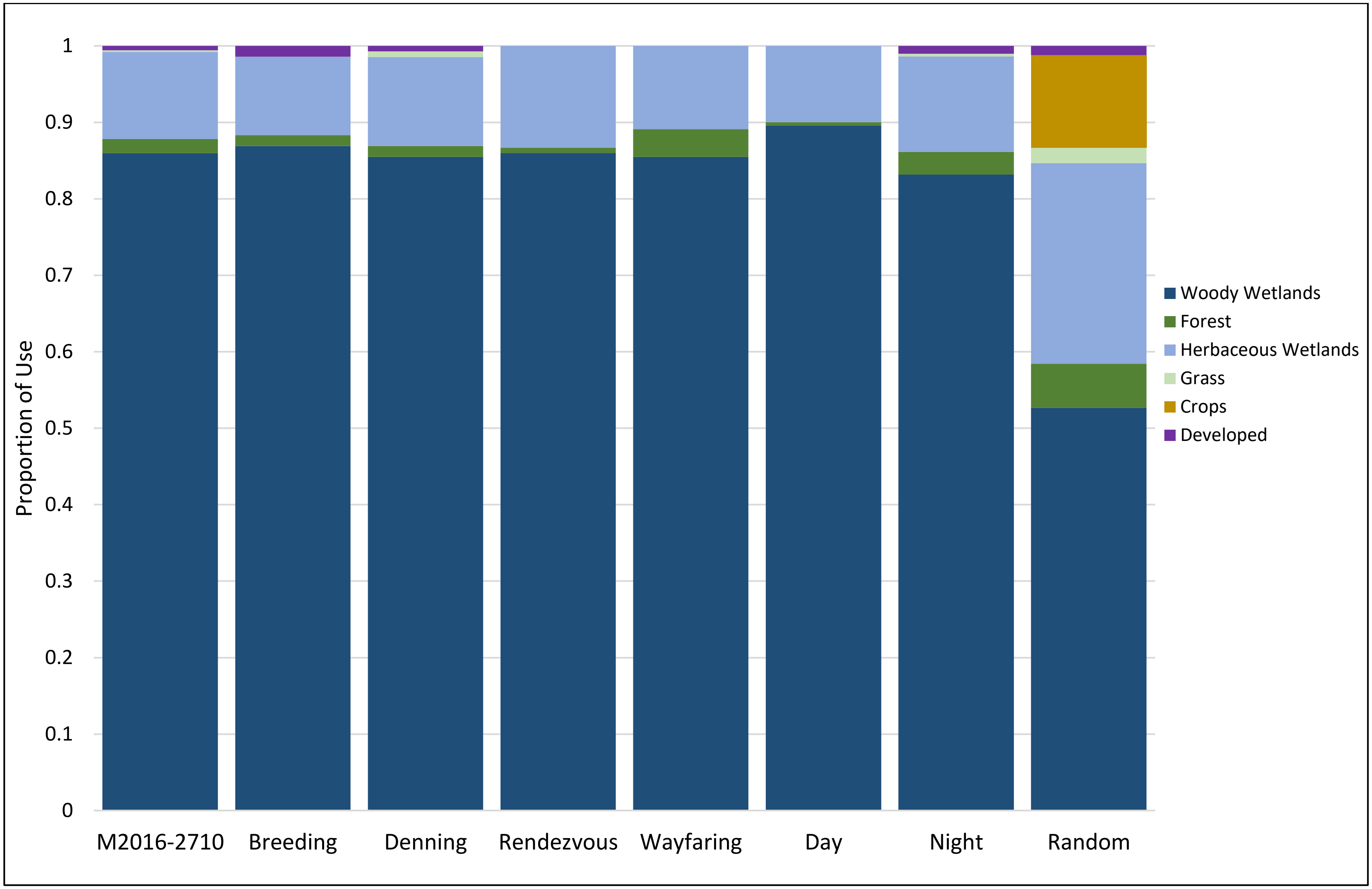


Figure 12k. Habitat use of wolf M2016-2710 during each applicable season and each diel period compared to the availability of habitat (Random) within the individual 30km buffer based on the reclassified 2016 NLCD.

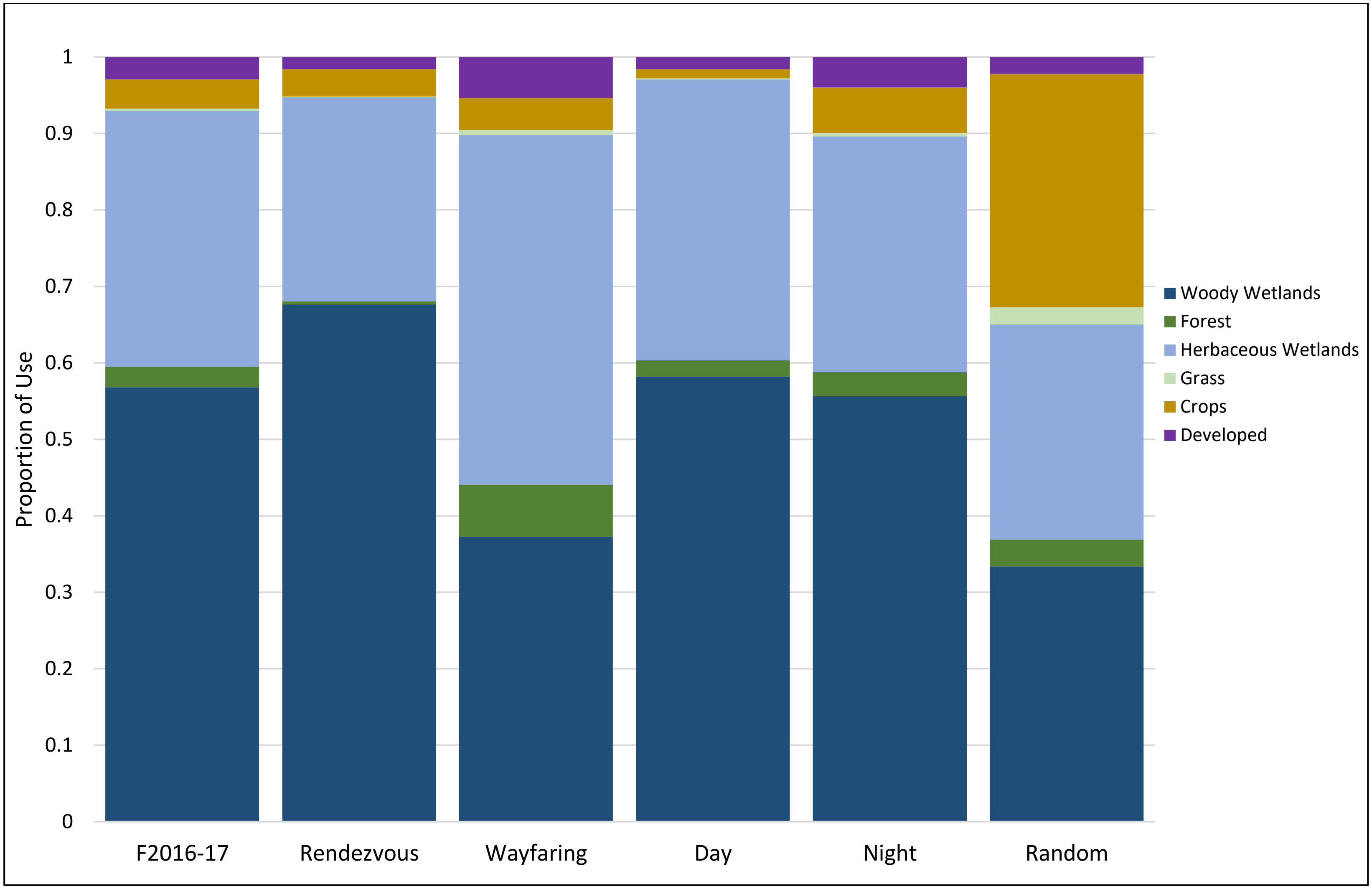


Figure 12l. Habitat use of wolf F2016-17 during each applicable season and each diel period compared to the availability of habitat (Random) within the individual 30km buffer based on the reclassified 2016 NLCD.

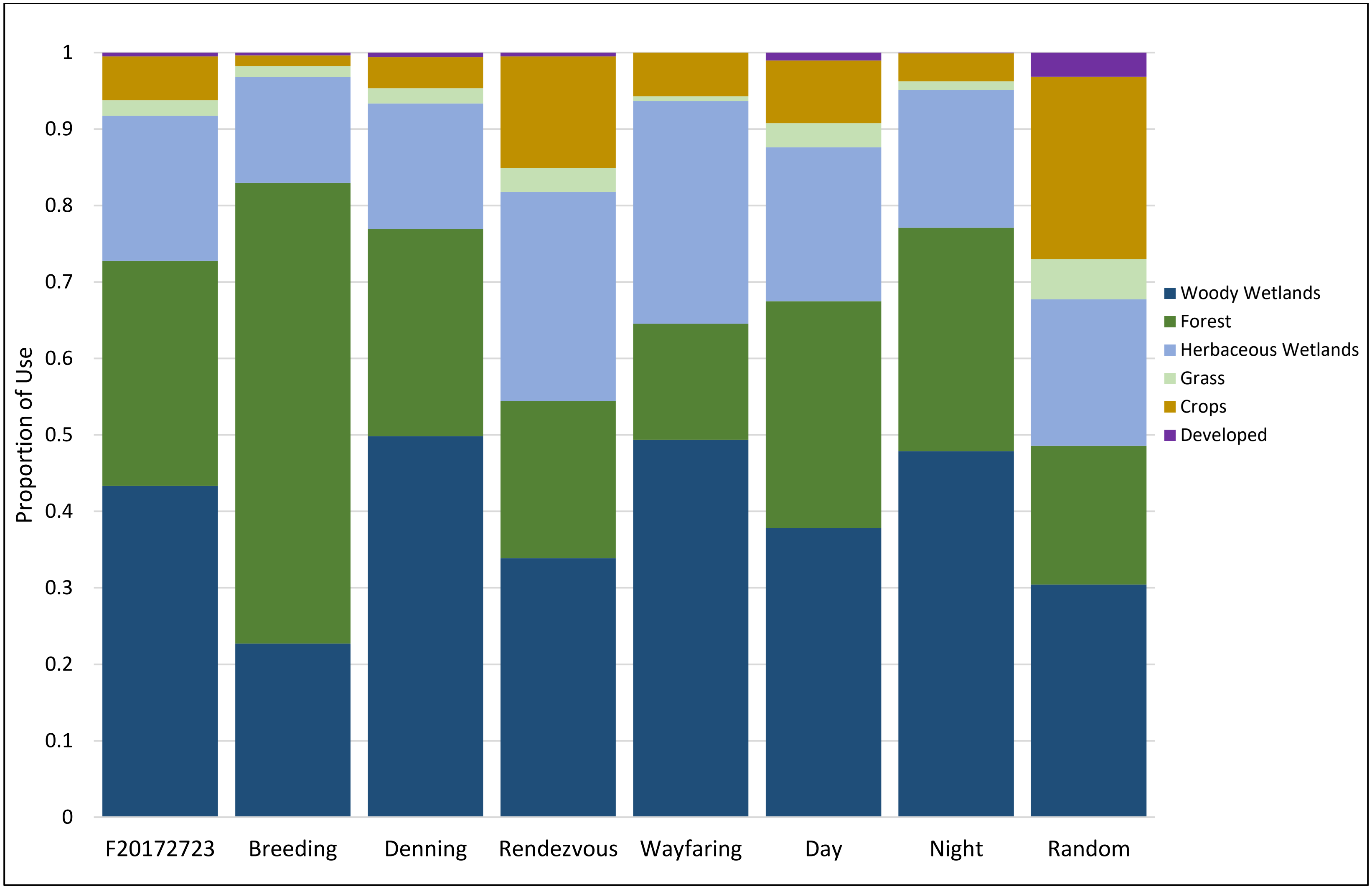


Figure 12m. Habitat use of wolf F2017-2723 during each applicable season and each diel period compared to the availability of habitat (Random) within the individual 30km buffer based on the reclassified 2016 NLCD.

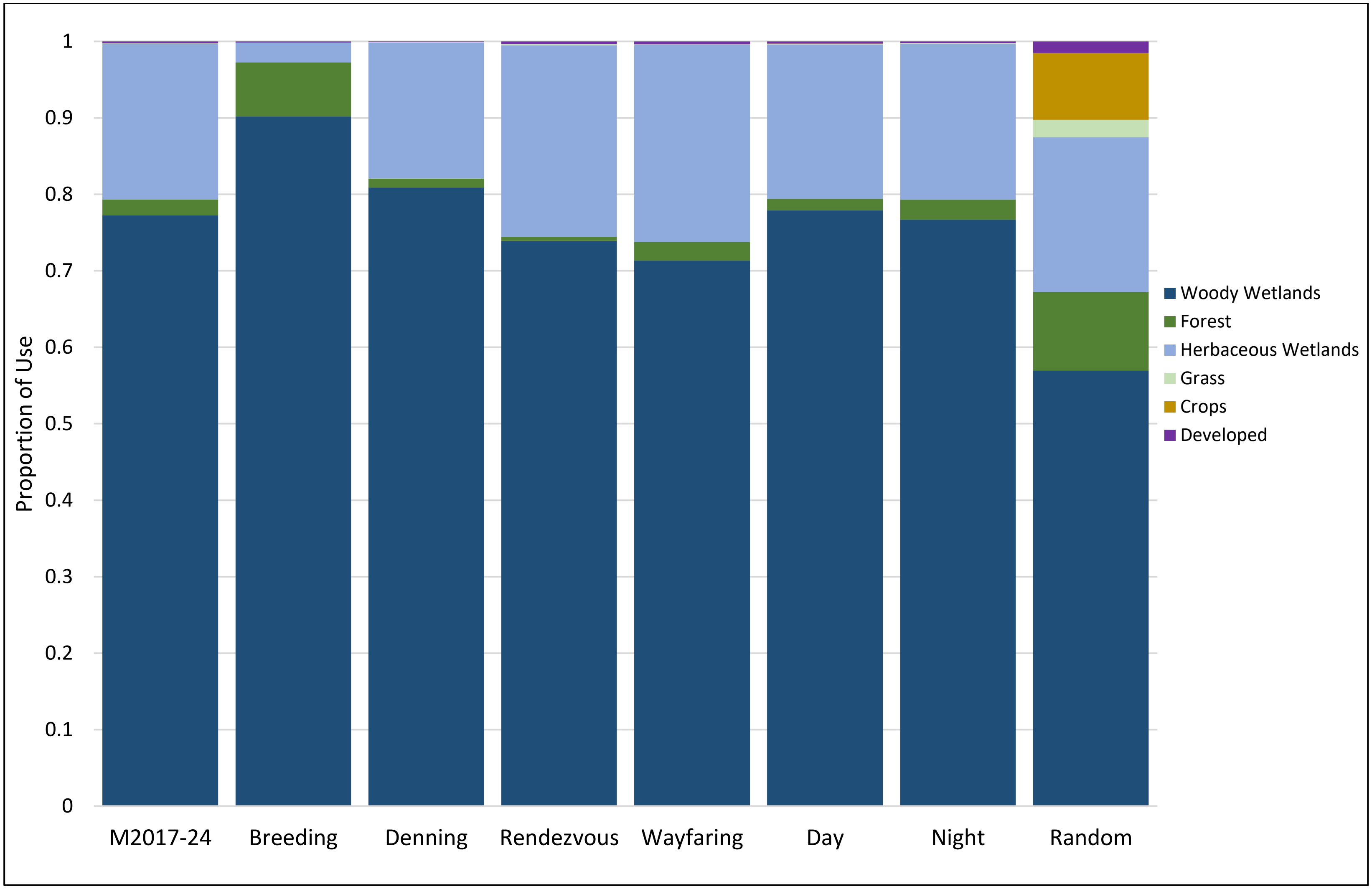


Figure 12n. Habitat use of wolf M2017-24 during each applicable season and each diel period compared to the availability of habitat (Random) within the individual 30km buffer based on the reclassified 2016 NLCD.

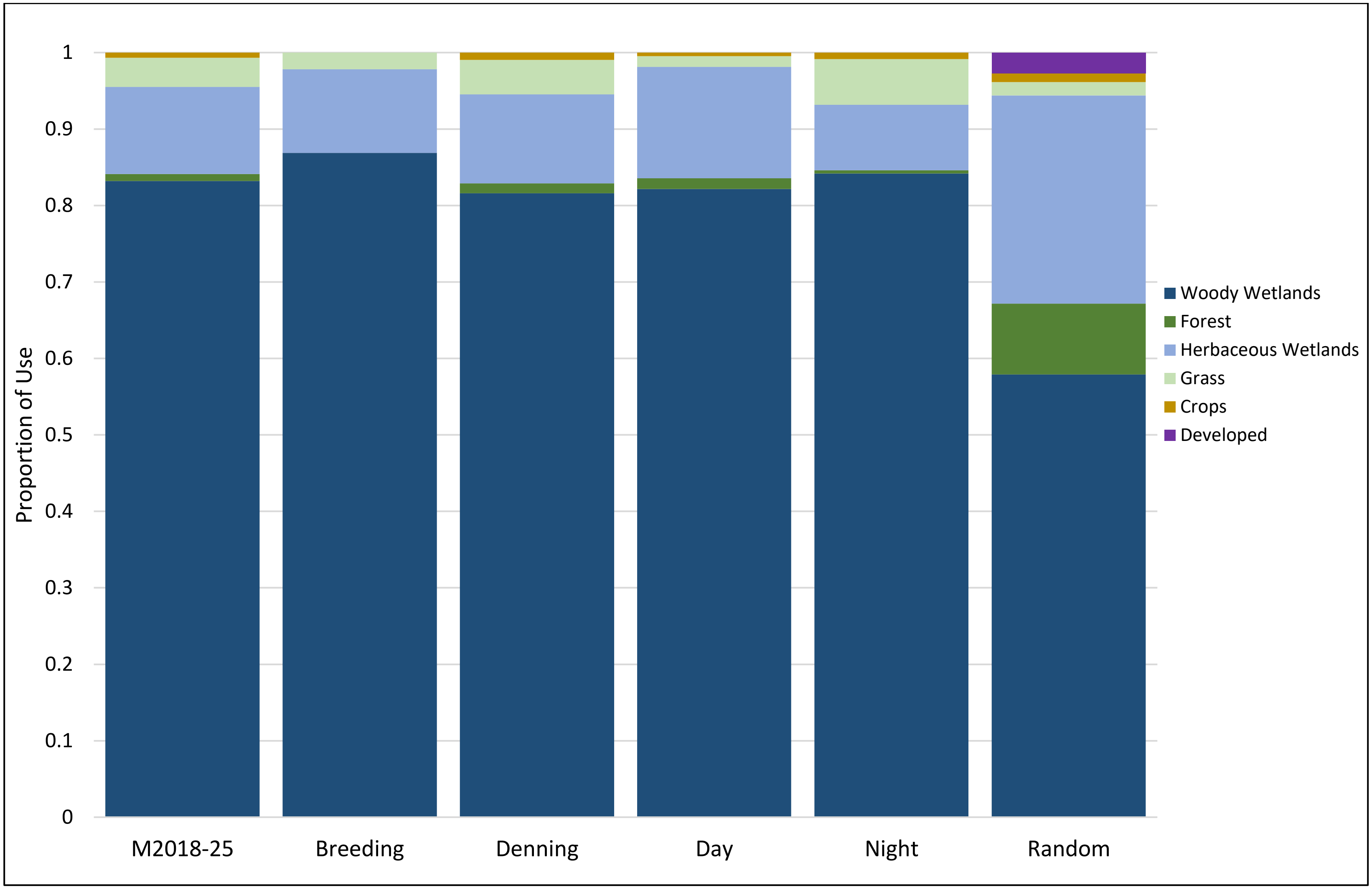
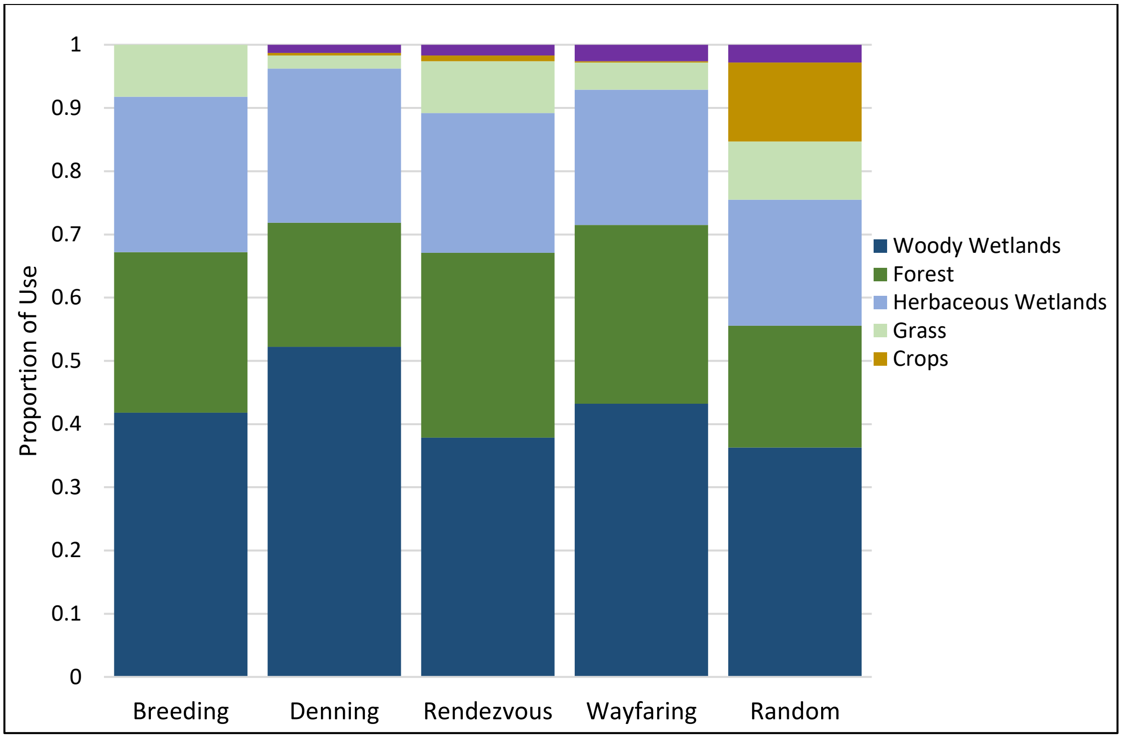
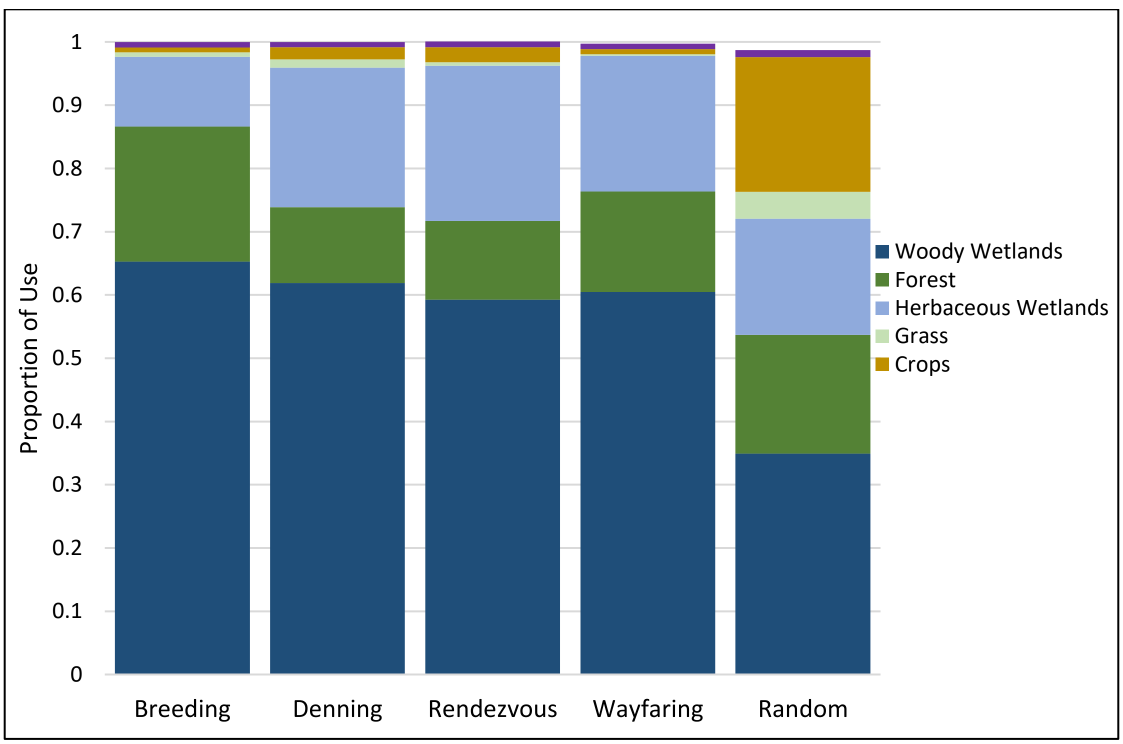


Figure 12o. Habitat use of wolf M2018-25 during each applicable season and each diel period compared to the availability of habitat (Random) within the individual 30km buffer based on the reclassified 2016 NLCD.

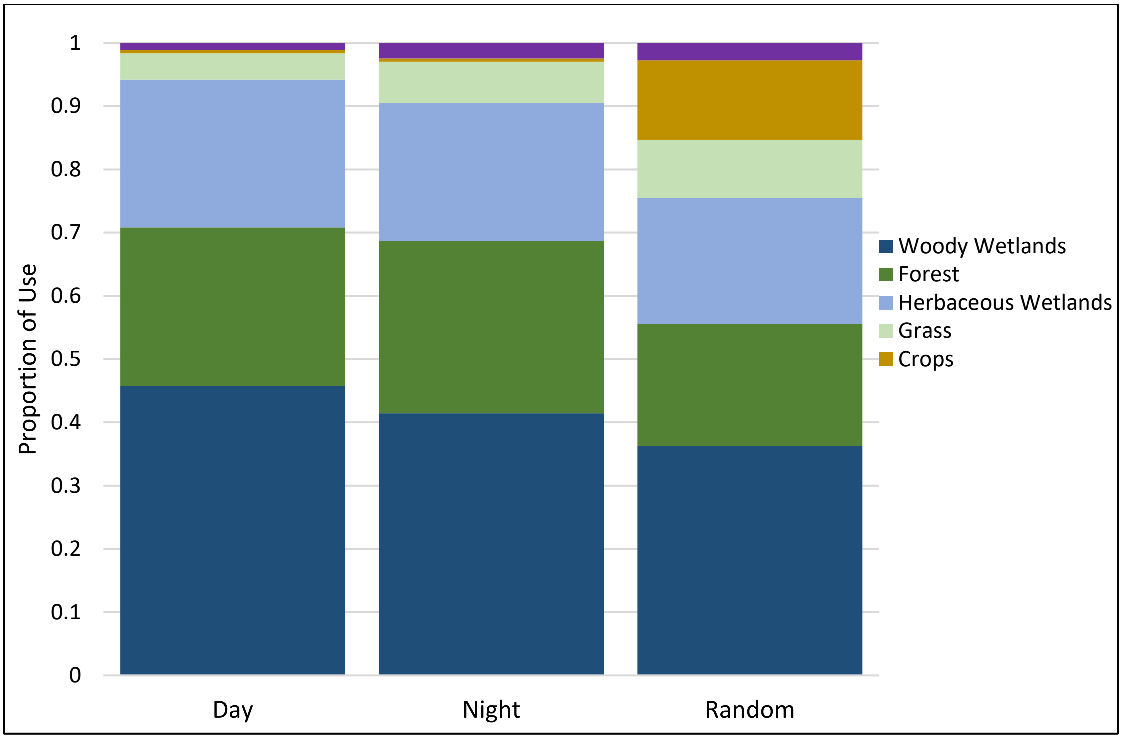


a.

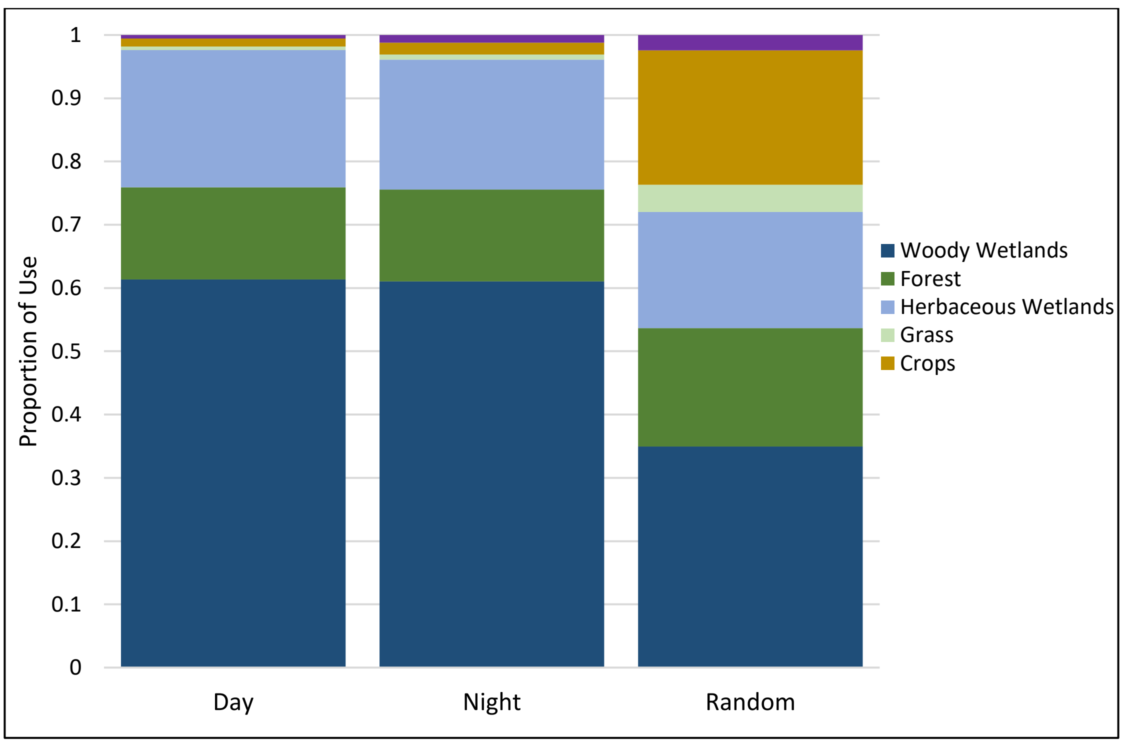


b.

Figure 13. Habitat use during each season within **a.** group 2011 and **b.** group 2016 compared to the availability of habitat (Random) within the 30km buffer based on the reclassified 2011 and 2016 NLCD, respectively.

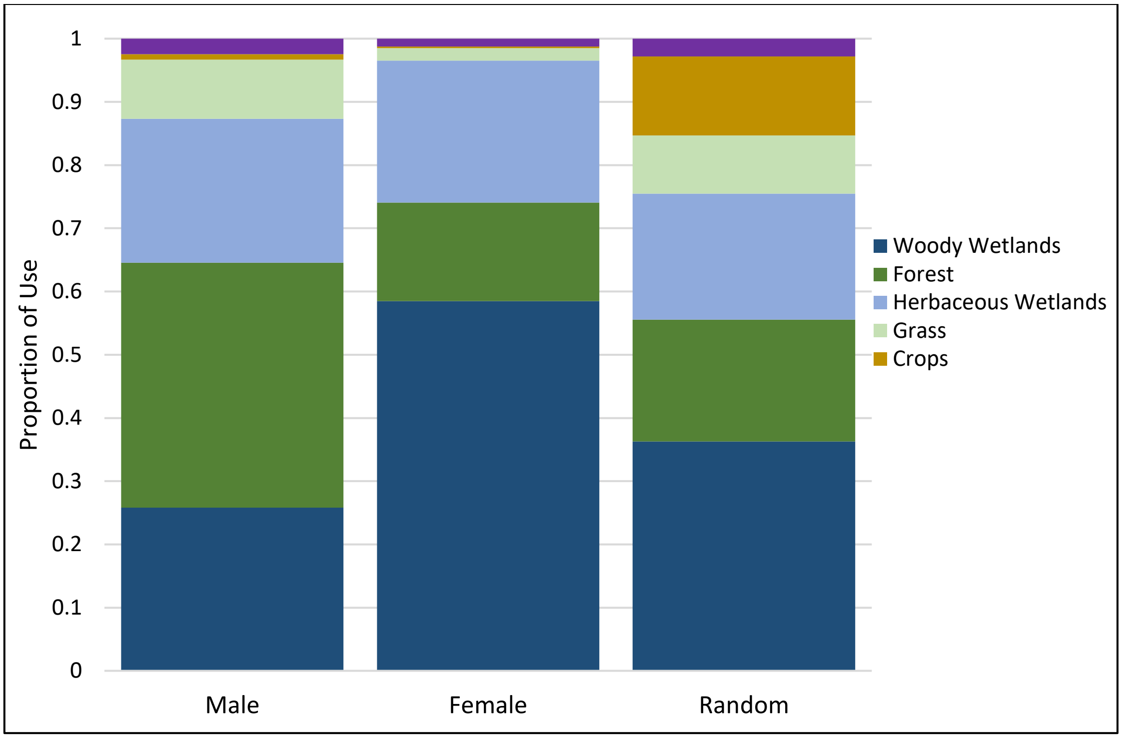


a.

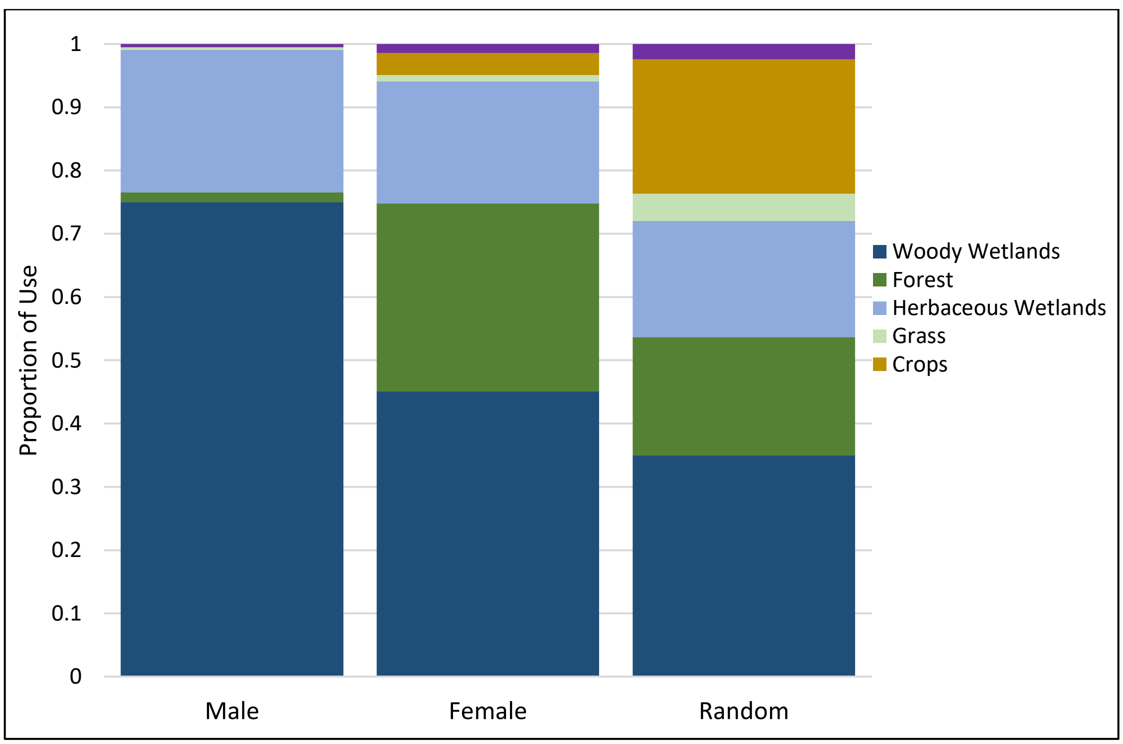


b.

Figure 14. Habitat use during each diel period within **a.** group 2011 and **b.** group 2016 compared to the availability of habitat (Random) within the 30km buffer based on the reclassified 2011 and 2016 NLCD, respectively.



a.



b.

Figure 15. Habitat use for each sex within **a.** group 2011 and **b.** group 2016 compared to the availability of habitat (Random) within the 30km buffer based on the reclassified 2011 and 2016 NLCD, respectively.

Appendix D

Model Selection Details for Testing for Habitat Selection and Effects on Speed

Table 15. The top individual level multinomial models for Red Lake Indian Reservation gray wolves in group 2011 based on Akaike's Information Criterion (AICc) and Akaike weights (ω_i). Predictor variables were all categorical fixed effects and included wolf (WF), season (SSN), and diel period (DP) as well as a season by diel period interaction. Response variable was land class at each relocation either from a wolf or from a randomly sampled point.

		Model Variables				log				Deviance	
Wolf	**Rank**	**WF**	**SSN**	**DP**	**K**	**Likelihood**	**AICc**	**ΔAICc**	ω_i	**Residual**	**Null**
M201201	1	+		+	3	-798.5	1627.9	0	0.335	1597.0	1682.9
	1			+	2	-798.5	1627.9	0	0.335	1597.0	1682.9
	2	+			2	-804.2	1628.8	0.85	0.219	1608.3	1682.9
F201322	1	+			2	-739.4	1499.1	0	0.942	1478.7	1542.4
F20132459	1	+			2	-2296.8	4613.7	0	0.244	4593.6	4848.6
	2	+		+	3	-2292.0	4614.2	0.48	0.191	4583.9	4848.6
	2			+	2	-2292.0	4614.2	0.49	0.191	4583.9	4848.6
	3	+	+		3	-2282.4	4615.4	1.73	0.103	4564.7	4848.6
	3		+		2	-2282.4	4615.4	1.73	0.103	4564.7	4848.6
F201304	1		+	+	3	-765.2	1571.7	0	0.467	1530.4	1581.8
	1	+	+	+	4	-765.2	1571.7	0	0.467	1530.4	1581.8
M201306	1		+	+	3	-1036.4	2124.5	0	0.393	2072.8	2164.0
	1	+	+	+	4	-1036.4	2124.5	0	0.393	2072.8	2164.0
M201315	1		+	+	3	-2136.2	4333.7	0	0.498	4272.4	4630.1
	1	+	+	+	4	-2136.2	4333.7	0	0.498	4272.4	4630.1
F201323	1		+		2	-1832.0	3704.5	0	0.427	3664.0	4057.6
	1	+	+		3	-1832.0	3704.5	0	0.427	3664.0	4057.6
M201307	1	+	+		3	-2004.9	4040.2	0	0.253	4009.8	4273.5
	1		+		2	-2004.9	4040.2	0	0.253	4009.8	4273.5
	2	+	+	+	4	-2000.2	4041.0	0.81	0.169	4000.3	4273.5
	2		+	+	3	-2000.2	4041.0	0.81	0.169	4000.3	4273.5

Table 16. The top individual level multinomial models for Red Lake Indian Reservation gray wolves in group 2016 based on Akaike's Information Criterion (AICc) and Akaike weights (ω_i). Predictor variables were all categorical fixed effects and included wolf (WF), season (SSN), and diel period (DP) as well as a season by diel period interaction. Response variable was land class at each relocation either from a wolf or from a randomly sampled point.

		Model Variables					**log**				**Deviance**	
Wolf	**Rank**	**WF**	**SSN**	**DP**	**SSN:DP**	**K**	**Likelihood**	**AICc**	**ΔAICc**	ω_i	**Residual**	**Null**
M201414	1		+	+		3	-4835.5	9731.4	0	0.495	9671.1	10304.6
	1	+	+	+		4	-4835.5	9731.4	0	0.495	9671.1	10304.6
F201516	1		+	+		3	-12204.4	24469.0	0	0.499	24408.8	26138.7
	1	+	+	+		4	-12204.4	24469.0	0	0.499	24408.8	26138.7
M20162710	1	+	+	+		4	-2904.5	5869.5	0	0.291	5808.9	6440.6
	1		+	+		3	-2904.5	5869.5	0	0.291	5808.9	6440.6
	2	+		+		3	-2920.0	5870.1	0.62	0.213	5840.0	6440.6
	3			+		2	-2920.0	5870.2	0.7	0.205	5840.0	6440.6
F201617	1	+	+	+		4	-4172.6	8385.5	0	0.332	8345.3	9142.8
	1		+	+		3	-4172.6	8385.5	0	0.332	8345.3	9142.8
	2	+	+	+	+	5	-4168.2	8386.9	1.37	0.168	8336.5	9142.8
	2		+	+	+	4	-4168.2	8386.9	1.37	0.168	8336.5	9142.8
F20172723	1	+	+	+	+	5	-6243.7	12578.4	0	0.456	12487.5	13276.8
	1		+	+	+	4	-6243.7	12578.4	0	0.456	12487.5	13276.8
M2014724	1	+	+			3	-9584.4	19218.9	0	0.397	19168.8	20715.0
	1		+			2	-9584.4	19218.9	0	0.397	19168.8	20715.0
M201825	1	+		+		3	-837.9	1706.2	0	0.329	1675.7	1800.7
	1			+		2	-837.9	1706.2	0	0.329	1675.7	1800.7
	2	+				2	-843.8	1707.8	1.54	0.152	1687.5	1800.7

Table 17. The top population level multinomial models for Red Lake Indian Reservation gray wolves in group 2011 and group 2016 based on Akaike's Information Criterion (AICc) and Akaike weights (ω_i). Predictor variables were all categorical fixed effects and included wolf (WF), season (SSN), diel period (DP), and sex (SEX) as well as all two way interactions. Response variable was land class at each relocation either from a wolf or from a randomly sampled point.

		Model Variables								log				Deviance	
Group	**Rank**	**WF**	**SSN**	**DP**	**SEX**	**ID:SSN**	**ID:DP**	**SSN:DP**	**K**	**Likelihood**	**AICc**	**ΔAICc**	**ω_i**	**Residual**	**Null**
2011	1	+	+	+	+	+			6	-12479.35	25212.20	0.00	0.494	24958.69	27367.70
	2	+	+	+		+			5	-12479.35	25212.21	0.01	0.490	24958.71	27367.70
	3	+	+	+		+	+		6	-12447.44	25321.11	8.42	0.007	24894.88	27367.70
2016	1	+	+	+		+	+		6	-42902.85	86127.10	0.00	0.918	85805.70	98744.87
	2	+	+	+		+	+	+	7	-42890.27	86132.30	5.12	0.071	85780.53	98744.87
	3	+	+	+	+	+	+	+	8	-42892.51	86136.80	9.61	0.008	85785.03	98744.87

Table 18. The top 3 linear mixed models for Red Lake Indian Reservation gray wolf speed based on Akaike's Information Criterion (AICc) and Akaike weights (ω_i). Predictor variables were all categorical and included land class (LC), season (SSN), diel period (DP), and sex (SEX), as well as all 2-way interactions as fixed effects and wolf as a random effect. Response variable was $\log_{10}$ transformed speed at each relocation timestamp derived from continuous-time movement models. Null deviance = -6780.38.

	Model Variables								log				Residual
Rank	**LC**	**SSN**	**DP**	**SEX**	**SSN:DP**	**SSN:SEX**	**DP:SEX**	**K**	**Likelihood**	**AICc**	**ΔAICc**	**ω_i**	**Deviance**
1	+	+		+		+		5	3437.78	-6845.50	0.00	0.44	-6875.56
2	+							2	3430.51	-6845.00	0.52	0.34	-6861.01
3	+	+	+	+	+	+	+	8	3441.51	-6842.90	2.57	0.12	-6883.02

Appendix E

Boxplots Depicting Variation in Gray Wolf Speed Across Various Categories

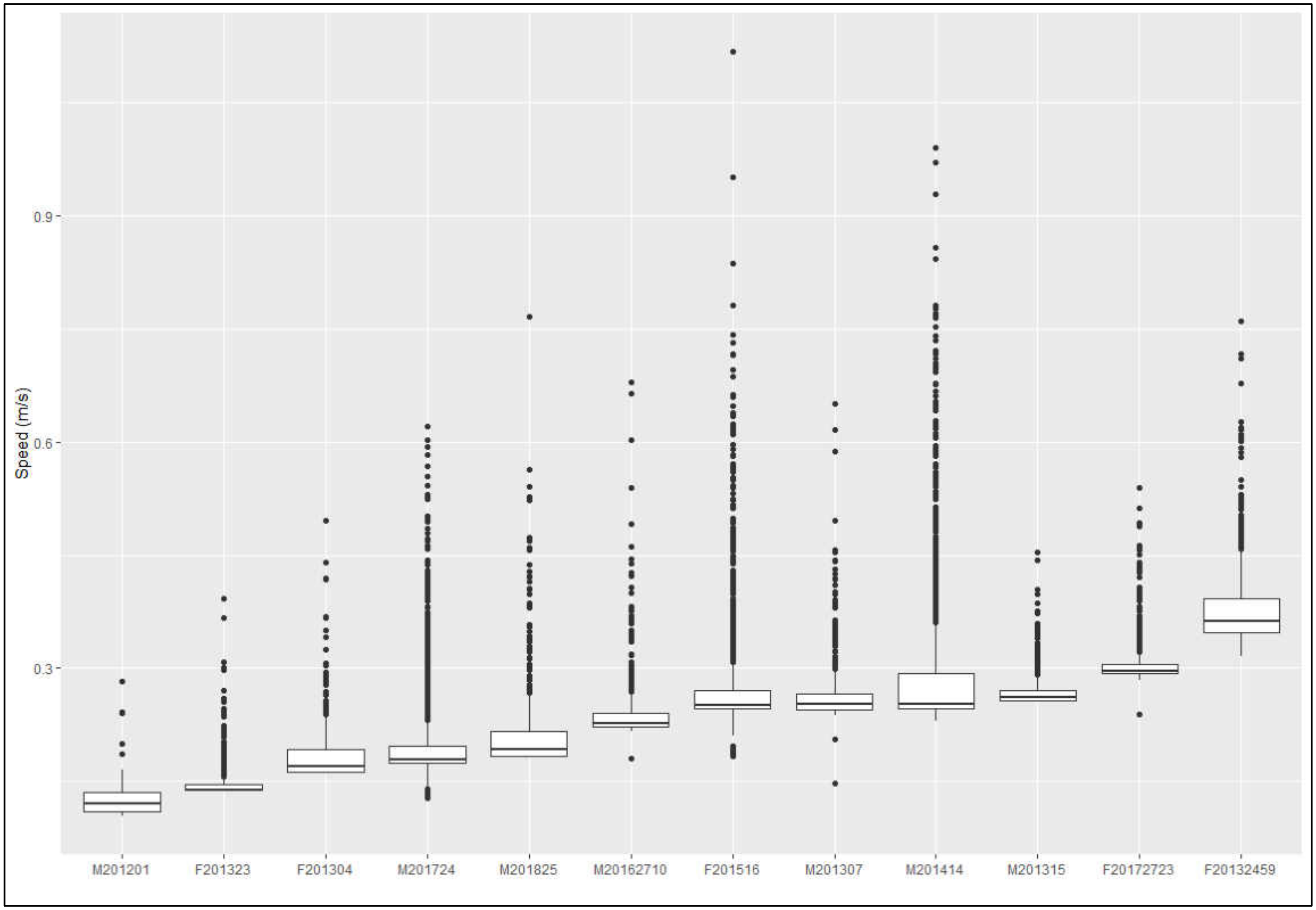


Figure 16a. Variation of speed of gray wolves on Red Lake Indian Reservation.

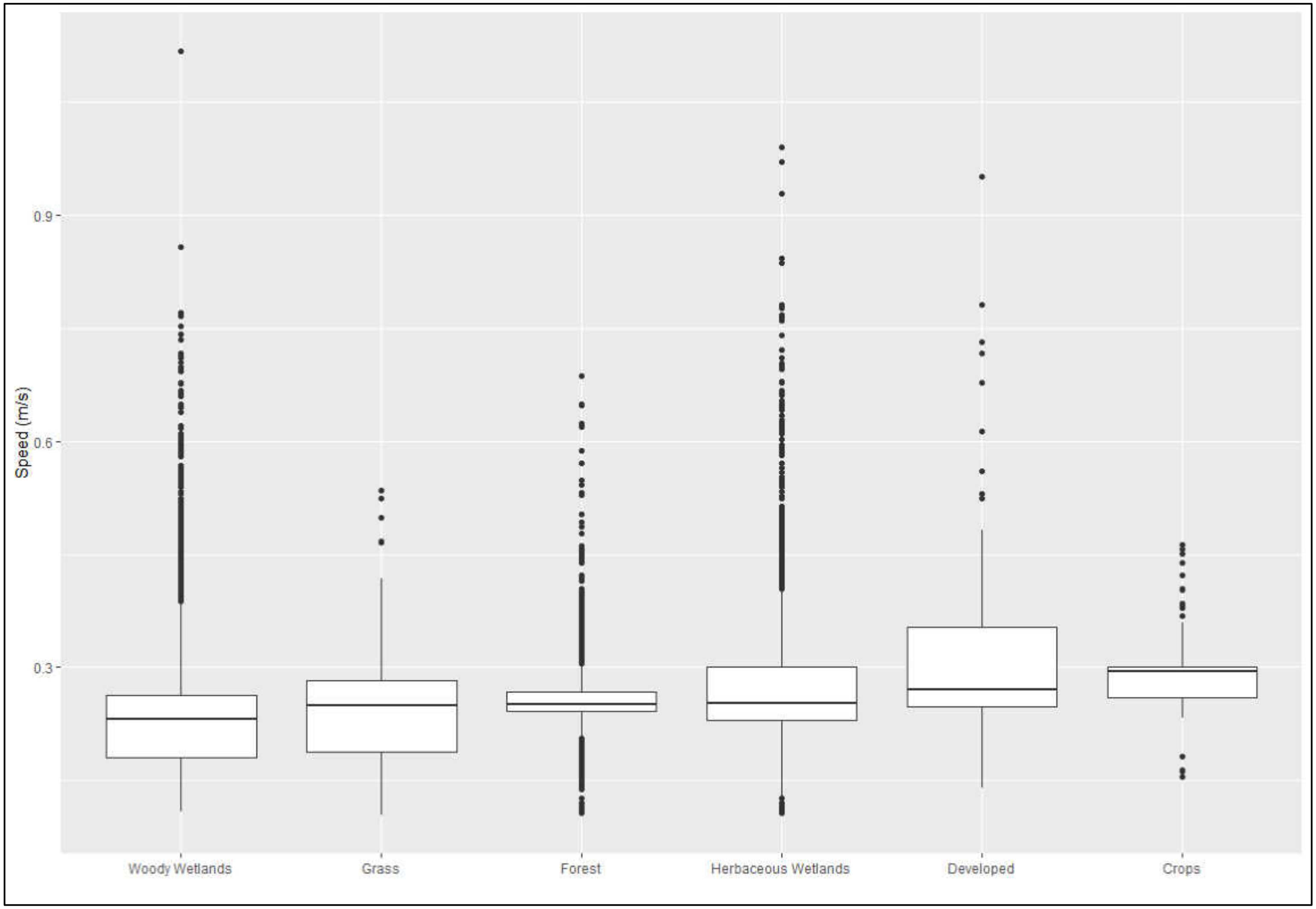


Figure 14b. Variation of speed of gray wolves on Red Lake Indian Reservation across land classes.

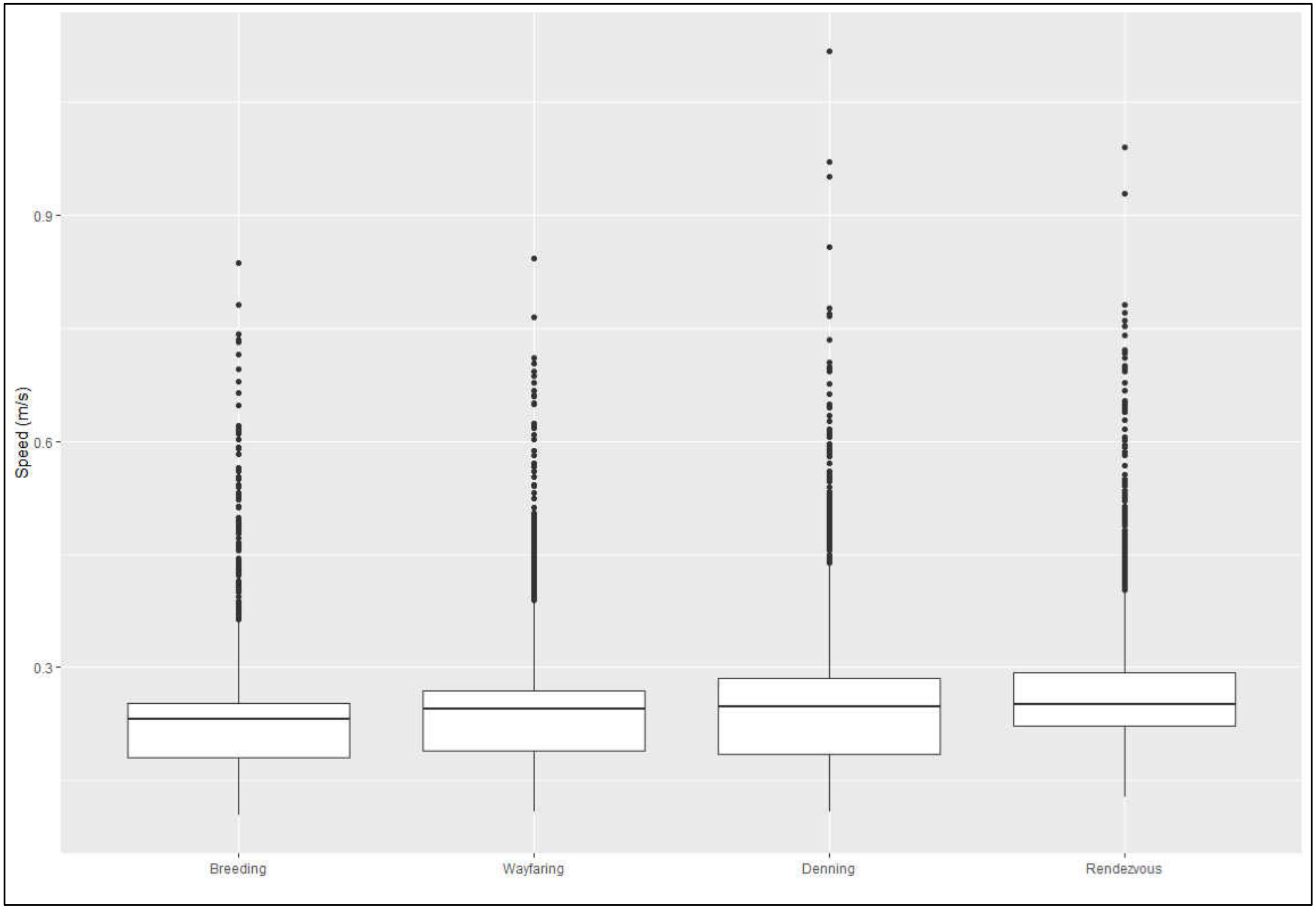


Figure 14c. Variation of speed of gray wolves on Red Lake Indian Reservation across seasons.

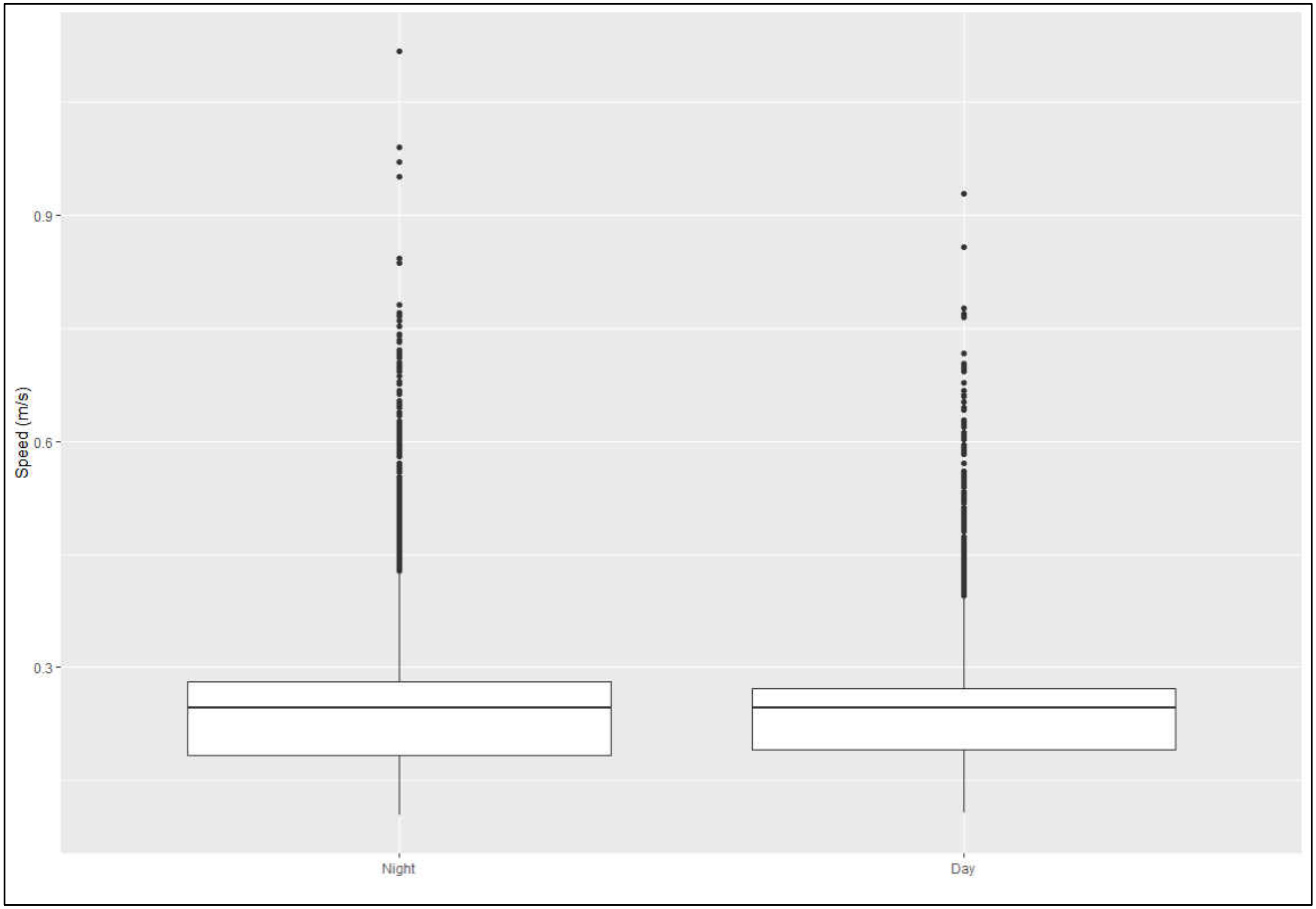


Figure 14d. Variation of speed of gray wolves on Red Lake Indian Reservation across diel periods.

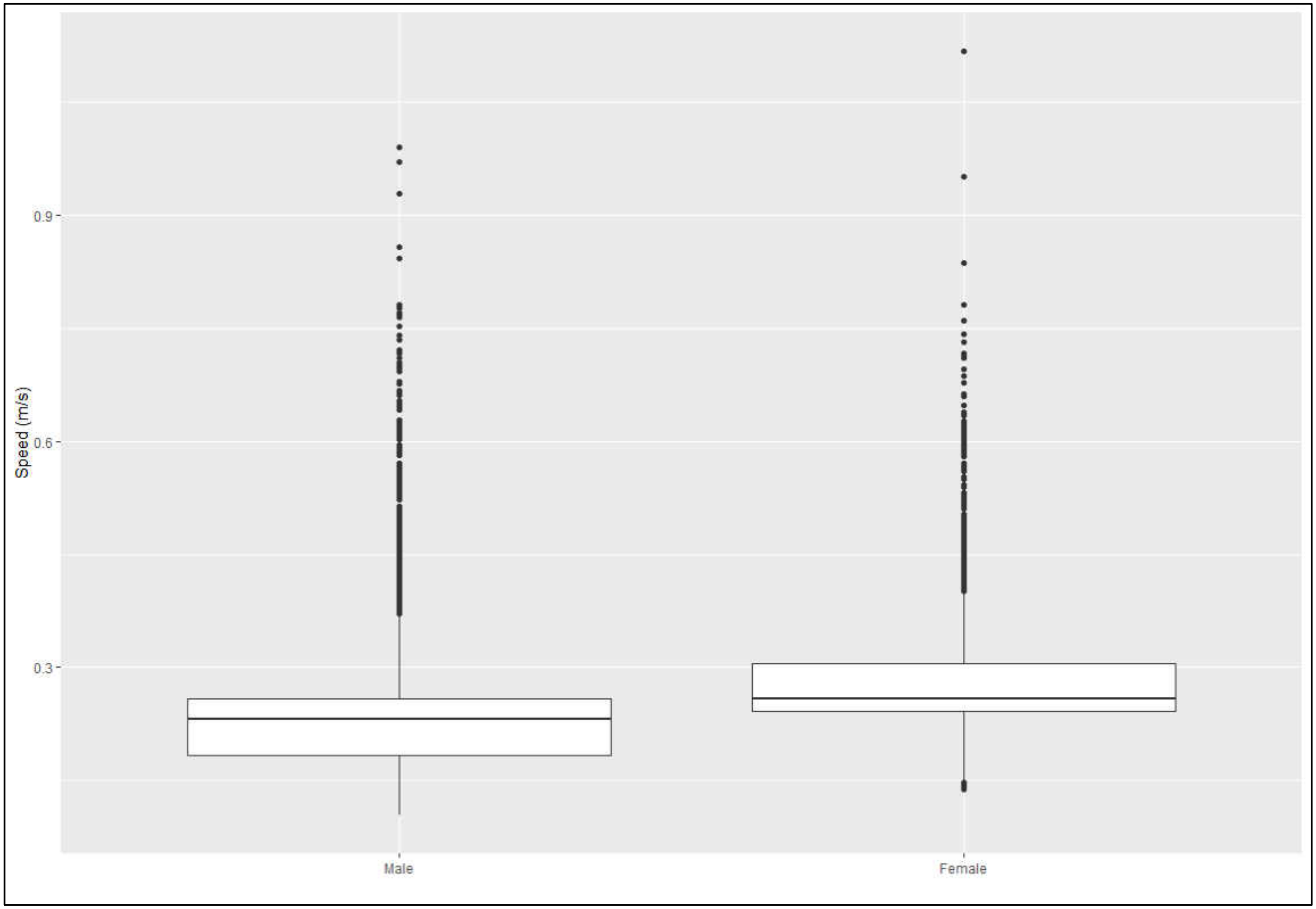


Figure 14e. Variation of speed of gray wolves on Red Lake Indian Reservation across sexes.