# American black bears: Strategies for living in a fragmented, agricultural landscape

A DISSERTATION
SUBMITTED TO THE FACULTY OF
UNIVERSITY OF MINNESOTA
BY
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IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

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August 2014

# Acknowledgements

Funding for this research was provided by the Minnesota Department of Natural Resources, University of Minnesota Graduate School, Minnesota Corn Growers Association, American Society of Mammalogists, the Bell Museum of Natural History, and the Rice Lake Area Sportsmen.

I would like to thank J. Huener, R. Prachar of the Minnesota DNR and G. Knutsen of the US Fish and Wildlife Service for housing us and providing support in the field. I'm grateful for the hard work of the technicians who helped me in the field: S. Rettler, D. Paige, T. Enright, A. Tri, M. Lyons, and M. Elfelt. A special thank you to K. Noyce, T. Laske and P. Iaizzo for the incredible amount of work, data sharing and collaboration during the course of this project. They helped to make the work even more enjoyable. Further acknowledgements specific to the work completed for each chapter can be found after the Discussion section of each.

There is little doubt this experience was greatly enhanced through the great friends I have made here: A. Swanson, J. Jungers, J. Keville, J. Vincent, H. Martin, M. Beck, L. Wallace, S. Stapleton, and L. Scotson just to name a few. Without the support and encouragement from S. Thompson, even when the enormity of the task put me in a bad mood, much of this would not have been accomplished. In addition, the four-legged friends that have been a part of my life (Bernard and Avalon) have been the best mood enhancers and reminders to relax and play from time to time I could have asked for.

My graduate committee was extremely insightful and supportive throughout the years. My advisors, Dr. Burk and Dr. Garshelis, took a major risk by accepting a recovering finance worker to a wildlife study and for that I am extremely grateful. Dr. Fieberg has been very generous with his time and provided great hands-on help and direction. I see a great future in syrup feeding to bears in case the "stats thing" doesn't work out. Dr. Arnold and Dr. Forester have offered insightful advice and encouragement throughout the years.

# Dedication

This dissertation is dedicated to my parents who supported my decision to do a career 180 and the man in Alaska only known in my stories as “Edgar Allan Busdriver.” He helped to encourage the change by mocking my life choices to move to Manhattan and work in economic consulting (something I was very proud of at the time) and planted the seeds of doubt that I was not meant to chase money for my career, but instead pursue my true passions, the ecology and conservation of wild things and places.

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# PREFACE

The general introduction provides the background motivation for this study and offers an overview of the larger scientific picture for which this dissertation fits into. The first three chapters of this dissertation represent manuscripts that are submitted for publication in a specific journal, and formatting within each chapter was done to meet the requirements of the specific journal. However, any citations to a chapter within this dissertation were altered to include the chapter number (e.g. Ditmer 2014, chapter X). The fourth chapter is intended for submission but does not follow a specific journal's formatting requirements. Each of these publications will have one or more coauthors, so plural pronouns are used throughout, but as senior author I am responsible for the content of each chapter. Chapter 1, "Foraging patterns by the American black bear in an agricultural landscape" was submitted for peer review during July 2014. Chapter 2, "Do innate food preferences and learning affect crop raiding by American black bears?" was submitted in July 2014. Chapter 3 "Behavioral and physiological responses of American black bears to landscape features within an agricultural region" was submitted in July 2014.

# INTRODUCTION

Understanding how species respond to anthropogenic features and alterations to their habitat is paramount for conservation because few places on earth remain unaffected by the expanding global footprint of humans. Anthropogenic influences to habitat including energy development, conversion to farmland, urbanization, road building, and climate change can lead to habit fragmentation. Fragmentation is a process where continuous suitable habitat is broken up into smaller parcels of varying sizes and shapes (Fahrig 2003). Fragmented landscapes require individuals to navigate among the remaining fragments to acquire necessary resources. Ultimately, fragments can become too small and widely separated to support some species (Pimm et al. 1988). Conservation biologists have long focused efforts on understanding the impacts of fragmentation on species (MacArthur and Wilson 1967) because it is critical to understand how to best manage and protect remaining habitat. However, few large-scale studies have been able to directly quantify the impacts of fragmentation on individuals and populations (Harrison and Bruna 1999).

Additionally, fragmentation or loss of habitat can alter or reduce the range limits of a species. Animals living at the edge of their range yield important insights into the requisites for species persistence and how they respond to human activities (Pe'er et al. 2014). It was previously assumed that animals living at the periphery of their range must suffer reduced fitness. However, recent research suggests that individuals can thrive even where the margins of primary range recede into fragmented habitat patches, if habitat quality remains high (Sexton et al. 2009).

The American black bear (*Ursus americanus*) is a forest-dwelling species, but also an ecological opportunist. Black bears' diverse and adaptable diet, (Garshelis and Noyce 2008) coupled with their high mobility enables them to persist from the shrublands of Mexico to the boreal forests of Canada. Black bear numbers across North America have increased in recent decades (Garshelis and Hristienko 2006) and populations in many regions have expanded in geographic range (Frary et al. 2011, Lackey et al. 2013, Scheick and McCown 2014) or re-colonized historical range (Hristienko and McDonald 2007). Many newly established populations of bears are thriving in areas once assumed to be uninhabitable and dominated by anthropogenic features (Lyons 2005, Baruch-Mordo et al. 2008, Shivik et al. 2011). Black bears general tolerance for, and even attraction to, human-dominated areas enable them to exploit several types of food that result from human activities, such as productive habitat edges created during forest fragmentation (Rogers and Allen 1987; Hellgren et al. 1991), garbage disposal sites (Baruch-Mordo 2008; Thiemann 2008), orchards (Garner and Vaughan 1987, Lyons 2005), bird-feeders (Merkle et al. 2011b), apiaries (Jonker 1998) and agricultural fields of cultivated crops (Maddrey 1995; Garshelis 1999; Obbard et al. 2010). These caloric hotspots provide bears increased fat reserves for hibernation, increased or earlier fecundity for females (Noyce and Garshelis 1994; Beckmann and Lackey 2008), a stable food alternative to seasonally or annually fluctuating natural food (Howe et al. 2012), and require less range or movement to find adequate forage (Beckmann and Berger 2003). The availability and abundance of wildland fall forage is believed to be the foremost driver of anthropognic food use by bears (Rogers 1976, Mattson 1990, Jonker et al. 1998), yet studies have found that some bears utilize these non-natural sources despite abundant natural food (Merkle et al. 2013). The recent increase in bear population growth and geographic expansion, coupled with human encroachment into bear habitat, has led to increased levels of human-bear conflicts and direct mortality of bears (Peine 2001, Hristienko and McDonald 2007, Spencer et al. 2007), ultimately resulting in a reduced human tolerance for coexistence with bears (Bowman et al. 2001).

Agricultural fields tend to be a major source of potential conflict between bears and people. Agricultural conversion is a primary cause of habitat loss and fragmentation but some crop fields can also provide the densest source of calories in a landscape, often without the attendant human presence typical of other anthropogenic food sources. Throughout the United States, wildlife managers and biologists have documented bear depredation of agricultural crops (Davenport 1953, Garshelis et al. 1999, Witmer and Whittaker 2001, Dobey et al. 2005, Benson and Chamberlain 2007). Areas of crop production increasingly overlap large, established bear populations, and studies have found bears utilizing corn to a significant degree in a number of U.S. states and Canadian provinces (Stowell and Willgang 1992; Jonker et al. 1998; Garshelis et al. 1999; McDonald and Fuller 2001; Obbard et al. 2010) because of improved farming and seed technology as well as more suitable growing conditions due to climate change (Almaraz et al. 2008, Malcom et al. 2012).

Despite the expansion of bear populations and increased levels of human-bear conflict in these fragmented regions, few studies have investigated the ecological requirements for American black bears living in these landscapes. My study took place in northwestern Minnesota, a site of recent range expansion located at the very western edge of the population of black bears occupying the eastern U.S. (westward there is an expansive gap in the range until western Montana). The study area marks a transition between the deciduous forest biome to the east and the tall grass prairie biome to the west. The former prairie habitat is now largely devoted to agricultural production (areal coverage ~ 52.5%); common crops included soybeans, wheat, corn, sugar beets, alfalfa, sunflowers and oats. The Minnesota Department of Natural Resources considers this area "secondary bear range" due to small parcels of natural bear habitat and lower bear density than the more forested parts of the state (Garshelis and Noyce 2011). In 1995, bear abundance in the region increased when bears moved into the area while seeking alternative foods during a statewide natural food failure. Since this initial influx, northwestern Minnesota has supported a growing and expanding bear population (Garshelis and Noyce 2008).

My dissertation, spurred by this intriguing increase and expansion of bears at the edge of their range, focuses broadly on two interrelated fundamental ecological questions: (1) how do bears respond to fragmentation of forested habitat, and (2) how (mechanistically) is the edge of a bear's geographic range delimited? My first chapter examines how the availability of anthropogenic foods alters bears' diets and links the degree of crop consumption with natural forage availability, demographics, size and health, space use patterns and landscape fragmentation surrounding the individual. This chapter relies upon stable isotope analysis to ascertain the contributions of different food categories in bear diets. By linking an individual’s willingness to consume anthropogenic foods (crops) with biological and ecological factors we tested hypotheses about the risks and rewards that govern foraging decisions near human presence. In addition, we were able to look for benefits accrued by crop-feeding bears in the form of increased fat reserves and body size, and reduced range sizes. Results of this chapter were supported with an appendix that showed farmer’s reactions to bears in their cropfields and the types of crops where farmers encountered the highest levels of damage from bears.

The second chapter investigates foraging decisions in a controlled environment, using captive bears offered equal access and quantities of fall foods (wild and agricultural) that were common in the study area.  This experiment eliminated many of the complicating factors that may influence an individual’s decision to forage on anthropogenic foods. I was able to test the hypotheses that food preference is based on familiarity and nutritional benefit. I also tested the hypothesis that under captive conditions, absent all of the competing factors that may influence food choices in the wild, males and females would show similar food preferences. Whereas the first hypothesis was supported, the second was not — males were much more apt to try novel, high-calorie foods, but females learned to do so after more exposure.

My third chapter focuses on how bears react physiologically to both natural and anthropogenic landscape features. I utilized advanced biologger technology to record and store heart rates of individual bears and linked changes in heart rate with the bear’s location on the landscape, determined using GPS-collars. I was able to test the hypothesis that bears felt more stressed when foraging in cropfields or in small patches of forest.

This was rejected, as heart rates in such areas were slower than expected given the movement rates. However, when crossing open fields without foods, their heart rates were typically faster than expected for their rate of travel, indicating a stress response.

My last chapter focuses on delineating the habitable landscape, or the ecological limit of this expanding population. I found that annual home range sizes of bears in this area were very large, compared to more forested areas.  I examined short-term (weekly) home ranges to estimate how landscape, habitat type, caloric availability and demographics affected the amount of area a bear used at different times of year. These weekly home ranges enabled me to assess short-term habitat needs in terms of cover and food abundance as well as the possible negative influence of roads. By sliding moving windows of weekly home range requirements across the landscape, I was able to identify areas that were habitable or not habitable in the long term. Ultimately, this process yielded regional maps of bear habitat quality under varying natural and anthropogenic food conditions, showing the probable geographic limit of this range. It appears that for bears to expand much farther west they would need to cross a large expanse of unsuitable habitat or slacken habitat requirements.

# CHAPTER 1

# FORAGING PATTERNS BY THE AMERICAN BLACK BEAR IN AN AGRICULTURAL LANDSCAPE

## 1.1 INTRODUCTION

Ecologists have long considered the multiple benefits of omnivory, not only for individual animals, but also for the stability of ecosystems and food webs (Fagan 1997; McCann and Hastings 1997; Singer and Bernays 2002). Omnivores benefit from greater forage availability and stability when they maintain a more diverse diet (MacArthur 1955). Dietary diversity increases the reliability and redundancy of functional food groups (Naeem and Li 1997; Naeem 1998) and reduces starvation risk by reducing reliance on a single dietary input (Doak et al. 1998; Lehman and Tilman 2000). Garshelis and Noyce (2008) found these benefits extend to a large terrestrial omnivore, the American black bear (*Ursus americanus*), by associating population growth with increasing diversity of food resources.

American black bear range stretches from the shrublands of Mexico to the boreal forests of Canada. Black bear numbers across North America have increased in recent decades (Garshelis and Hristienko 2006) and populations in many regions have expanded in geographic range (Frary et al. 2011; Lackey et al. 2013) or re-colonized historical range (Hristienko and McDonald 2007). Though typically an obligate forest-dwelling species, black bears exhibit a diverse and adaptable diet, high mobility, and tolerance for and even attraction to human-altered landscapes with rich sources of food. Bears make use of the foraging opportunities created by human activities, such as productive habitat edges created during forest fragmentation (Rogers and Allen 1987; Hellgren et al. 1991), garbage disposal sites (Baruch-Mordo 2008; Thiemann 2008), orchards (Garner and Vaughan 1987; Lyons 2005), bird-feeders (Merkle et al. 2011b), apiaries (Jonker 1998) and agricultural fields of cultivated crops (Maddrey 1995; Garshelis 1999; Obbard et al. 2010). Crop fields can provide the densest source of calories in a landscape, often without the attendant human presence of other anthropogenic food sources. Bears are most often known to utilize corn, oats, and barley crops across the United States and Canada (Mattson 1990).

Agricultural crops can provide stable food sources and a hyper-abundance of calories. In some populations, anthropogenic food sources comprise a majority of bear diets (Landers et al. 1979), or at least a majority for certain groups within the population (Merkle et al. 2013). Abundant calories provide increased fat reserves for hibernation, and may yield increased or earlier fecundity for females (Noyce and Garshelis 1994; Beckmann and Lackey 2008). However, the ability to exploit these caloric hot-spots often comes with increased risk (Woodroffe and Ginsberg 2000; Beckmann and Lackey 2008). Risks include mortality from vehicle-collisions (McLellan and Shackleton 1988), poaching (Muth and Bowe 1998), and lethal control for nuisance activity (Hristienko and McDonald 2007). The cost of human-bear conflict can be large for both bears and humans when bears begin to seek out or rely on anthropogenic food sources (Gunther 1994; Hristienko and McDonald 2007). Thus, determining what types and how much anthropogenic foods bears consume may help wildlife managers understand movement patterns, range expansion, and demographics of bears living in or colonizing agricultural landscapes.

Stable isotope analysis can be used to determine the relative contribution of different food sources to an animal's diet (Ben-David and Flaherty 2012). Stable isotope compositions can characterize consumer tissue samples and food sources using the ratio of naturally occurring heavy to light isotopes. The $\delta^{15}N$ values of animal tissues indicate trophic position because animals preferentially incorporate dietary $^{15}N$ and excrete $^{14}N$, thus top predators have the highest $\delta^{15}N$ values within the ecosystem (DeNiro and Epstein 1981; Ambrose 1991). Consumer $\delta^{13}C$ values reflect the relative consumption of resources derived from plants using $C_3$- photosynthesis (trees, shrubs, cool-season grasses) versus $C_4$-photosynthesis (warm-season grasses; O'Leary 1981). $C_4$ plant-derived resources, such as corn (*Zea mays*) or human garbage containing high-fructose corn syrup or cane sugar (Merkle et al. 2011b) yield more positive $\delta^{13}C$ values (Smith and Epstein 1971). This makes it possible to use stable isotope analysis to distinguish bears that have consumed these anthropogenic foods (Partridge et al. 2001; Mizukami et al. 2005; Merkle et al. 2011a, Hopkins et al. 2012; Bentzen et al. 2014).

Stable isotopes provide information on assimilated rather than consumed nutrients and better represent actual nutritional sources after the effects of differential rates of digestion and absorption of different food sources in the gut (Peterson and Fry 1987). Moreover, a single sample of metabolically inactive tissues like hair, bone, and claws can provide a record of an individual's dietary composition through time (Roth and Hobson

2000; Mizukami et al. 2005). This makes it possible to reconstruct both historical diets of populations (Hopkins et al. 2014) and, by sectioning fast-growing tissues like hair, seasonal changes in diet (Fortin 2013).

Only recently has stable isotope analysis been used to distinguish foraging preferences of individual animals (Urton and Hobson 2005; Newsome 2009; Edwards et al 2011). Individual foraging decisions exist on a continuum of risk and reward (Mayor et al. 2009), where high-risk – high-reward strategies are positively correlated with expected daily energy budget (Caraco et al. 1980). Bears' additional caloric requirements during hyperphagia in the fall, a time when they seek to amass fat for hibernation, can result in a heightened propensity for high-risk behavior, including use of anthropogenic food sources. Foraging decisions are influenced by caloric needs, but may also vary by sex (Merkle et al. 2013), age-class (Mattson 1990), social status (Beckmann and Berger 2003), physical size (Seger et al. 2013), availability of natural foods (Merkle et al. 2013), and cub rearing (Blanchard and Knight 1991; Wielgus and Bunnell 1994). Habitat quality and fragmentation may also play important roles in these foraging decisions.

We tested relationships between external factors and the high-risk high-reward behavior of agricultural foraging within a geographically expanding, growing population of American black bears living in a wild-cropland interface in northwestern Minnesota. Based on prior data from GPS –collared bears and interviews with local farmers we learned that some individuals foraged on domesticated corn and sunflower (*Helianthus annuus*) fields extensively in the fall, while other bears rarely moved outside of natural habitats (Ditmer 2014, chapter 4). Our first objective was to determine population-level, seasonal and sex-specific variation in the relative consumption of natural versus anthropogenic food sources. Second, we sought to understand factors associated with individuals' dietary selection of corn and sunflowers, and to elucidate the consequences of agricultural foraging. We thus explored relationships between crop consumption and physical size, body condition, food availability, landscape fragmentation, habitat use, and home range size. We hypothesized that bears would increase crop consumption with age, size, regional crop abundance, and higher levels of habitat fragmentation. We further hypothesized that crop use would decrease in years with high natural food availability, decrease with increased availability of oak stands, and lead to reduced home range size and increased fat reserves. We expected that females with cubs would rely less on agriculture than females without cubs due to increased risks, including the potential for infanticide by adult males at sites with spatially-concentrated forage (Ben-David et al. 2004).

## 1.2 MATERIALS AND METHODS

*Study area*.— Northwestern Minnesota marks the western edge of the American black bear's eastern population (Scheick and McCown 2014). The region was once a transition biome of deciduous forests to the east and tall grass prairies to the west. Today, the region is primarily agricultural (areal coverage ~ 45%). During our study period (2006-2012) soybeans ($\bar{x}$= 37%, range = 22-47% of annual crop coverage) and wheat ($\bar{x}$= 37%, range = 26-46% of annual crop coverage) were the primary annual crops (United States Department of Agriculture 2012). The percentage of cropland dedicated to corn production averaged 2.3% and increased over the course of our study (2006-2012: 1.1 to

4.9 %) but still only makes up a small fraction of the entire landscape ($\bar{x}$ = 1.0%, 2006-2012: < 0.1 to 2.1 %). Corn grown in the region was primarily field corn for animal feed but sweet corn production is increasing. Sunflowers were historically a major crop in the region until disease reduced their popularity to about 1/6th of their historical high, averaging 2.4% of areal crop coverage during our study but declining (2006-2012: down from 5.6% in 2007 to 1.1% in 2012) and only covering 1.1% of the total area on average (range: < 0.01 to 2.5%). In 2012, the remaining agricultural lands were primarily pasture/hay (11%), alfalfa (7%), sugarbeets (3%), and dry beans (2%). The remaining 55% of the region included human developments (4%), open water (1%) and natural vegetation (50%). Aspen/white birch forests (~26%, *Populus tremuloides*/*Betula papyrifera*), lowland deciduous shrub (~23%, primarily willow *Salix* spp., alder *Alnus* spp., red-osier dogwood *Cornus sericea*), herbaceous wetlands (~22%), grasslands (~ 15%) and bur oak forests (~ 7%, *Quercus macrocarpa*) make up the majority of natural cover types (Minnesota Department of Natural Resources 2012).

Bears in forested parts of Minnesota consumed mainly young green vegetation during spring (Garshelis and Noyce 2008). This was true as well in northwestern Minnesota. Ants (primarily *Lazius* spp.) dominated bear scats during June and July (Noyce et al. 1997). White-tailed deer (*Odocoileus virginianus*) were abundant throughout the region (Carstensen and DonCarlos 2011) and bears in Minnesota preyed on newborn fawns in the spring (Garshelis and Noyce 2008). The majority of the small forest stands in northwestern Minnesota were young and abutted open fields or roads, providing abundant sunlight for production of fruits and nuts in the shrub layer.

Serviceberry (*Amelanchier* spp.*)*, chokecherry (*Prunus virginiana)*, raspberry (*Rubus strigosus)*, red-osier dogwood (*Cornus sericea)*, sarsaparilla (*Aralia nudicaulis)*, gray dogwood (*Cornus racemosa)*, and high-bush cranberry (*Viburnum trilobum)* were the most common plants producing fruits consumed by bears. These ripened during July and August. Hazelnuts (*Corylus cornuta*, *Corylus americana*) were abundant and available during August–October. Acorns from bur oak trees ripened and fell during late August or early September, but acorn abundance varied significantly annually. Corn becomes attractive and palatable to bears in the "milk stage" which begins early-to-mid-August dependent on weather conditions and date of planting (Stowell and Willging 1992, Ditmer 2014, appendix 1). Sunflower fields attract bears starting in late-August to mid-September (Ditmer 2014, appendix 1).

Our study area, which included portions of Kittson, Roseau, Marshall, Pennington, Red Lake, and Polk counties encompassed an area of about 10,000 km$^2$. Unlike the more forested portions of the state, there were no quotas on the number of bear hunting licenses in this region because the area was not considered primary bear range (Garshelis and Noyce 2011). The hunting season spanned 6-7 weeks from 1 September through mid-October. Most hunters attracted bears with bait, and some hunted near cornfields where bears were known to occur. Hunting was the primary source of mortality for bears in this area (Garshelis et al. 2013). Bears were also frequently killed as nuisances. It was legal for people to shoot bears to protect their property, notably their crops.

*Bear capture and handling*.— We captured bears using baited barrel traps during May–July, 2007–2011. We immobilized bears with a combination of ketamine hydrochloride and xylazine, or premixed tiletamine hydrochloride and zolazepam (Telazol®, Elkins-Sinn, Cherry Hill, NJ, USA). We fit bears with either VHF radio-collars (Telonics Inc., Mesa, AZ, USA), GPS store-on-board collars (Telemetry Solutions Concord, CA, USA; Lotek Wireless Inc., Newmarket, Ontario, Canada**;** Advanced Telemetry Systems, Isanti, MN, USA) or GPS Iridium satellite collars (Vectronic Aerospace, Berlin, Germany). We programmed GPS collars to acquire a location once every 1−6 h during the non-denning seasons; we often increased the sampling rate during fall to capture fine-scale movements when bears might have foraged on agricultural crops.

During the initial capture, we extracted a first upper premolar to estimate age (Coy and Garshelis 1992), gave each bear a unique identification number, and marked individuals with numbered plastic ear tags. Each winter (Dec–Mar, 2007–2013) we used Telazol to anesthetize collared bears in dens in order to download GPS data from store-on-board units. We classified females as being with cubs if cubs were present in the den in March (cubs were born in January) or if the female was lactating when captured during the summer, even if cubs were not observed. All animal handling was approved by the University of Minnesota’s Institutional Animal Care and Use Committees (permit no. 1002A77516) and all methods conform to the guidelines of the American Society of Mammalogists regarding use of wild animals in research (Sikes and Gannon 2011).

We used hanging spring scales to weigh bears and we measured total length (from nose-tip to tip of tail) and head girth to the nearest cm. We assessed bone prominence and skin-fold thickness as indices of body fat (Noyce et al. 2002). During each handling we pulled out a hair sample (including the roots) from between the shoulders using pliers. Most hair samples were collected during winter den handling sessions but when samples were taken during spring trapping we only collected the previous year's molting hair. Therefore, all hair samples were representative of the entire previous year's diet.

*Natural food availability.*— We created an index of fall food availability based on an annual survey of the abundance of natural fruits and nuts coordinated by the Minnesota Department of Natural Resources (Noyce and Garshelis 1997). Survey participants subjectively scored each fruit/nut species' production on a 0–4 scale. We used the regional productivity indices of oak, hazel, and dogwood (*Cornus rugosa, C. sericea, C. alternifolia, C. racemosa*) each year as an annual index of fall food availability.

We calculated an independent index for acorn abundance by counting the number of fallen acorns (or caps) within 1-m$^2$ sampling plots in oak stands. Plots were established along the open edges of stands (along roadways or clearings) and deeper into stands to capture variation in production related to light penetration. Bears foraged for acorns mainly on the ground, rather than in trees, so we conducted counts shortly after the peak in acorn fall. We sampled at least 10 stands per year during 2007–2012.

*Isotopic analysis of hair and bear foods.*— We collected samples of 25 principal wild bear foods from various sites within our study area for isotopic analysis (Table 1). General categories included spring vegetation, ants and pupae (*Lasius* spp.), summer fruits, and nuts. We obtained white-tailed deer flesh from the abdominal wall and hair from the hindquarter at a hunter check station in our study area. We collected corn and sunflower samples from agricultural fields during late August to early October.

We obtained hair samples from 21 female and 30 male bears, with individuals sampled up to seven times ($\bar{x}$ = 2.2 hair samples per individual), but never more than once per year, yielding samples for 54 male and 56 female bear-years in total. We cut each hair into 2 segments: 1/3 of the hair length on the root-end represented the most recent growth corresponding approximately with the autumn diet, and the remaining 2/3 distal end, corresponding with the spring and summer diet (Mizukami et al. 2005). To remove dirt, lipids, and oils, hairs were soaked and rinsed in deionized water, then soaked in a 2:1 chloroform:methanol solution for ca. 2 h, rinsed with deionized water, and allowed to dry (after Scwertl et al. 2003). We trimmed visible follicles from root ends then cut each hair segment into small pieces using scissors.

Samples were analyzed for elemental concentrations of C and N (% dry wt, values used in mixing model but not presented), and for $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios, expressed in standard $\delta$ notation as permil difference between the ratios in a sample and a standard material differential from international standards for these isotope ratios (Vienna PeeDee Belemnite for carbon and air for nitrogen). Samples and corresponding standards were analyzed using either a Thermo-Electron Delta V Advantage IRMS configured through a Finnigan CONFLO III, using a Carlo Erba NC2100 elemental analyzer at the Colorado Plateau Stable Isotope Laboratory of Northern Arizona University, or at the University of Minnesota Stable Isotope Laboratory in the Department of Earth Sciences using a Costech 4010 Elemental Analyzer coupled to a Thermo-Finnegan Delta V Plus mass spectrometer. Based on replicate analyses of laboratory standards at both labs, precision for $\delta^{13}C$ analyses is <0.15% and <0.2% for $\delta^{15}N$ analyses.

To analyze food samples, we removed indigestible components (e.g., seeds, hulls, shells), rinsed in distilled water to remove dirt, then freeze-dried at -50˚C for >24 h before grinding into a fine powder. Deer hair samples were prepared in the same manner as the bear hair samples (but not sectioned). We analyzed all food samples at the University of Minnesota Stable Isotope Laboratory for C and N dry weight %, and for $\delta^{13}C$ and $\delta^{15}N$. Based on replicate analyses of a peach leaves standard, precision for $\delta^{13}C$ analyses is <0.15‰ and <0.2‰ for $\delta^{15}N$ analyses, respectively.

*Isotopic mixing models for estimating dietary composition.*— We created 2 mixing models to separately estimate diet during spring/summer and fall (represented by the 2 segments of hair). Bears' established seasonal diets allowed us to include only the seasonally available food sources that correspond with the season of hair growth. Prior to running models, we first assigned foods to isotopically distinct groups (Phillips et al. 2005). Food groups incorporated into the spring/summer model included: 1) early season spring vegetation and summer fruits, 2) ants and ant pupae, 3) deer, and 4) corn. Fall foods were grouped into: 1) autumn fruits and nuts, 2) corn, and 3) sunflowers. We also tested whether acorns could be distinguished from other natural fall forage, and whether oil and confection sunflowers could be differentiated. We used the package ‘SIAR’ (Stable Isotope Analysis in R) in program R (Parnell et al. 2008; R Core Team 2013), which uses Bayesian inference to solve for the most likely dietary contributions of the separate food groups, given the isotopic ratios of each. We ran all models for 1,000,000 iterations with a burn-in of 1,000. SIAR allows for the incorporation of sources of uncertainty by accounting for variation surrounding the isotopic values of source groups, elemental concentrations of sources (wt%C, wt%N) and the enrichment values for each source. Enrichment values adjust isotopic values to account for the isotopic fractionation that occurs when a consumer assimilates dietary components into body tissues, in this case, hair (Phillips 2012). Enrichment values vary by species and tissue type (Caut et al. 2008). Determining proper enrichment values is important because mixing models are sensitive to these assumptions. We used equations derived for American black bears and polar bears (*Ursus maritimus*) (Hilderbrand et al. 1996) to adjust the mean values of $\delta^{13}C$ and $\delta^{15}N$ in food samples to $\delta^{13}C_{hair}$ and $\delta^{15}N_{hair}$. The only exception was for corn’s carbon isotopic signature, which we used the smallest positive adjustment recommended for carbon (+0.4‰ for plasma, which has similar enrichment as hair; Hilderbrand et al. 1996).

*Spatial data.*— We overlaid locations from GPS-collared bears (whose hair had been sampled) onto a land cover map (Minnesota Department of Natural Resources 2012) and a crop cover map (United States Department of Agriculture 2012) using a geographic information system (ArcMap 10.1, Environmental Systems Research Institute, Redlands, CA, USA). We only plotted sequential locations that were at least 4 h apart. We quantified fall (15 Aug until denning) use of oak, upland shrub (primarily *Corylus* spp.) and crops by counting the number of locations in each of these habitats and dividing by the total number of locations during the fall time interval.

We estimated home range metrics for bear-years with ≥200 GPS locations during fall. We used the package adehabitat in program R (Calenge 2006, R Core Team 2013) to create and estimate the area (km$^2$) of 50% and 95% fixed kernel density estimators (KDE) using the ad-hoc method for smoothing (Worton 1989, 1995) and 50% and 95% minimum convex polygons (MCP). Within each 95% MCP we calculated the mean patch size of each natural cover type and the average distance between natural habitat patches to serve as indices of habitat fragmentation. We defined natural habitat as any land-cover type not classified as either crop, developed, or within 15m of roads (Minnesota Department of Transportation 2012).

We associated each hair sample with a single location on the ground. For GPS collared bears this location was the centroid of the 95% MCP home range. Hair from bears without GPS collars were assigned the den location, trap location, or kill site where the hair was collected. We used X and Y coordinates separately as proxies for home range center in order to relate general location within the study area to diet; agricultural land use generally increases from east to west and north to south in northwestern Minnesota.

*Statistical analysis.*— We tested for differences in $\delta^{15}$N and $\delta^{13}$C between root versus distal ends of hairs and between sexes using a 2-factor multivariate analysis of variance (MANOVA). We obtained posterior distributions of likely dietary contribution from each food group for the population and for each bear-year. We report population estimates using the 95% credible-interval for each food group and annual estimates of diet from crop were calculated by multiplying lower and upper values of corn and sunflowers by 2/3 for the spring/summer estimates (corn only) and 1/3 for the fall. To report dietary fall estimates for individual bear-years (IDEs), we used the median estimate within food groups for each bear-year.

As a means of validating our isotopic mixing models, we tested for a relationship between fall IDEs for crops (corn + sunflowers) and the percent of time each GPS-collared bear spent in corn or sunflower fields. We quantified uncertainty in the estimated regression coefficient using a cluster-level bootstrap (resampling individuals) to account for non-independence among observations from the same bear (i.e., data collected from different years). We also fit a series of linear mixed models to explore relationships between crop consumption and several individual, physical and spatial covariates (Table 2). Physical measurements were associated with the proximal end of hair collected at the time of measurement and therefore reflect the influence of diet from the preceding fall. We used a binary variable to distinguish females with cubs of the year (COY, “1”), and (“0”) for males or females when without COY. Many predictor variables were correlated and/or had varying levels of missing data (Table 2), thus we used a series mixed effects models with single fixed effect predictors for male and female bears separately to explore the relationship between crop consumption and attributes of individual bear-years: age, having cubs of the year, fat thickness, bone prominence, weight, total body length, head girth, fall food abundance, use of oak habitat, location of activity center within the study area, fall home range size, and metrics of habitat connectivity. We included a random intercept for each bear ID and fit the models using the ‘lme’ function in the nlme package of Program R (Pinheiro et al. 2013; R Core Team 2013). To present relationships graphically and provide a better comparison of correlation with dietary crop reliance among predictors, we used the scaled and centered version of all covariates (Schielzeth 2010).

*Post-hoc analysis.*— Results from our initial statistical analyses suggested that grouping bears into 4 categories: adult males, adult females without COY, adult females with COY and juveniles (age ≤ 3), was more appropriate than grouping by sex alone. Thus, we re-ran the mixing models as described above to obtain dietary estimates for these four groups. We report differences between groups and provide dietary estimates (± 95% credible-intervals) for the 4 groups from spring/summer and fall mixing models.

To determine which grouping was most appropriate, we used Akaike’s Information Criterion to compare model fit (Burnham and Anderson 2002) of linear mixed models relating IDEs of fall crop consumption to sex only versus the four demographic groups. We used the same model structure as described above, using IDE as the response variable with a random intercept included for each different bear-year.

## 1.3 RESULTS

We analyzed 141 samples of bear foods to distinguish food groups for spring/summer and fall mixing models. Distinctions among food groups were based on both $\delta^{13}$C and $\delta^{15}$N values. Acorns were not isotopically different from fall fruit and nuts, and oil and confection sunflowers were not significantly different from each other so their values were combined (Table 2). Average spring/summer vegetation and fruit $\delta^{15}$N values were isotopically unique from other spring food sources (Table 3). Corn was differentiated from other spring/summer and fall food sources due to a higher $\delta^{13}$C values (Table 3). Sunflower seeds and corn had higher $\delta^{15}$N values relative to fall fruit/nuts (Table 3).

The $\delta^{13}$C and $\delta^{15}$N values from bear hairs were significantly different between sexes (Wilks $\lambda = 0.95$; $F_{4,106} = 5.30$; $P < 0.01$) and seasons (Wilks $\lambda = 0.86$; $F_{2,108} = 13.99$; $P < 0.01$). Male bears' higher $\delta^{13}$C values throughout the seasons indicate more crop use than for female bears (Fig. 1). More positive $\delta^{13}$C values in fall, for both sexes, coincide with the timing of crop maturation. Females showed a marked drop in $\delta^{15}$N values from spring/summer to fall, despite consumption of corn (as indicated by $\delta^{13}$C), which has higher $\delta^{15}$N values (Fig. 1). Higher $\delta^{15}$N values represent consumption at a higher trophic level, such as ants and deer.

Despite differences in isotopic signatures among food sources, spring/summer mixing models (Fig. 2A) did not detect significant dietary differences between males and females (Table 4). Both sexes relied mainly (~80–90%) on green vegetation and fruits in spring and summer. Ants and deer comprised a small component of assimilated spring/summer diet; credible intervals bounding the estimates of their consumption always included zero except in the case of ant consumption by female bears (Table 4). Corn consumption in spring/summer was at least as prevalent as ants, and did not significantly differ between males and females.

Fall diets were also not significantly different between the sexes (Table 4). Fall fruits and nuts were the dominant component (75–90%), but corn became a more major contribution (Table 4). Sunflowers comprised up to 5% of the diet. However, the fall mixing model (Figure 2B) shows several points near the isotopic source values for sunflowers and corn suggesting that either only a few outliers consumed crops or grouping dietary estimates by sex alone does not adequately capture consumption trends within the population.

Fall individual dietary estimates varied widely for wildland foods (range: 1–93%), corn (range: 1 – 95%) and sunflowers (range: < 1 – 43%). Mean and median IDEs of crop consumption were 25% (95% CI = 20.6−29.2%) and 18%, respectively. This skewed distribution suggests that some individuals heavily used crops: crops composed at least half the fall diet for 13.9% of the bear-years (Fig. 3). The relationship between a bear's IDE of crop consumption and the percentage of its respective GPS locations in corn and sunflower fields (Fig. 4) was significant and positive ($\beta = 1.99$, 95% CI = 1.44 – 2.74, $p < .001$, $r^2 = 0.43$, $n = 33$), providing strong evidence that our fall isotopic mixing model and dietary discrimination assumptions were appropriate.

We observed positive relationships between crop IDEs and the age and physical size of bears of both sexes, but more strongly for males (Fig. 5). For females, body mass and bone prominence were the only physical attributes with a definitive positive relationship to crop consumption (Fig. 5). Females with COY showed less consumption of crops than solitary females (Fig. 5). IDEs for males showed a weak negative relationship with our subjectively-rated fall food indices, but females had a significant negative relationship, indicating less consumption of crops in years with high natural food abundance (Fig. 5). IDEs showed no relationship to our quantitative counts of acorns on the ground in oak forests (Fig. 5).

Consumption of crops by females varied with the general proportion of the area near their home range dedicated to agricultural production. Female bears in the western and southern portions of the study area consumed more crops than females elsewhere (X and Y centroids, Fig. 6). Male consumption of crops was unrelated to local areal coverage of agricultural production.

Males that consumed more crops had smaller fall home ranges (both MCP and KDE; Fig. 6); this effect was larger using 95% MCP or KDE home ranges than for core 50% home ranges. This relationship was less apparent for females. Conversely, time spent in oak and upland shrub habitats was negatively associated with crop use in females, but not males (Fig. 6). Crop use did not vary significantly with measures of habitat fragmentation (Fig. 6).

The post-hoc model, including a covariate with four categories representing sex, age and reproductive status, had more support than the model with categories for gender only (AIC = -35.0 vs. -10.9). Juvenile bears ($\beta = -0.24$, SE = 0.05, $p \leq 0.01$) and females with COY (-0.24, SE = 0.06, $p \leq 0.01$) had significantly lower estimated crop consumption than males but females without COY had similar estimated crop consumption as adult males ($\beta = -0.04$, SE = 0.05, $p = 0.51$). Dietary estimates confirm a wildland-focused foraging strategy in juveniles and females with COY, but extensive use of agriculture by adult males and solitary adult females without COY (Table 5).

## 1.4 DISCUSSION

Black bears are a forest-dwelling species, yet in a landscape that is roughly half agriculture, much of their ecology and behavior is driven by the 2% of the area that produces specific crops. We obtained dietary estimates for bears from stable isotope analyses by aligning the isotopic compositions associated with sectioned hairs with corresponding seasonal food sources. We then validated our results by comparing space use by bears (using locations from GPS collars) in isotopically unique areas of the landscape (corn and sunflower fields) with dietary estimates. We found that bears' proclivity to forage in crop fields can vary seasonally and throughout their lifespan related to reproductive status and the availability of natural forage. By combining disparate data sources from stable isotope analysis, locational data from GPS-collars and GIS cover maps, physical measurements of bears, and field observations of resource availability, we were able to develop a more complete picture of how bears have been able to thrive in an agricultural, human-dominated landscape.

*Spring and summer diet.*— Although the spring/summer diet was mainly composed of green vegetation and fruits, elevated $\delta^{15}N$ values were indicative of consumption of animal matter, which was absent in the fall. Hobson et al. (2000) reported this same finding for bears feeding on ants and deer flesh in British Columbia, Canada. In Minnesota, estimated dietary contribution from white-tailed deer was minor across all demographic groups despite a high deer density in the region. Kunkel and Mech (1994) found that bears in northeastern Minnesota consumed newborn fawns for only a few weeks in spring (May–June), and ceased feeding on deer once fawns were more mobile. Thus, although the $\delta^{15}$N confidence intervals for deer and ants broadly overlapped (Fig. 2), we surmised that the elevated $\delta^{15}$N during spring/summer (Fig. 1) was due mainly to ingestion of ants. Noyce et al. (1997) found that ant remains comprised ≥ 33% of bear scat volume during a 4 week period of June and July in a forested region of Minnesota. Likewise, we observed that during these same months ants were common in bear scats in our study site. However, we also noticed early season fruits in the scats, which may have been more abundant in our study area due to the young age of the forest and high edge to area ratio, owing to small patch sizes which may explain our small estimated dietary contribution from ants.

*Fall diet.*— Although bears in this region had access to calorically rich crops, crops dominated the diet of only a small percentage of bears (Fig. 3); nevertheless, crops were an important dietary component for many bears. Corn is usually consumed by bears during the milky phase of growth (prior to starch formation; Mattson 1990), which typically begins in early August in northwestern Minnesota. However, it has been identified as a major component of diet at other times of year as well (Davenport 1953; Landers et al. 1979; Hellgren and Vaughan 1988; Maddrey 1995). Our estimates of corn consumption are similar to those of Benson and Chamberlain (2006) who found that corn comprised 30–33% of scat volume in summer/fall scats in an agricultural landscape in Louisiana. They reported bears continuing to feed on waste corn in the fall following harvest. Our isotope data indicated that some bears consumed considerable corn in spring/summer as well. Data from GPS-collared bears and visual observations of bears in fields corroborated that bears fed on unharvested corn from the previous fall and spillage from harvested fields in the spring.

Corn production in North America has traditionally been concentrated in areas that are not home to black bears, such as Iowa, Illinois, Nebraska, southwestern Minnesota, and South Dakota (U.S. Department of Agriculture 2013a). However, all states (except Nevada) produce some corn and total acreage of production is expanding within the United States (U.S. Department of Agriculture 2013b). Much of the expansion is occurring at northern latitudes because of improved farming and seed technology as well as more suitable growing conditions due to climate change (Almaraz et al. 2008, Malcom et al. 2012). Areas of commercial corn production increasingly overlap large, established bear populations, and studies have found bears utilizing corn to a significant degree in a number of U.S. states and Canadian provinces (Stowell and Willgang 1992; Jonker et al. 1998; Garshelis et al. 1999; McDonald and Fuller 2001; Obbard et al. 2010). Increased availability of corn can benefit individuals metabolically by providing calorie-dense forage that improves body condition and, potentially, reproductive productivity, as well as reducing the distances bears must travel to find adequate forage.

Sunflowers are a $C_3$ plant, so $\delta^{13}C$ values were similar to wild foods; however, they exhibited higher $\delta^{15}N$ values relative to other $C_3$ plants. These higher $\delta\ ^{15}N$ values enabled us to distinguish consumption of sunflower seeds, although with less confidence than corn because sunflowers are only differentiable with respect to $\delta^{15}N$ and along that axis sunflowers have a high variance. As a result, our estimated sunflower consumption may be conservative. For example, bears that ate both corn and sunflowers, or a bear that foraged in a sunflower field with a low $\delta^{15}N$ value may not have been correctly identified by our mixing models. This high variation in sunflower $\delta^{15}N$ values is not unexpected (Unkovich et al. 2008; Choi et al. 2003) and is likely related to the application of chemical fertilizer. Most nitrogen fertilizer used in northwest Minnesota is chemical urea (Bierman et al. 2012), which should contain a $\delta^{15}N$ value of 0‰ (i.e. atmospheric $N_2$; Bateman et al. 2005), however, the interaction of fertilizer and rooting depth, soil history, and small differences of $\delta^{15}N$ in plants can create variable effects (Evans 2001).

*Individual dietary estimates.*— Previous studies combining animal locations to validate individual dietary estimates from stable isotope analysis are rare. Edwards et al. (2011) linked faster movement speeds of GPS-collared polar bears (*Ursus maritimus*) with greater percentages of meat consumption based on higher values of $\delta^{15}N$. Cerling et al. (2006) combined 5mm sectioned isotopic values of elephant (*Loxodonta africana*) tail hairs with GPS locations to determine migration patterns and seasonal dietary shifts.

Our regression of observed use (GPS locations) of corn and sunflower fields versus the estimated assimilation of these crops had a slope of 1.99, suggesting that 1% time spent in a cropfield provided ~2% of a bear’s fall diet (Fig 4). This relationship provides evidence that foraging in crop fields is more efficient than in natural vegetation, a reasonable interpretation given the calorically rich nature of the crops. Despite the overall strong relationship, a few points deviated greatly from expectations. Some deviations may have been due to bears consuming hunters' baits that contained high-fructose corn syrup; baiting by hunters occurred coincident in time with maturing of crops. Also, some GPS points may have been improperly categorized due to misidentification of type of croplands on GIS layers. Finally, individual differences in isotopic fractionation or the rate at which bears can physically consume different crop types may have also caused variation in the relationship.

*Size, age, and sex related to crop consumption.*— The positive association between crop consumption and physical size of male bears was expected. Seger et al. (2013) used stable isotopes to link black bear body mass with meat consumption, another highly valued and calorically beneficial food source. The relationship we observed was strong because it was self-reinforcing: males got heavier and fatter (but not longer; Fig. 5) when feeding on crops, and large males fed on crops more than other bears. Males are known to dominate high-value food sources, often excluding females and smaller males (Garshelis and Pelton 1981; Powell et al. 1997; Beckmann and Berger 2003; Costello et al. 2009). For females, crop use enabled them to gain weight faster, but physically larger females had no apparent advantage in using cropfields (Fig. 5). Females with COY were less likely to use cropfields probably due to the risks of infanticide from the large males that tended to be found there (Blanchard and Knight 1991; Martin et al. 2013). We witnessed one case of a male attempting to kill a COY, defended by its mother, in a cornfield.

Explanation of the positive relationship between crop use and age (Fig. 5) likely involves influences of both size (smaller bears avoiding larger bears) and learning. Some young bears, especially females with small home ranges may be unaware of crop fields, and also may not recognize crops as a food source if they never fed in a crop field with their mother. Mother-offspring social learning appears to be important in whether bears use anthropogenic foods (Hopkins 2013). These small bears may also fear the unnatural structure, lack of tree cover, and threatening scents of humans and large bears. We observed some young male bears in cropfields at the western periphery of the study area (which is the western periphery of bear range), possibly because they felt safe with the low bear density in this area; these observations fit with Mattson's (1990) hypothesis that young bears feed more on anthropogenic foods when bear density is low.

*Effects of natural food availability on crop use.*— The availability of natural forage plays a role in most animals' foraging decisions. A negative relationship between natural food abundance and the propensity for bears to forage on anthropogenic food sources has been well documented (Elowe and Dodge 1989; Mattson 1990; Zack et al. 2003, Baruch-Mordo et al. 2014). Whereas bears are opportunistic omnivores, we found that different demographic groups regarded anthropogenic food sources differently. Natural food availability had little influence on males' attraction to crops. Males appeared willing to take foraging risks to rapidly increase caloric intake both because they require more calories (Welch et al. 1997) and because their fitness is closely tied to larger physical size (Kovach and Powell 2003). Hence, they used their physical size to compete for these peculiarly rich food sources, even if other natural foods were adequate.

Females, in contrast, appeared to view crops mainly as a fallback, when natural foods were lacking. Likewise, female black bears in Massachusetts sought crops only during shortages of natural fall mast (McDonald and Fuller 2001). Females in Minnesota were also less attracted than males to hunters' baits, and female attraction to baits, like crops, was more strongly influenced by natural food availability (Noyce and Garshelis 1997). Bear behavior toward these rich food sources represented a trade-off between risk and reward: hunters' baits and cropfields expose bears to their primary sources of mortality in Minnesota, hunting and depredation killing.

Females exhibited a trade-off between time spent foraging in agricultural fields versus oak forests. However, our acorn abundance indices showed little or no association with bears' crop consumption levels. These seemingly contradictory results may be explained by the abundance of hazelnuts in the area. Along with dogwood berries and high-bush cranberries, hazelnuts are a principal natural fall food and typically occur in the drier soils associated with oak forests. Ditmer (2014, chapter 4) found that hazelnuts comprised nearly 40% of the biomass of available berries and nuts and contained the highest caloric content per gram of all sampled forage options (including crops) for bears in northwestern Minnesota. The abundance of this food may in part be due to the patchy mosaic of forested lands, providing extensive edges where light penetration promotes fruit production.

*Spatial aspects to foraging in an agricultural landscape.*— Optimal foraging theory predicts that home range size should decrease where high-calorie foods are clustered (Pyke et al. 1977). Beckmann and Berger (2003) found that bears using rich food resources in urban areas maintained smaller home ranges than bears subsisting on wild foods. Dobey et al. (2005) observed smaller home range sizes for black bears that had access to corn feeders than those that relied exclusively on natural foods. Results of our study indicated that edible crops affected bears' home ranges, but suggest that males and females viewed the landscape differently and thus made foraging decisions at different spatial scales. The fall home ranges of females were not significantly influenced by agricultural availability but females located in the regions of the study area with more agriculture (farther west and south) and smaller patches of natural habitat tended to consume more crops. In contrast, male home ranges shrunk if they found a crop field to feed in, indicating that their foraging strategy was directed toward finding and staking out these choice, but relatively rare and scattered feeding areas.

Understanding population dietary requirements and factors that may influence individual dietary preferences are instrumental for informing conservation efforts in human-altered landscapes. The diet of American black bears is especially complex because of their omnivory and mobility, which along with demographics have prompted range expansions into areas with abundant anthropogenic food sources. Isotopic analysis provides several benefits over traditional scat analysis for determining diet because it incorporates assimilated nutrients, allows for dietary reconstruction over longer time intervals, which can be associated with space use, body condition, and reproduction. Sectioning bear hair into seasonal components and comparing the isotopic composition of these to respective seasonal available foods via a mixing model added precision to dietary estimates. Future work should continue to integrate stable isotopes and spatial information from GPS data to ascertain relationships between diet and space/habitat use. Studies should also include individual survival estimates to better discern the risk component of the high-risk high-reward continuum facing species that utilize anthropogenic food sources.

*Acknowledgments*

We gratefully acknowledge our funding sources: Minnesota Department of Natural Resources, Minnesota Corn Growers Association, and the American Society of Mammalogists. We especially thank Carolin Humpal, Spencer Rettler, and Michael Saxton for assistance with lab work, and Doug Page and Thomas Enright for fieldwork. Tom Gulya of the United States Department of Agriculture, Russ Severson and Howard Person at University of Minnesota Agricultural Extension, and Joel Huener and other employees of the Minnesota Department of Natural Resources provided samples, helped with logistics, and provided food abundance assessments. Sarah Thompson and John Vincent provided helpful insights on earlier versions of the manuscript.

Table 1. —Mean and standard deviation of isotopic values of bear food sources from northwestern Minnesota. Sources were assigned to a mixing model dependent on chronology of availability to bears (spring/summer:SS and fall). Samples were collected from spatially independent areas or crop fields.

| Common name | Species | Sample type | Mixing model | Samples | $\delta^{15}$N (SD) | $\delta^{13}$C (SD) |
|---|---|---|---|---|---|---|
| | | Spring wildland foods | | | | |
| sedge | *Cyperaceae* | vegetation | SS | 4 | 1.40 (0.77) | -29.76 (0.70) |
| horsetail | *Equisetum spp* | vegetation | SS | 3 | 4.54 (0.11) | -30.48 (2.06) |
| aspen buds | *Populus tremuloides* | vegetation | SS | 2 | -3.21 (0.93) | -26.92 (1.16) |
| dandelion | *Taraxacum* spp. | vegetation | SS | 2 | -0.49 (2.83) | -32.06 (0.13) |
| grass | *Gramineae* | vegetation | SS | 2 | 0.14 (1.84) | -27.65 (3.34) |
| northern bedstraw | *Galium boreale* | vegetation | SS | 2 | 0.42 (1.76) | -32.14 (0.56) |
| serviceberry | *Amelanchier humilis* | fruit | SS | 2 | -1.30 (0.61) | -29.42 (0.29) |
| veiny pea | *Lathyrus venosus* | vegetation | SS | 2 | -0.26 (0.05) | -29.36 (1.30) |
| dwarf raspberry | *Rubus pubescens* | vegetation | SS | 1 | -2.91 (--) | -30.56 (--) |
| false soloman's seal | *Maianthemum racemosum* | vegetation | SS | 1 | 0.32 (--) | -31.23 (--) |
| | | Protein | | | | |
| adult ants | *Lasius* spp. | ants | SS | 9 | 3.84 (0.98) | -26.83 (0.52) |
| ant pupae | *Lasius* spp. | pupae | SS | 2 | 4.17 (0.90) | -26.94 (0.50) |
| deer hair | *Odocoileus virginianus* | hair | SS | 28 | 5.80 (0.93) | -26.95 (1.45) |
| deer flesh | *Odocoileus virginianus* | flesh | SS | 6 | 4.98 (1.10) | -26.85 (0.99) |
| | | Spring/Summer & fall wildland foods | | | | |
| red-osier dogwood | *Cornus sericea* | fruit | SS & Fall | 3 | 0.25 (1.08) | -28.40 (1.49) |
| sarsaparilla | *Aralia nudicaulis* | fruit | SS & Fall | 3 | -1.66 (0.36) | -29.68 (0.36) |
| raspberry | *Rubus strigosus* | fruit | SS & Fall | 2 | 0.11 (0.72) | -28.85 (0.02) |
| | | Fall wildland foods | | | | |
| acorns | *Quercus macrocarpa* | nuts | Fall | 5 | -0.53 (0.88) | -26.45 (1.55) |
| chokecherry | *Prunus virginiana* | fruit | Fall | 4 | -1.33 (1.85) | -27.24 (1.78) |
| hazelnuts | *Corylus cornuta, Corylus americana* | nuts | Fall | 4 | -1.40 (0.92) | -30.75 (1.10) |
| nannyberry | *Viburnum lentago* | fruit | Fall | 3 | -0.57 (0.13) | -30.22 (0.80) |
| arrowood | *Viburnum dentatum* | fruit | Fall | 1 | -4.03 (--) | -30.46 (--) |
| gooseberry | *Ribes hirtellum* | fruit | Fall | 1 | -3.99 (--) | -31.13 (--) |
| gray dogwood | *Cornus racemosa* | fruit | Fall | 1 | 0.85 (--) | -31.62 (--) |
| high-bush cranberry | *Viburnum trilobum* | fruit | Fall | 1 | -1.36 (--) | -24.76 (--) |

|  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|
| pagoda dogwood | *Cornus alternifolia* | fruit | Fall | 1 | -0.43 (--) | -29.44 (--) |
| plums | *Prunus americana* | fruit | Fall | 1 | 1.67 (--) | -29.22 (--) |
| Corn |  |  |  |  |  |  |
| corn | *Zea mays* | kernel | SS & Fall | 24 | 6.98 (4.80) | -12.07 (0.39) |
| Sunflowers (oil and confection grouped in mixing models) |  |  |  |  |  |  |
| oil & confection | *Helianthus annuus* | dehulled kernel | Fall | 21 | 9.86 (3.84) | -28.52 (1.56) |
| oil |  |  |  | 15 | 9.63 (4.22) | -28.28 (1.51) |
| confection |  |  |  | 6 | 10.45 (2.97) | -29.13 (1.65) |

Table 2.— Variables and corresponding data sources and sample sizes used in analyses relating outside factors to percent diet of corn and sunflowers. All variables under Space use, Home range area and Habitat connectivity were derived from GPS locations from fall only (mid-August – November).

| Category | Variable | Description | Data source[a] | Sample size (unique individuals, bear-years) |
|---|---|---|---|---|
| Age/status | Age | Age of bear | BH | 50, 109 |
|  | COY | With cubs of the year | BH | 20, 56 |
| Body condition | FatThick | Skin-fold thickness | BH | 42, 81 |
|  | Bone | Bone prominence | BH | 42, 84 |
| Size metrics | Weight | Weight of the bear at time of handling | BH | 48, 91 |
|  | Total Length | Total length(from nose-tip to tip of tail) | BH | 43, 83 |
|  | Head | Head girth | BH | 44, 84 |
| Fall food abundance | Fall Food | Indices of primary fall foods (hazelnut, dogwood, oak) | Annual manager survey | 51, 110 |
|  | Acorn | Estimate of annual acorn mast (acorns/m2) | Annual acorn counts | 51, 110 |
| Location in study area | X-Cent | Center of activity (east - west) based on trap location, kill site, den or home range centroid | BH & GPS | 32, 80 |
|  | Y-Cent | Center of activity (north-south) based on trap location, kill site, den or home range centroid | BH & GPS | 32, 80 |
| Space use | Oak | % of locations in oak and upland shrub habitats | GPS | 24, 33 |
| Home range size | KDE50 | 50% fixed kernel density estimate | GPS | 24, 33 |
|  | KDE95 | 95% fixed kernel density estimate | GPS | 24, 33 |
|  | MCP50 | 50% minimum convex polygon estimate | GPS | 23, 33 |
|  | MCP95 | 95% minimum convex polygon estimate | GPS | 24, 33 |
| Habitat connectivity | NN | Average shortest distance between each natural habitat patch | GPS | 24, 33 |

| | | | |
|---|---|---|---|
| PATCH | Mean size of natural habitat patches | GPS | 24, 33 |

[a] HB = data were obtained from handled bears either during winter den visits or initial captures. GPS = data obtained from GPS collars. Annual manager survey and Annual acorn counts are described in the methods.

Table 3.−Mean (± 95% confidence interval) isotopic values of food source groups used in spring/summer and fall isotopic mixing models. Food sources were grouped based on similarity of source and availability for consumption to bears. Samples were collected from spatially independent areas or crop fields in northwestern Minnesota from 2011 -2012. Values presented here are not corrected for fractionation.

| Source group | Mixing model | n | $\delta^{13}C$ 95% CI | $\delta^{15}N$ 95% CI |
|---|---|---|---|---|
| Spring veg & summer fruit | SS | 29 | -29.63 (-30.28−-28.98) | 0.11 (-0.68−0.90) |
| Ants | SS | 11 | -26.85 (-27.15−-26.56) | 3.90 (3.35−4.45) |
| Deer | SS | 28 | -26.95 (-27.49−-26.41) | 5.80 (5.46−6.15) |
| Corn | SS & Fall | 24 | -12.07 (-12.22−-11.91) | 6.98 (5.06−8.90) |
| Fall fruit & nuts | Fall | 30 | -28.73 (-29.49−-27.97) | -0.89 (-1.41−-0.36) |
| Sunflowers | Fall | 21 | -28.52 (-29.19−-27.86) | 9.86 (8.22−11.50) |

Table 4.– Dietary contributions on a population level (95% credible intervals) of spring/summer and fall foods for male and female black bears in northwestern Minnesota.

| Food source | Males | Females |
|---|---|---|
| Spring/Summer mixing model | | |
| Ants | 0 - 9% | 2-10% |
| Corn | 4 - 13% | 2-11% |
| Deer | 0 - 2% | 0 - 2% |
| Spring veg. & summer fruit | 81 - 90% | 83-91% |
| Fall mixing model | | |
| Sunflowers | 0-5% | 0-5% |
| Corn | 10-24% | 7-18% |
| Fall fruit & nuts | 75-85% | 81-90% |
| Annual diet from crops | 6-18% | 4-15% |

Table 5) Dietary contributions (95% credible intervals) of spring/summer and fall foods broken down by four demographic groups (FWOC = Females w/o cubs, FWC = Females with cubs; bear-years in parenthesis).

| Food source | Adult males (n=27) | Juvenile males (n=24) & females (n=9) | FWOC (n=21) | FWC (n=25) |
|---|---|---|---|---|
| Spring/Summer mixing model | | | | |
| Ants | 0-11% | 2-12% | 0-13% | 0-7% |
| Corn | 9-23% | 0-7% | 3-16% | 0-11% |
| Deer | 0-3% | 0-2% | 0-3% | 0-2% |
| Spring veg. & summer fruit | 70-85% | 84-94% | 75-90% | 84-95% |
| Fall mixing model | | | | |
| Sunflowers | 0-7% | 0-5% | 0-10% | 0-2% |
| Corn | 19-39% | 1-11% | 10-30% | 0-11% |
| Fall fruit & nuts | 59-75% | 87-96% | 67-83% | 88-99% |
| Annual diet from crops | | | | |
| Corn + sunflowers | 12-31% | 0-10% | 5-24% | 0-12% |

Fig. 1.— Isotopic mean values of $\delta^{13}C$ and of $\delta^{15}N$ from 110 bear-year hair samples grouped by sex and season. Error bars correspond to standard errors.

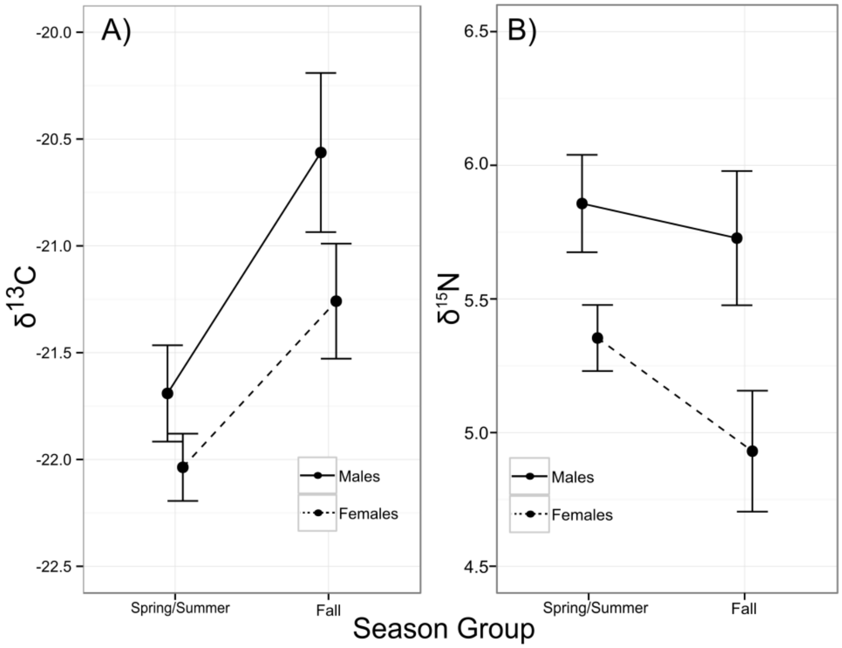


Fig. 2.─ Isotopic signatures of bear-hair and bear foods used in isotopic mixing models for 56 female and 54 male bear-years using food sources available for consumption (Tables 2, 3) from A) spring through mid-August and B) mid-August until winter in northwestern Minnesota. Isotopic values of hair samples correspond to A) the distal 2/3 of the hair and B) the 1/3 root end of the hair.

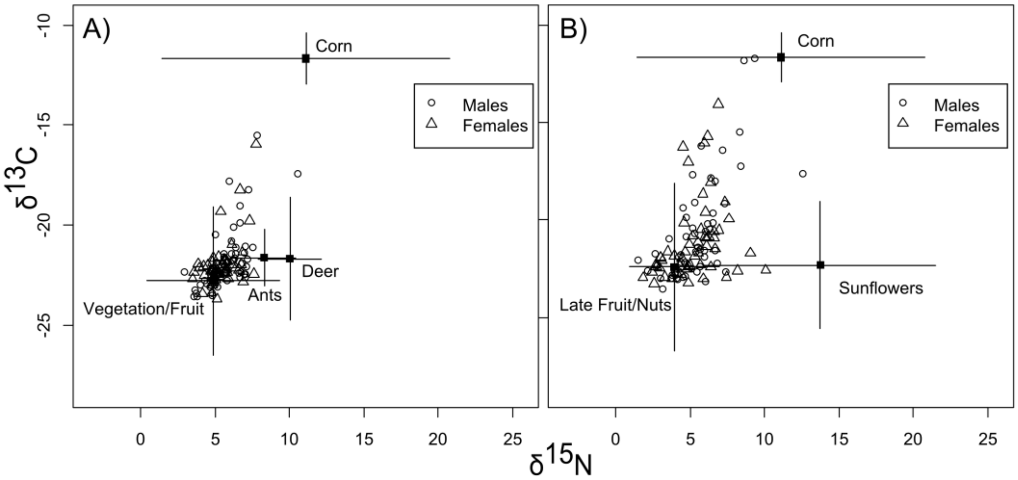


Fig. 3.– Individual dietary estimates (IDEs) proportions of fall crop (corn + sunflowers) from 110 bear-year hair samples from northwestern, Minnesota. The vertical lines represent the median (black) and mean (gray).

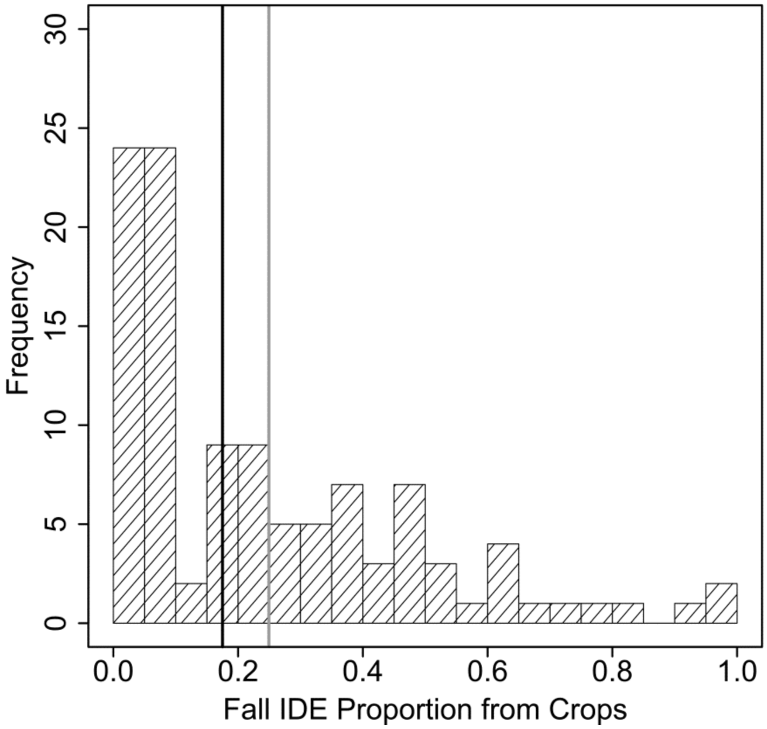


Fig. 4. – Simple linear regression showing relationship between proportion of fall GPS locations of collared bears in corn and sunflower fields in northwestern Minnesota and the estimated proportion of these two crops in their diet derived from stable isotope analysis of the fall growth of their hair.

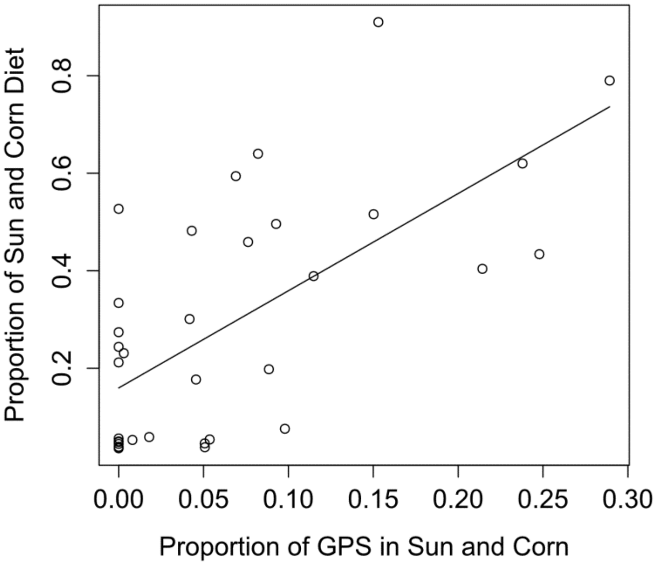


Fig. 5.─ Parameter estimates (β –hat; 95% confidence intervals) from linear mixed model regressions between estimates of individual bears' consumption of crops (IDE) and covariates relating to food availability and physical status of animals (Table 1). Covariates were scaled and centered (Schielzeth 2010) for comparison purposes.

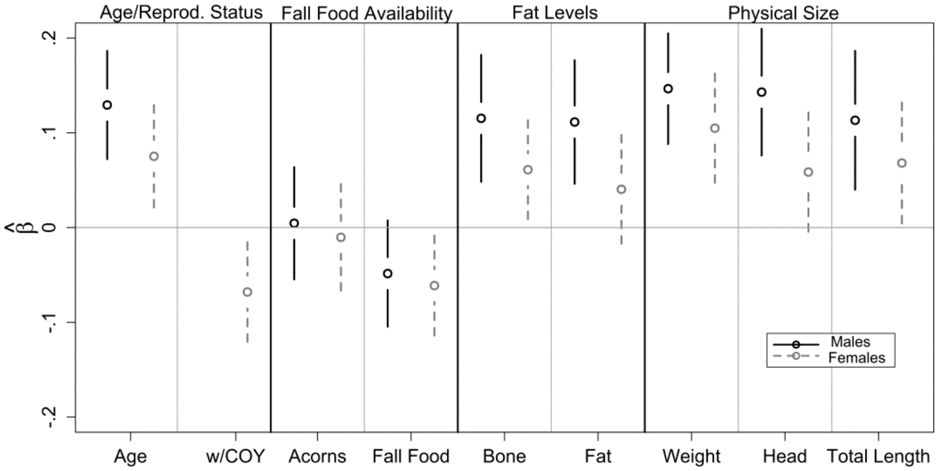
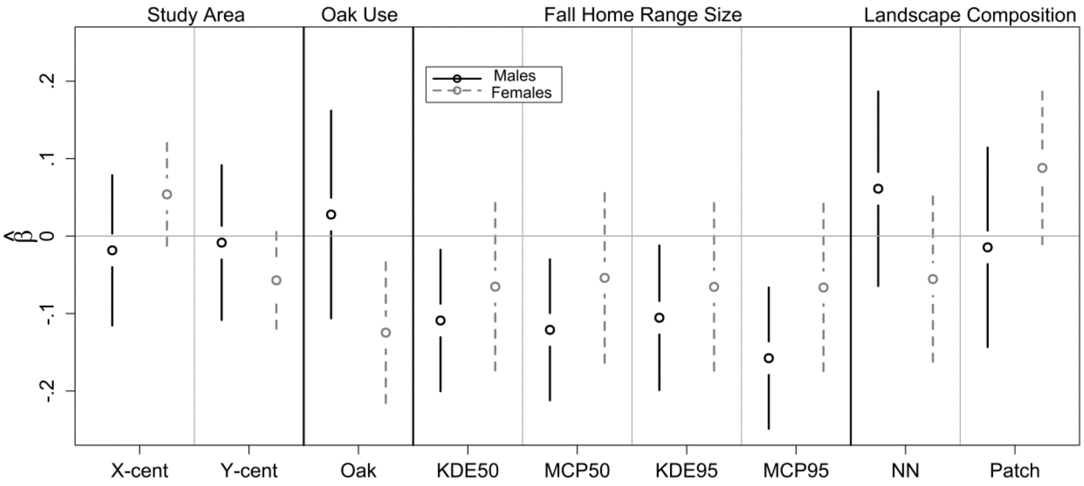


Fig. 6. − Parameter estimates (β –hat; 95% confidence intervals) derived from linear mixed model regressions relating estimate of individual bears' consumption of crops (IDE) with spatial covariates based on GPS data from radio-collars (Table 1). Covariates were scaled and centered (Schielzeth 2010) for comparison purposes.



## CHAPTER 2

# DO INNATE FOOD PREFERENCES AND LEARNING AFFECT CROP RAIDING BY AMERICAN BLACK BEARS?

## 2.1 INTRODUCTION

Populations of American black bears (*Ursus americanus*) have expanded both geographically (Williamson 2002, Scheick and McCown 2014) and numerically (Garshelis and Hristienko 2006) in recent decades. Bear population growth coupled with human encroachment into bear habitat has led to increased levels of human-bear conflicts (Peine 2001, Hristienko and McDonald 2007, Spencer et al. 2007). Many populations are thriving in areas once assumed to be uninhabitable by bears and dominated by anthropogenic features (Lyons 2005, Baruch-Mordo et al. 2008, Shivik et al. 2011). Throughout the United States, wildlife managers and biologists have documented bear depredation of agricultural crops (Davenport 1953, Garshelis et al. 1999, Witmer and Whittaker 2001, Dobey et al. 2005, Benson and Chamberlain 2007) resulting in financial losses for farmers, and ultimately to a reduced human tolerance for coexistence with bears (Bowman et al. 2001).

The availability and abundance of wildland fall forage is believed to be the foremost driver of crop depredation by bears (Rogers 1976, Mattson 1990, Jonker et al. 1998). Maturation of crops that bears eat, such as corn, oats, and sunflowers, occurs when bears are in a state of hyperphagia, a period of intense foraging to add fat reserves for winter (Hilderbrand et al. 1999). When bears cannot acquire adequate calories by foraging on natural foods, they seek calorie-rich alternatives, where they can amass fat quickly. If calorie requirements are unmet, cub production and growth may be reduced (Eiler et al. 1989, Elowe and Dodge 1989, Noyce and Garshelis1994, Costello et al. 2003) and risky behavior, including use of anthropogenic foods, may increase (Noyce and Garshelis 1997, Baruch-Mordo et al. 2014). Other factors that influence the timing and amount of crop depredation include the types of available crops (Warburton and Maddrey 1994) and landscape configuration (Retamosa et al. 2008, Takahata et al. 2014).

Individual bears vary in their propensity to exploit crops, likely related to their knowledge of cropfields, how far they are willing to wander to find a cropfield, how driven they are to gain weight, how much risk they are willing to take, and how they fit within the social hierarchy. Male bears seem to be the primary crop depredators (Garshelis 1989, Maddrey 1995, Ditmer 2014, chapter 1), likely due to their more wide-ranging movements, their need to eat more to maintain large size and enhance future reproductive success, their greater boldness, and their ability to sequester the resource for themselves. Female bears tend to be more risk-averse, especially when accompanied by cubs (Beckmann and Berger 2003). Noyce and Garshelis (1997) found that both sexes were willing to take more risks to find food when natural food availability was low, and although females were always more wary than males, their riskiness changed more than males when food conditions were poor. Size of the individual may also play an important role in crop use in terms of caloric needs (Kovach and Powell 2003), social interactions (Garshelis and Pelton 1981, Costello et al. 2009), and foraging efficiency (Welch et al. 1997).

Individuals may also learn to exploit anthropogenic food sources as a routine foraging strategy (Mazur and Seher 2008, Hopkins 2013). Merkle et al. (2013) found that some bears engaged in risky behavior to obtain anthropogenic foods despite abundant wildland food options. During our study of black bears in northwestern Minnesota, where natural habitat is highly fragmented within a matrix of over 50% agriculture, we found that crop use varied widely among individuals: half of GPS-collared bears (*n* =16 bears) used sunflowers and corn extensively ($\bar{x}$ = 16.8% of fall locations [95% CI: 10.8% - 22.9%]), whereas the other half (n=16 bears) showed nearly no use of corn or sunflowers during this same period ($\bar{x}$ = 0.6% of locations [95% CI: 0.1% - 1.1%]) (Ditmer 2014, chapter 4). Exploitation of crops in this atypical bear habitat benefits this population through increased individual size and fecundity, yielding the highest population growth rate in the state of Minnesota (Garshelis et al. 2012). Our observations of bears using crops in northwestern Minnesota's agricultural matrix raised a number of questions and hypotheses, which motivated the study here.

To a bear, a crop field adjacent to a forest may seem like a convenient food-rich patch of habitat. On the other hand, it is likely that bears are also aware that crop fields are riskier in terms of human presence and lack of cover, possibly explaining why bears use crop fields less if natural foods in the forest are sufficiently abundant. Additionally, bears may view crops as a foreign food that they are not accustomed to, and therefore find them less attractive. We sought to test this hypothesis with bears in captivity, by offering them choices between a preferred natural food (acorns; Vaughan 2002) and agricultural foods that bears consumed in our northwestern Minnesota study site (corn and sunflowers). We hypothesized (hypothesis #1) that without the confounding effects of human threats, cover, presence of other competing bears, and travel distance to a crop field, bears in captivity would choose foods based on familiarity and possibly nutritional benefit (Coogan et al. 2014). We further hypothesized (hypothesis #2) that under captive conditions, absent all of the competing factors present in the wild, males and females would show similar food preferences. In the wild, males appear to be much more inclined to feed on crops, so if controlled feeding experiments showed no sex-related difference in food preference, then we can look to other explanations for sex-related differences in crop use.

## 2.2 MATERIAL AND METHODS

We conducted experimental food preference trials with 9 captive black bears (*n* = 6 females, 3 males) housed at 2 facilities managed by the Wildlife Science Center (WSC) headquartered in Forest Lake, Minnesota. Each facility houses the bears in groups but we were able to single out bears into a separate enclosure for the feeding trials. Bears ranged in weight ($\bar{x}$ = 157 kg, range: 55 – 273 kg) and age ($\bar{x}$ = 9.5 yr, range: 1 – 20 yr). Six of the 9 bears were wild-born but arrived at the facility as cubs and thus were not exposed to many natural foods. The other bears were brought to the facility at various ages after being held as pets.

We assessed preference among 4 fall foods that wild bears commonly consumed in our northwestern Minnesota study site: bur oak acorns (*Quercus macrocarpa Michx.*), corn, and 2 types of sunflowers (confection and oil). We conducted 20 trials in 2010 and

29 in 2011 during September – October each year. This corresponds to a period when wild bears in northwestern Minnesota would be feeding on these foods. Bears at the WSC hibernated over winter, so like wild bears, were hyperphagic during the fall. None of these bears had previously been exposed to corn or sunflower seeds except potentially in the stomachs of road-killed deer (*Odocoileus virginianus*), which they were commonly fed throughout the year. The WSC staff provided acorns to bears during the fall; other typical food items included a variety of fresh fruits and vegetables, beaver carcasses, fish, aspen (*Populus tremuloides*) cuttings, beef trimmings, and occasionally dog food. Bears were fed less than their normal portions for 24 hours prior to the trials.

We collected the majority of acorns for the feeding trials from under bur oak trees in northwestern Minnesota and supplemented them with others collected in Saint Paul, Minnesota. We obtained oil and confection sunflower seeds that were grown in northwestern Minnesota. We gathered grain corn from a farm field and wildlife food plot in northwestern Minnesota.

For each feeding trial, we coaxed the individual subject into a separate pen in which there was a feeding station containing 200 g of each of the 4 food choices, each in a separate bowl 55 cm apart (Fig. 1). We attached the feeding station to a flat wooden platform to prevent tipping and to help catch spilled food. Each food type was randomly assigned a bowl to avoid bias due to spatial arrangement. Food items were removed from their parent plant but not otherwise modified; cupules were not removed from acorns if still attached, sunflower seeds were not removed from their pericarp (shell), but corn was shaved from the cob and sunflower seeds were separated from the flower in an attempt to equalize handling time among food options. We conducted 6 feeding trials on 5 bears, 5 trials on 3 bears, and 4 trials on 1 male. All bears received at least 2 trials each in 2010 and 2011.

Two or 3 observers stood 2–3 m away from the bear and outside the pen. One observer watched the bear and called out what food it was consuming, while another recorded the time of each event, to the second. We defined the “first bite” as the first 5 consecutive bites from a single food option. We noted every time the bear switched to a different food item.

During early trial replicates we aimed to remove bears from the feeding trial pen after 20 min, but shortened the targeted trial time to 10 min after the first 2 sets of trials. We were not always successful at removing bears from the enclosure at the specified time. Also, some bears stopped feeding before the target time period due to outside distractions or satiation.

After removal of the bear, we collected the remaining uneaten samples in individual bags and weighed them to determine the amount of each food type consumed. Before weighing, we removed inedible portions (acorn and sunflower shells) that the bear had discarded while eating. We did not weigh the discarded samples because we were unable to collect all discarded waste after each trial (e.g. discarded sunflower hulls were often scattered and trampled into the soil by the bear). All methods were approved by the University of Minnesota’s Institutional Animal Care and Use Committees (1002A77516).

## Calorimetry

We estimated caloric content per gram dry weight of each of the 4 food types. We separated and weighed the inedible portions of each food type (e.g. acorn shells and cupules if attached, sunflower shells) and used at least 30 samples to calculate the average amount of refuse. We estimated moisture content of the edible portions by freeze-drying the samples for a minimum of 48 hours. We crushed the samples and measured caloric value using a Parr Calorimetric Thermometer (Model#:1672, Parr Instrument Company, Moline, Illinois USA). We ran 2 replicates of each food sample and calculated the standard deviation among the replicates. Calorimetry results for bur oak acorns from our 2 collection sites did not differ, so we combined them.

### Statistical analyses

We calculated the time spent foraging on each type of food, number of food types consumed (1–4), number of switches between food types, and consumption (g) of each food type for each trial. We used the average bite rate (total bites/total time feeding on that food type), bite size (grams consumed/total bites), and intake rate (bite rate × bite size = grams consumed/time feeding) for each food option to estimate consumption of each food type during the first 6 min of each trial. This was the duration of the shortest feeding trial; we refer to these as time-corrected consumption values. By using these values, we eliminated confounding issues related to bears that stopped feeding or emptied a food bowl before the end of the trial, or bears that switched to another food because a food bowl became full of shells. We compared average bite rate and bite size among food types and between the sexes across all trials and tested whether differences significantly affected intake rate using an analysis of variance (ANOVA). A significant result ($P <$

0.05) from the ANOVA test for either factor (sex or food type) or the interaction (sex × food type) would suggest that average handling time influenced intake rates and thus might influence food preference.

We averaged the time-corrected consumption proportions of each food type across trials for each individual, so that each bear was a sample unit. We used the resulting values in a compositional analysis with multivariate analysis of variance (MANOVA) in Program R using the package adehabitat (Aebischer et al. 1993, R Development Core Team 2012, Calenge 2006). Though typically used in habitat selection studies to properly account for the lack of independence between used and available habitat, compositional analysis is also appropriate for use in experimental feeding preference trials (Woods 2009, Pearson et al 2011). Food preferences were assessed by comparing the log-ratio–transformed average proportions of consumption by individual for each food choice to the starting availability (equal availability in our trials = 0.25). Proportions <0.01 were changed to 0.01 because compositional analysis is sensitive to outliers and requires a logarithmic transformation. We conducted a second compositional analysis using only females ($n = 6$), but lacked sufficient sample size ($n = 3$) to do so for males (Aebischer et al. 1993). We also examined how selection changed over time by plotting the percent consumption of food types through the multiple trials.

## 2.3 RESULTS

Duration of feeding trials ranged from 6 min 16 sec to 36 min 20 sec ($\bar{x}$ =15 min 45 sec). Variation was due to bears quitting early or remaining after the designated trial duration (not being able to remove the bear), and our changing the targeted trial duration from 20 to 10 min. Corresponding with reduced access time to the feeding station, total food consumption varied from the first feeding trials ($\bar{x}$ = 389 g, SE = 62 g) to the last 2 feeding trials ($\bar{x}$ = 338 g, SE=44 g). During the first 6 min, bears consumed, on average, 3.5 food types per trial; both sexes switched between food bowls often (females: $\bar{x}$ = 6.3, males: $\bar{x}$ = 7.2 times per 6 min) indicating that bears tasted most food options and then decided which food(s) to select.

Compositional analysis of the time-corrected data indicated differential selection among the 4 food options ($L_3 = 0.033$, $P < 0.001$). Oil sunflowers ranked highest (Table 1), constituting an average of 45% (95% CI: 25 – 65%; Fig. 2) of the food consumed. Oil sunflowers also had the highest caloric content and largest percent of edible dry mass (Table 2). Oil sunflowers had a higher seed to shell biomass ratio than the larger, confection sunflowers, and shells were also thinner and likely more palatable.

Bears preferred the agricultural options in order of caloric density. Bears largely did not select corn: it ranked last in compositional analysis (Table 1), averaging 8.9% (95% CI: 0 – 22%) total consumption (Fig. 2); only 1 individual selected corn first (Tables 3 and 4). All other food choices were selected first at least once by 6 of 9 individuals (67%).

The only natural food option, acorns, had the second lowest caloric content and highest amount of refuse per sample (Table 2). This food type was selected first most often (41%, Tables 3 and 4). Acorns ranked second in both compositional analysis (Table 1) and time-corrected consumption, at 30% (95% CI: 16 – 43%; Fig. 2).

Males preferred oil sunflowers ($\bar{x} = 61\%$ of consumption, SE: 18%) to all other options. However, their first bites did not show this selection (Table 3). Their focus on oil sunflowers occurred after some initial tasting.

Conversely, acorns had the highest ranking in the compositional analysis for the 6 females ($L_3 = 0.02$, $P < 0.001$; Table 5). However, the average consumption of acorns by females progressively diminished with each of the 6 trials (80, 43, 33, 30, 24, 12% for trials 1–6 respectively). With experience (more trials), females increasingly consumed oil and confection sunflowers over the course of this 2-year study (Fig. 3), so that by the end of our experiment, females consumed similar amounts of oil sunflowers ($\bar{x} = 37\%$, SE: 12%) and acorns ($\bar{x} = 35\%$, SE: 9%). First selection for females also favored agricultural options in later trials but acorns were selected first in 15 of 34 trials (44%) overall (Table 4).

Males had a higher average caloric consumption ($\bar{x} = 643$ kcal, 95% CI: 545−742) than females $\bar{x} = 475$ kcal, 95% CI: 313−636) during the first 6 min of each trial. This difference was driven by their selection of calorically-rich oil sunflowers, not higher intake rates. Females had a higher bite rate ($\bar{x} = 14.9$ bites/min, 95% CI: 7.9−21.9) than males ($\bar{x} = 11.4$ bites/min, 95% CI: 3.8−19.1), whereas males had a larger bite size (females: $\bar{x} = 6.2$ g/bite, 95% CI: 4.3−8.2, males: $\bar{x} = 7.4$ g/bite, 95% CI: 4.3−10.4). Bite rates for corn were the quickest ($\bar{x} = 22.7$ bites/min, 95% CI: 16.5−28.9) and those for acorns were slowest ($\bar{x} = 7.9$ bites/min, 95% CI: 7.1−8.7), because corn required no handling time whereas bears manipulated acorns in their mouth to remove and spit out the shell. However, average edible bite size was largest for acorns ($\bar{x}$ = 8.7 g/bite, 95% CI: 6.5−10.8) and smallest for corn ($\bar{x}$ = 4.1 g/bite, 95% CI: 0.6−7.6). As a result of the inverse relationships between bite sizes and rates among the sexes and food types, intake rates did not significantly differ between the sexes ($F_{1,28}$ = 0.55, $P$ = 0.47), food options ($F_{3,28}$ = 1.62, $P$ = 0.21), or their interaction ($F_{3,28}$ = 0.20, $P$ = 0.89).

## 2.4 DISCUSSION

Results of these controlled feeding trials support our hypothesis (hypothesis #1) that food preferences of bears during hyperphagia are influenced both by familiarity and caloric reward. Possibly, the smell or taste of the oil sunflowers signaled their rich caloric content, and made them especially attractive. Males' first bites, for the first 3 trials, showed a testing strategy, but further into each trial and with more trials, they ate increasingly more oil sunflowers. Females were less inclined to eat anthropogenic foods early in the experiment, but grew more attracted to sunflowers with experience.

These results from captivity fit with observations from the wild. Studies of free-roaming bears found males to be generally less wary of anthropogenic foods and smells (Beckmann and Berger 2003). Consistent with this, males tend to be more exploratory, more prevalent at range edges (Kojola and Heikkinen 2006, Jerina and Adamič 2008), and more likely to use urban areas (*Merkle et al. 2013, Baruch-Mordo et al. 2014)* and agriculturally dominated regions (Benson and Chamberlain 2007). Data from GPS-collared bears in our northwestern Minnesota study indicated that males used agricultural crops significantly more than females (Ditmer 2014, chapter 4). Males may be especially motivated to find calorically-rich fall feeding sites in order to gain mass quickly, which may increase body size the following year, and ultimately enhance mating success (Kojola and Heikkinen 2006, Kovach and Powell 2003). Competition for mates is likely to be especially keen at the edge of the range, which is male-dominated. Oil sunflowers may be sought after by males because they provide nearly 1.5 times the caloric density of acorns (Table 2). Males are seemingly more driven to consume a calorie-rich food, which in the wild entails overcoming risks; in our captive experiments this was manifested as being more willing to try a novel food.

In the wild, caloric density relates not only to calories/gram of biomass of the food, but also the density of the food in the foraging area and the handling time of the food. In our experiment, all foods were presented in bowls, so were at similar densities. In the wild, agricultural crops like sunflowers and corn are densely packed on the plant, and stalks closely planted in neat, dense rows, providing easy access for bears. By contrast, oak trees are generally more scattered in the forest, and acorns spread throughout the leaf litter (bears generally eat acorns from the ground after they fall) and under brush. It is unlikely that a bear in the wild would find acorns at a density equal to what we provided in this experiment. Thus, actual caloric intake rates for all of these foods are certainly less in the wild, especially for acorns.

Our field studies indicated that female bears tended to select natural fall foods (acorns, other nuts and some fleshy fruits) over agricultural foods when abundance of these foods was sufficient to satisfy their caloric demands (Ditmer 2014, chapters 1 and 4). They appeared to be deterred from cropfields, likely due to the sparse cover, presence of people (farmers and hunters) and a few large, dominant male bears. Innate preferences for certain tastes also likely influenced their food selection. Bacon and Burghardt (1983) found that captive bears preferred wildland foods with high levels of starches, sugars or carbohydrates, whereas they selected for more protein-rich non-wildland foods. We did not measure protein and carbohydrates for our sample foods, but based on published values, the selection ranking that we observed was not correlated with either (United States Department of Agriculture 2012).

We found the low corn consumption in our trials surprising because corn has been commonly reported as a crop targeted by bears (Davenport 1953, Landers et al. 1979, Stowell and Willging 1992, Garshelis et al. 1999, Benson and Chamberlain 2006). Bears in northwestern Minnesota frequently foraged in corn fields during late summer and fall (Ditmer 2014, chapter 4), so we expected bears would readily eat the corn (which we obtained from northwestern Minnesota fields) in our trials. The lack of preference for corn in our study may have been due to the use of long-maturity silage hybrids, compared against sunflowers and an unusually high density of acorns. Wildlife managers in Wisconsin reported drastic increases in bear damage to corn fields when shorter maturity grain corn was grown in bear range (Stowell and Willging 1992). Other reports of corn consumption by bears occurred without overlapping regional production of sunflowers. Northwestern Minnesota may be the only region in the United States to have large areal spatial overlap of corn and sunflower production and a resident population of bears. However, oak stands, and corn and sunflower fields are often spatially separated, and offer different access and threats to bears, depending on nearby forest cover, roads, and houses. Weather conditions dictate planting dates and phenology of the agricultural options, but generally, corn is targeted by bears during the "milk stage" which can begin in early-to-mid-August (Stowell and Willging 1992, Ditmer 2014, appendix 1). However, we also documented GPS-collared bears foraging in corn fields in October and November, just prior to denning.

Female bears' initial preference for acorns over agricultural foods is consistent with observations in the wild that they are more wary foraging in crop fields. Research has suggested several potential factors for this reluctance. Dominant males in free-roaming populations may socially exclude females from small, food-rich sites. Social exclusion has been documented in black bear populations when highly valued resources are limited (Garshelis and Pelton 1981). Alternatively or additionally, females may show more reluctance to use agricultural fields because they fear humans more than males do. Lack of horizontal cover (Mysterud and Østbye *1999),* scent of male bears (Wielgus and Bunnell 1994), age (Rode et al. 2006), or the immobility and vulnerability of cubs (Blanchard and Knight 1991) may also influence foraging behavior. Finally, females have smaller, and often more stable home ranges (Baruch-Mordo et al. 2014) suggesting they are less willing to travel widely, so they may be less prone to discover fields of edible crops, especially as farmers change what they plant in fields year to year. Most fields are not crops that bears consume.

None of these were factors in our study, so our results (counter to our hypothesis #2) suggest that females were also more inclined to eat natural foods because of taste familiarity or innate taste preferences. This alone could explain the lower use of crop fields by females in the wild. But it is likely that all of these factors are intertwined.

Males have more pressure to gain weight, and also are not burdened with cub-rearing, so it is advantageous for them to range widely to find rich sources of food, to assert dominance over these foods, to accept increased threats associated with these foods, and to identify and adapt their diet to novel, calorie-rich foods on the landscape. Females may require more positive feedback to overcome their tendency to stay with safe, familiar foods.

These findings predict that in an expanding black bear population, males are likely to be first to exploit agricultural foods, but with time and experience, females will do the same. Accordingly, their reproduction will likely increase as documented in other populations with access to a hyper-abundance of calories (Beckmann and Berger 2003), and their cubs will learn these foods as a normal component of their diet (Hopkins 2013). In this way, this forest-dwelling omnivore eventually adapts to living in an agricultural landscape.

## 2.5 MANAGEMENT IMPLICATIONS

The expansion of American black bear population numbers and geographic range has resulted in increasing numbers of human-bear conflicts and complaints to wildlife managers. This is especially true for managers in more northern latitudes where crops that bears may consume, such as corn, are increasing in popularity because of the availability of shorter maturity seeds and longer growing seasons. Our experimental study using captive black bears demonstrated the greater tendency for male bears to try novel, calorie-rich foods, confirming field observations that such foods may pave the way for population expansion, initially by males, but later followed by females. It is unlikely that farmers can prevent bears from eating these crops, especially males who appear especially driven to find caloric hotspots. However, growing these crops in fields as far away as possible from natural bear habitats may dissuade female bears from developing a taste for them, and thereby reduce some crop damage.

### *Acknowledgements*

We thank the founder and executive director of the Wildlife Science Center, P. Callahan, and staff members especially M. Row for allowing us to use their captive bears in this study, and their assistance with the experiment. The Minnesota Corn Growers Association provided funding for the materials. Several farmers in northwestern Minnesota and the Thief Lake Wildlife Management Area staff of the Minnesota Department of Natural Resources allowed us to collect their field corn. We thank the numerous students at the University of Minnesota who assisted in field work. We thank J. Jungers, S. Thompson, K. Noyce and J. Fieberg for helpful suggestions on previous drafts.

**Table 1.** Ranking matrix based on compositional analysis[a] of 4 fall foods offered in equal quantities (grams) to captive male and female bears in Minnesota, September – October, 2010 and 2011.

| **Food type** | **Oil sunflowers** | **Acorns** | **Confection sunflowers** | **Corn** | **Rank**[b] |
|---|---|---|---|---|---|
| Oil sunflowers | | + | + | +++ | 1 |
| Acorns | - | | + | +++ | 2 |
| Confection sunflowers | - | - | | + | 3 |
| Corn | --- | --- | - | | 4 |

[a] Values indicate positive (+) or negative (-) Student's t-values from mean differences. Triple signs (+++ or ---) indicate significance at the alpha = 0.05 level. Student's t-values were derived using the log ratios comparing percent of biomass consumed versus the percent available (25%) of each of the 4 offered foods.

[b] Rank was calculated by summing the number of columns with positive signs for each row (food type). Higher rank indicates greater preference.

**Table 2.** Gross energetic content and total available calories of food samples presented to captive Minnesota black bears during food preference trials. Each sample included a replicate run in the bomb calorimeter.

| **Food type** | **Inedible portion** | **Moisture content** | **Overall edible dry weight %** | **kcal/g (dry wt.)** | | **Available kcal per trial**[a] |
|---|---|---|---|---|---|---|
| | | | | **Mean** | **SD** | |
| Corn | 0.0% | 33.7% | 66.3% | 4.23 | 0.04 | 560.8 |
| Acorns | 38.5% | 51.6% | 31.7% | 4.43 | 0.09 | 281.1 |
| Confection sunflowers | 44.9% | 2.4% | 53.8% | 5.89 | 0.01 | 633.4 |
| Oil sunflowers | 27.0% | 2.9% | 70.9% | 6.60 | 0.01 | 935.8 |

[a] Based on 200 grams per trial per food option.

**Table 3.** Percent of first choice selections (defined as the first 5 consecutive bites of any 1 food type) among 4 food choices offered in equal quantities to captive male black bears (*n* = 1–3) during 6 trials in 2 years (September –October, 2010 and 2011).

| **Trial** | **Oil sunflowers** | **Acorns** | **Confection sunflowers** | **Corn** | **No. of bears** |
|---|---|---|---|---|---|
| 1 | 33.3% | 33.3% | 33.3% | 0% | 3 |
| 2 | 33.3% | 33.3% | 33.3% | 0% | 3 |
| 3 | 33.3% | 33.3% | 33.3% | 0% | 3 |
| 4 | 66.7% | 0% | 33.3% | 0% | 3 |
| 5 | 50.0% | 50.0% | 0% | 0% | 2 |
| 6 | 0% | 100% | 0% | 0% | 1 |
| All | 40.0% | 33.3% | 26.7% | 0% | 15 |

**Table 4.** Percent of first choice selections (defined as the first 5 consecutive bites of any 1 food type) among 4 food choices offered in equal quantities to captive female black bears (*n* = 4–6) during 6 trials in 2 years (September –October, 2010 and 2011).

| **Trial** | **Oil sunflowers** | **Acorns** | **Confection sunflowers** | **Corn** | **No. of bears** |
|---|---|---|---|---|---|
| 1 | 16.7% | 83.3% | 0% | 0% | 6 |
| 2 | 33.3% | 50.0% | 16.7% | 0% | 6 |
| 3 | 33.3% | 50.0% | 0% | 16.7% | 6 |
| 4 | 50.0% | 33.3% | 16.7% | 0% | 6 |
| 5 | 50.0% | 33.3% | 0% | 16.7% | 6 |
| 6 | 0% | 0% | 75.0% | 25.0% | 4 |
| All | 32.4% | 44.1% | 14.7% | 8.8% | 34 |

**Table 5.** Ranking matrix based on compositional analysis[a] of 4 fall foods offered in equal quantities (grams) to captive female bears in Minnesota, September – October, 2010 and 2011.

| **Food type** | **Oil sunflowers** | **Acorns** | **Confection sunflowers** | **Corn** | **Rank[b]** |
|---|---|---|---|---|---|
| Oil sunflowers |  | - | + | + | 2 |
| Acorns | + |  | + | +++ | 1 |
| Confection sunflowers | - | - |  | + | 3 |
| Corn | - | --- | - |  | 4 |

[a] Values indicate positive (+) or negative (-) Student's t-values from mean differences. Triple signs (+++ or ---) indicate significance at the alpha = 0.05 level. Student's t-values were derived using the log ratios comparing percent of biomass consumed versus the percent available (25%) of each of the 4 offered foods.

[b] Rank was calculated by summing the number of columns with positive signs for each row (food type). Higher rank indicates greater preference.

**Figure 1.** Captive black bears in Minnesota were offered 4 different fall foods in bowls to test food preferences, September – October, 2010 and 2011. Photo credit: S. Thompson.

**Figure 2.** Average proportions (±SE) of 4 different food types consumed by black bears during the first 6 min of captive feeding trials, where each food type was offered in equal proportions, September – October, 2010 and 2011.

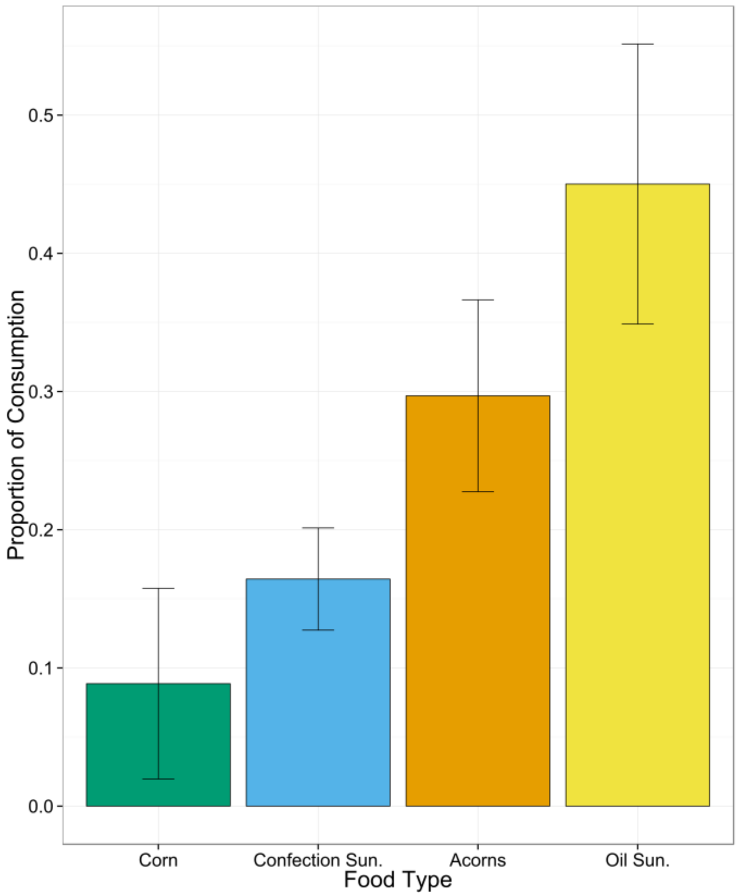
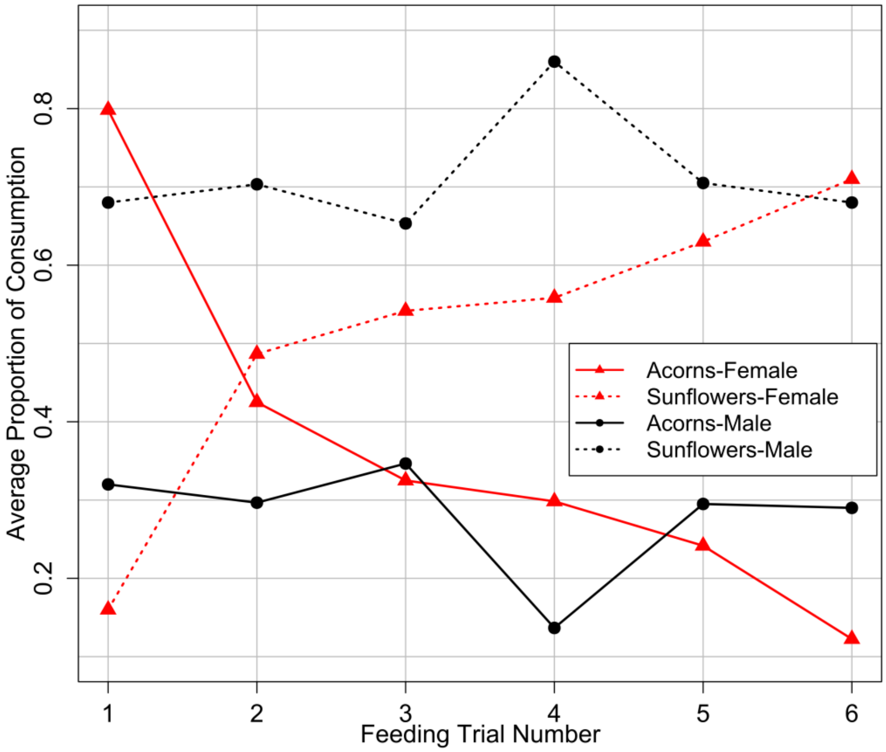


**Figure 3.** Proportions of acorns and sunflowers (oil and confection combined) that captive male (*n* = 3) and female (*n* = 6) bears consumed when offered in equal quantities, during the first 6 min of 6 feeding trials conducted in Minnesota during September – October, 2010 and 2011.



# CHAPTER 3

# BEHAVIORAL AND PHYSIOLOGICAL RESPONSES OF AMERICAN BLACK BEARS TO LANDSCAPE FEATURES WITHIN AN AGRICULTURAL REGION

## 3.1 INTRODUCTION

Understanding the relationship between an organism and its natural environment is fundamental to addressing many questions in applied and theoretical ecology (Costa and Sinervo 2004, Brown et al. 2004). Telemetry studies have increased our understanding as to how various organisms interact with their environment by providing locational information on free-roaming individuals. However, our relative knowledge concerning physiological responses of organisms to stimuli in their natural habitat is lacking, often because most studies of physiology are confined to laboratory settings. In contrast to other visible measures of health (e.g., weight loss, illness, population decline), physiological measurements can capture more immediate changes to an organism's health and thus provide an early warning system for deleterious influences in a changing environment. Advances in biologger technology, which can remotely measure physiological parameters, can be combined with locational data to examine physiological responses to intrinsic and extrinsic factors over extended time periods and in natural settings (Cooke et al. 2004b, Block 2005).

Recently, much research has been focused on determining how landscape configuration (Ellis et al. 2011) and habitat types (Huey 1991, Homyack 2010) may in turn influence innate physiology. For example, heart rate (HR) measurements can provide an indirect measure of field metabolic rates (Butler et al. 2004) and when connected with locational information could predict the relative energetic costs of locomotion (Fortin et al. 2005, Durner et al. 2011) or stressors (Nimon et al. 1996, Cooke et al. 2004a). Understanding the nuances of the direct and indirect costs of locomotion is particularly important for species living in fragmented landscapes where individuals often require more space to obtain required resources (Taylor et al. 1993). Additionally, it has been reported that human presence is often more prevalent in fragmented landscapes, exacerbating stress (Wikelski and Cooke 2006, Arlettaz et al. 2007). Stress can affect breeding success (Giese 1996), habitat use (Thiel et al. 2008), population size (Fefferman and Romero 2013) or space use (Andersen et al. 1996, Angelier et al. 2007).

In recent decades, American black bear (*Ursus americanus*) populations have been expanding geographically (Scheick and McCown 2014), and in the process have come into greater contact with human-occupied or modified landscapes; their interaction with these landscapes has thus far been measured in terms of altered activity patterns (Beckmann and Berger 2003a, Baruch-Mordo et al. 2014), diets (Jonker et al. 1998), habitat use (Obbard et al. 2010, Merkle et al 2013) and survival (Van Manen et al. 2012, Beckmann and Lackey 2008). This species is highly mobile, enabling access to spatially varying resources (Garshelis and Pelton 1981, Noyce and Garshelis 2010). Black bears are also relatively human-tolerant and take advantage of anthropogenic food resources (Maddrey and Pelton 1995; Garshelis et al. 1999). In Minnesota, USA, black bears recently expanded into an agriculturally-dominated region in the northwestern corner of the state and exploited crop fields (Ditmer 2014, chapter 1). Here, bears range over especially large areas (Ditmer 2014, chapter 4) and are exposed to a variety of habitat types, levels of human influence, and forage options, making this an ideal site to examine physiological effects of the environment.

Here we describe the combined use of GPS collars and cardiac monitors to provide unique insights as to how bears react to a human-altered habitat at both physiological and behavioral levels. This investigation involved the portion of the year when bears were actively moving around the landscape, whereas most previous physiological measurements of bears focused on the denning period (Nelson et al. 1983, Laske et al. 2010, Laske et al. 2011). Our first objective was to quantify the influence of movement on heart rate. We hypothesized that a bear's HR will increase with faster movement speeds. Second, we compared seasonal changes in the relationship between movement and HR over the course of the active period of the year. We hypothesized that the relationship would change seasonally with activity patterns (Amstrup and Beechum 1976, Garshelis and Pelton 1980), especially in the fall during hyperphagia (a period of intense caloric intake and consequent fat gains prior to hibernation). We posited that bears follow a similar pattern to that found in small hibernators in which metabolic rate diminishes prior to reductions in food intake, enabling significant gains in body mass (Florant and Healy 2012).

Our third objective was to discern the effects of anthropogenic features (e.g., roads, crop fields, habitat fragmentation), habitat type, weather, and temporal factors (season and time of day) on bear behavior and physiology. These can influence HR either directly or indirectly, by causing changes in movement rates. We predicted that habitats with different food density and understory density (i.e., obstruction to movement) would have distinct effects on their heart rates. We expected that roads, highly fragmented habitat, and agriculture fields would increase heart rate and movements of bears, as they have been shown to increase movement rates in other species (MacArthur et al. 1979, Coffin 2007, Dussault et al. 2007). We predicted that this effect would be gender-specific, as males tend to encounter these features more often due to their larger home ranges (Powell et al. 1997) and their tendency to be less risk-averse (Beckmann and Berger 2003b, Ditmer 2014, chapter 2). Finally, we hypothesized that heart rates would increase, but movement decrease, when bears encountered high temperatures, winds or other extreme weather events (Speakman et al. 2003, Zub et al. 2009, Wingfield et al. 1998, Theil et al. 2004). Our novel use of new biologger technology, coupled with routinely deployed GPS-collars, provided an unique opportunity for enhanced understanding of bear behavior and physiological relationships with their environment.

## 3.2 MATERIALS AND METHODS

### *Study area*

Northwestern Minnesota marks the western edge of the eastern population of the American black bear. Agricultural crops in this area attracted large numbers of bears during a statewide failure of wild bear foods in 1995, and bear numbers have remained high and growing ever since, even while statewide bear numbers have declined (Fieberg et al. 2010, Garshelis and Noyce 2011). The landscape of northwestern Minnesota is comprised of agricultural fields and small woodlots with a few larger areas of state and federal land. A majority of the landscape is dedicated to agricultural production (52.5%), primarily soybeans and wheat with small amounts of corn, oats and sunflowers [collectively ~2–4% dependent on year]). A total of 17.3% of the landscape is forested, comprised of mainly aspen/white birch (*Populus tremuloides*/*Betula papyrifera*, 12.9% of the total area) and bur oak (*Quercus macrocarpa*, 3.6% of the total area). The region was once below glacial Lake Agassiz and the resulting flat landscape has many areas that are poorly drained, at least seasonally, and covered by lowland deciduous shrub (11.5%, primarily willow *Salix spp.*, alder *Alnus spp.*, red-osier dogwood *Cornus sericea*), wetlands (11.2%), and grasslands (7.4%, Conservation Reserve Program land, temporarily fallow fields, or remnant prairie). Urban areas make up a small percentage of the total land cover (0.2%), but the road network is extensive (0.55 km road/km$^2$).

### *Animal location and heart rate data*

During the summer of 2007−2011, we captured bears in baited barrel traps, and fit them with either store-on-board GPS devices (Telemetry Solutions, Concord, CA) or GPS collars that relayed fixes via the Iridium satellite system (Vectronic Aerospace, Berlin, Germany). We visited all collared bears in winter dens to change or refit collars, download stored GPS data, obtain morphometric and physiological measurements, and check on their general health status. We programmed GPS collars to collect fixes at 1–6-hour intervals, depending on the model of collar and time of year. Locations were accurate to within 15 m. Vectronic collars were also equipped with activity sensors that recorded acceleration on the X-Y axis in 5-min intervals during collar deployment.

During den visits in 2008–2013, we surgically implanted cardiac monitors developed for humans (Medtronic Inc., Reveal XT Model 9529, Minneapolis, MN, USA; specifications: nine cc; eight mm x 19 mm x 62 mm; 15 grams). Monitors were sterilized in ethylene oxide and inserted subcutaneously in a peristernal location using aseptic techniques. Monitors provided two data points per day, representing the average heart rate (HR) during daytime (08:00–20:00) and night-time (00:00–04:00) hours throughout the year (henceforth night or day HR interval). These two HR intervals were of different duration, and excluded eight hours per day, a constraint stemming from the intended use of these devices in humans. Data were downloaded noninvasively during subsequent winter den visits using transcutaneous telemetry (CareLink Model 2090 Programmer with software Model SW007, Medtronic Inc., Minneapolis, MN; details in Laske et al. 2011). All methods and animal handling were approved by the University of Minnesota's Institutional Animal Care and Use Committees (1002A77516).

### *Measured variables*

We created two data sets for analysis using the same measured variables. The first, which we analyzed to discern factors affecting movement rate, included all GPS-locations from all hours of the day, each as separate record. The values associated with each location or movement step were modeled for relationship to bear movement rate (see section: *Movement Rate Models*). In the second data set, which we used to discern effects on HR (including the effect of movement speed), we partitioned the data into daily day/night intervals that were aligned with HR intervals and used the average values of any variable measured more than once across that interval (see section: *Heart Rate Models*).

Accordingly, we estimated movement rate (MOVEALL, meters/hour) by dividing measured step lengths (i.e., straight-line distances between consecutive GPS observations) by the time-interval between locations for any locations occurring within six hours of one another. We created a second movement variable that averaged movement speeds within HR intervals (MOVEHR) for use in HR analyses. For this variable we included GPS locations from one hour before and after the HR intervals for store-on-board GPS units because these units had lower fix success than the Iridium satellite collars.

We used ArcMap 10.1 (Environmental Systems Research Institute, Redlands, California, USA) to overlay GPS locations onto a GIS land-cover layer (Upper Midwest

Gap Analysis Program, Minnesota Department of Natural Resources 2012). We classified locations as occurring within one of six composite cover types: 1) aspen-dominated forest (ASPEN: aspen, birch, black ash, *Fraxinus nigra*), 2) oak (OAK: bur oak, upland shrub), 3) marsh (WET: aquatic and marsh), 4) lowland shrub (SHRUB: lowland deciduous and coniferous shrubs), 5) grassland (GRASS) or 6) agriculture (AGFIELD). We added another covariate for distinguishing locations in three types of crops that bears consumed — corn, oats or sunflowers (CROP); this distinction was based on year-specific cover maps created by the United States Department of Agriculture, National Agricultural Statistics Service (United States Department of Agriculture 2012). We classified land-cover types as anthropogenic (agricultural, urban, roadsides) or natural (all other classifications). We used the Minnesota Department of Transportation (2012) map of roads to buffer an anthropogenic swath of habitat 25m to each side.

For each bear GPS location, we calculated mean patch size ($km^2$) for natural habitats, distance (m) to the nearest edge of a patch of natural habitat and distance to the nearest road. We recorded patch size and distance to edge as zero for locations in agricultural areas or the roadway buffer. We created a metric of habitat fragmentation (FRAG) using the first principal component, combining patch size, distance to habitat edge and distance to road; larger values of FRAG were indicative of bear locations in more fragmented areas of the landscape or the edge of a habitat patch. We created a road crossing variable (ROADX) by counting the number of roads crossed over a movement path of connected consecutive locations.

We created kernel density estimators of home range using least-squares cross-validation to create isopleths (5–100%) of annual locations for each bear-year (Geospatial

Modeling Environment; Beyer 2012). We averaged the corresponding values of each GPS location with the underlying isopleth boundaries (ISO) and assigned them to the HR interval in which the location occurred. The isopleth value associated with the final location of each movement step was used when analyzing movement rates. Smaller values for ISO represent locations within the most-used part of each home range.

We used the pheno package in program R (Schaber 2012, R Core Team 2013) to assess photoperiod (PHOTO). We converted all dates to Julian (JULIAN), and for analyses including HR, we created a variable to match the day or night HR interval (DAYNITE). We created a variable (LIGHT) to categorize each hourly increment in the day as either before or after sunset ("sun" or "moon"; movement analysis only).

We obtained weather data from weather stations in Gatzke and Thief River Falls (http://www.wunderground.com/), Minnesota. We utilized data including daily maximum, minimum, and mean temperatures (degrees Fahrenheit, MAXTEMP, MINTEMP, MEANTEMP); maximum and mean humidity (% relative humidity, MAXHUMID, MEANHUMID); total precipitation (cm, PRECIP); average level of cloud cover (0-10, CLOUD); average wind speed (mph, WIND); and a binary value for thunderstorm events (TSTORM).

### *Modeling approach*

We created separate models for assessing the influence of measured covariates on movement rate and HR to better understand direct and indirect effects on bears' HR's. We hypothesized that movement rate would have a strong positive influence on HR, so variables affecting movements necessarily had indirect effects on HR. We also sought to identify factors that directly influenced HR, after we controlled for movement rate (MOVEHR) by including it as a predictor.

We used a two-step modeling approach: 1) first we fit models to individual bear-years using a stepwise selection process; then 2) we fit a mixed model to all the data, including only those covariates supported by ≥ four individual bear-year models. Our decision to first create models for each bear-year was a conservative choice due to the large number of degrees of freedom associated with fitting mixed models using all variables and all bear-years. Step two allowed us to test a subset of the variables using the full dataset of bear-years, while also allowing for random coefficients (i.e., coefficients specific to each bear-year).

Covariates representing natural and anthropogenic landscape attributes were modeled differently for movement and HR models. In the HR model, we constructed covariates using the proportion of GPS locations occurring within each habitat type during the HR intervals. In the movement model, we created binary covariates to represent the cover type associated with the last GPS location of each movement step. We divided ROADX by the number of hours in a HR interval for HR models and divided ROADX by the number of hours in a movement step for movement models.

Before fitting models we checked for collinearity among measured variables using variance inflation factors (VIF). If two variables caused a large increase in VIF (10+), we chose the most biologically appropriate to include in analyses (Table 1).

### *Heart rate models*

We created model sets for each bear-year by regressing average HR in beats per minute (bpm) as a function of: 1) movement rate (MOVEHR, m/h), 2) temporal variables

(DAYNITE, splines based on JULIAN), 3) weather conditions (TEMP, WIND, PRECIP, CLOUD, TSTORM), 4) percentage of habitat use by habitat type (OAK, LLS, GRASS, MARSH), 5) road crossings per hour (ROADX), 6) degree of habitat fragmentation (FRAG), 7) location within the home range (ISO), and 8) percentage of time spent in agricultural (AGFIELD, not used for bear foraging) and crop fields (CROP, consumed by bears: corn, sunflowers and oats, Table 1). We expected bears to respond differently to roads and habitat fragmentation, depending on time of day since bears may be less stressed when moving through these areas at dark so we included interactions for ROADX × DAYNIGHT and FRAG × DAYNIGHT. Bears are known to seasonally change activity patterns, so we included the interaction DAYNIGHT × splines for JULIAN. We also hypothesized that the relationship between HR and ambient temperature as well as HR and agricultural areas might change seasonally so we tested the interactions MEANTEMP × splines for JULIAN and AGFIELD × splines for JULIAN.

We fit models using generalized least squares (GLS) to allow for temporally autocorrelated residuals via the gls function in the nlme package of program R (R Core Team 2013, Pinheiro et al. 2013). We used regression splines with five degrees of freedom when modeling the effect of JULIAN, to allow for nonlinear seasonal trends in the relationship between movement and HR. Additionally, we explored the seasonal changes in heart and movement rate data by fitting loess curves to the data based on Julian date. We excluded day or night periods with inadequate data to calculate movement rate. We accounted for autocorrelation among HR averages by including a first order autoregressive correlation structure (AR1). For this purpose, we started at the first HR interval in each bear-year and created a count of HR intervals as discrete units, skipping periods that were excluded due to insufficient data. We included CROP in individual bear-year models if >5% of HR intervals included at least one observation in CROP.

For each set of models, we used backwards stepwise elimination to remove the least significant covariates. We considered covariates with $p \leq 0.05$ to be significant. If a covariate had a p-value near this threshold, we looked at its effect on the residuals and the magnitude of influence on the predicted response to determine if it should be included in the model.

### *Movement rate models*

We modeled log-transformed movement rate (MOVEALL, m/hour) for each season and bear-year as a function of a cyclic smoother based on: 1) HOUR of the day, 2) habitat types including agricultural fields (HABITAT), 3) whether the agricultural area contained potential bear forage (CROP), 4) habitat fragmentation (FRAG), 5) road crossings per hour (ROADX), 6) weather conditions (TEMP, WIND, PRECIP, CLOUD, TSTORM), and 7) location within the home range (ISO). We included an interaction between SUN × ROADX because we hypothesized that bears might interact with roads differently at night (Table 1).

We used generalized additive models (GAM) in program R with package mgcv (Wood 2006) to model spring (den exit in March or April – July1), summer (1 July – 1 Sept.), and fall (1 Sept – den entrance in Oct or Nov) movement rates in separate model sets. We used GAMs to model non-linear relationships instead of regression splines as in the HR models, owing to the larger number of observations per individual (i.e., step length values instead of HR interval averages). We incorporated a cyclic cubic spline smoother to model the nonlinear effect of hour of day (following Martin et al. 2013) on movement rates. We assumed errors followed an autoregressive correlation structure and used time (in minutes) since the first observation to account for this feature. We required 3% of locations within a season to be in the CROP classification for consideration in an individual's model set. We used the same process as the HR models to determine the best supported covariates for each bear-year model set.

### *Mixed models*

The commonly supported covariates in the individual HR models were included in a linear mixed model fit using the lme function in the nlme package of program R (R Core Team 2013, Pinheiro et al. 2013). We used the commonly supported covariates in the individual movement models in a generalized additive mixed model (GAMM) in program R with package mgcv (Wood 2006) for each season. For both model sets, we used bear-year (BEARYEAR) as a random intercept and included a first order autoregressive correlation structure, formulated in the same manner as in the GLS and GAM models. To incorporate individual variation in the relationship between movement and HR, we modeled movement rate (MOVEHR) as both a random (slope) and fixed effect in the HR model. To better account for differences between the sexes we considered additional interactions in the global model (e.g., HABITAT × SEX [movement model], FRAG × SEX × DAYNIGHT [HR model]). We initially fit mixed models using maximum likelihood during model selection process then refit the best fitting model using restricted maximum likelihood to obtain unbiased parameter estimates (Zuur et al. 2009). We used the effects package (Fox 2003) to generate model-based predictions of the movement and HR values with associated 95% confidence intervals using the best fitting models. We inspected relationships between individual covariates and the response variable, while holding all other covariates at their mean values, to assess a covariate's strength of influence on predicted HR.

### *Model validation*

To test the validity of our models, we repeated our analyses of HR and movement rate using three additional bear-years obtained in 2013. We fit our top HR model to the new data using the same mixed modeling methodology and compared the results with our significant findings from the data obtained between 2009–2012. We re-fit our heart mixed model utilizing all available data and reported updated results. We modeled the movement rates from the 2013 data using the same individual GAM models and compared the seasonal results with our previous significant findings.

### *Post-hoc analysis*

To further investigate what turned out to be an unexpected relationship between bear HR and landscape fragmentation (FRAG), we utilized data from activity sensors on seven bears (five female, two males) during 2012-2013. An activity value was reported every 5 minutes, from which we calculated an average activity value (ACT) for each HR interval. We modeled HR as a function of activity and movement (MOVEHR), again controlling for seasonal patterns by modeling JULIAN with regression splines. We also included a random intercept for BEARYEAR, and we used the same autocorrelation structure as in the other HR models. We included MOVEHR as a covariate in all models despite correlation with activity to discern any residual effects of activity on HR beyond locational movement. To allow for the possibility of a FRAG × DAYNIGHT × SEX interaction, we fit separate models to males and females and for day and night HR intervals.

## 3.3 RESULTS

We obtained paired locational and HR data for seven different bears (three male, four female), representing nine bear-years (four males, four female with cubs, one solitary female) during 2009 – 2012. In seven bear-years, HR data spanned an entire year of activity (den emergence to den entry); mean number of monitored days was 172 (SE = 11, range = 118 - 221) and mean number of useable HR intervals for the nine bear-years was 308 (SE = 34, range = 169 – 439). For our movement analysis we incorporated an average of 1868 (SE = 436, range = 446 – 3658) movement steps per individual annually, 564 (SE = 126, range = 166 – 1,065) in the spring, 644 (SE = 138, range = 158 – 1,290) in the summer and 743 (SE = 186, range = 68 – 1,520) in the fall.

Spring movement rates (MOVEALL, Figure 1A) were low from sunrise through the middle of the day, increased rapidly near sunset for about 4 hours (~19:00 – 23:00 h), then declined sharply in the hours approaching sunrise. Spring movements were slower and had less variation throughout the day than during summer or fall (range: spring: -0.5 – 1.0, summer: -1.5 –1.5, fall: -1.0 –1.0, Figure 1). Trends around sunset and sunrise continued into summer, but bears became more active during daylight hours and movement rates reached the maximum values of any season (Figure 1B). In fall, daytime activity greatly diminished, and bears returned to a diurnal movement pattern similar to spring, but with extended hours of activity after dark (Figure 1C). Bears moved the least in the hours immediately pre-dawn in spring and summer, but in mid-day during fall.

HR and movement rate, both day and night, exhibited parallel seasonal trends from April–August (Figure 2). From September to den entrance, however, as bears reduced activity prior to denning, HR fell earlier and more quickly than corresponding movement rates, particularly during the night (Figure 2). The average HR started to decline 16 days earlier than movement rate (nighttime data: 5 September vs. 21 September). All bears except the largest individual, exhibited this relationship (Figure 3A-3H).In some cases, movement rates increased even after HR started to decline for the season.

### *Direct effects on bear heart rates*

Movement rate (MOVEHR) positively affected HR for all bear-years and was significant in the mixed model ($\hat{\beta}$= 1.87, SE = 0.35, p < 0.001, Figure 4A). The best fitting model included a random intercept for bear-year and a random slope for movement rate (likelihood ratio test, no random slope vs. random intercept: L = 93.79, p < 0.001). Mean predicted HR was 21% higher for bears moving at 66 m/h (median movement rate) than at 0.1 m/h (slowest movement rate for a non-stationary bear) and 34% higher when moving at the fastest observed rate of 3.2 km/h (Figure 4B).

After accounting for the influence of movement rate (MOVEHR) and the seasonally changing influence of the day-night cycle, bear HR provided further information about bears' responses to crop fields, habitat fragmentation, ambient temperature, and location within their home range (Table 2, Figure 5). Both sexes were infrequently located in agricultural fields that did not contain corn, sunflowers, or oats (AGFIELD; $\bar{x}_m$ = 5.6% of all locations, 95% CI: 2.4 – 8.7%; $\bar{x}_f$ = 4.7%, 95% CI: 0.0 – 8.3%). However, because these fields were the dominant feature on the landscape (areal coverage ≈ 48.5 – 50.5%) bears crossed them regularly ($\bar{x}_m$ = 42.6% of movement steps,

$\bar{x}_f$ = 26.1%). Conversely, despite being a small portion of the landscape (~2 – 4%), males were located in corn, sunflower and oat fields (CROP) more often ($\bar{x}$ = 10.2%, 95% CI: 10.6 – 21.0%); females, however, rarely used CROP ($\bar{x}$ = 1.2%, 95% CI: 0 – 3.2%). Females moved across AGFIELD particularly quickly, whereas males did not (summer, Figure 6B vs 6C). Movements across AGFIELD prompted higher than expected HRs in both sexes (Table 2, Figure 6), whereas when bears were located in CROP, they tended to have lower or no greater than expected HR (Figure 6; three of five bear-years had significant negative relationships).

During the summer, female and male bears responded differently to landscape fragmentation: whereas movement rate of females declined, males moved more quickly within natural habitat with the highest levels of fragmentation (e.g., small patch of aspen forest surrounded by roads and agricultural fields); no other significant effects of FRAG on movements were apparent (Figure 7). Additionally, HR was lower when bears used more fragmented portions of the landscape, but the significant interaction terms in this relationship suggested that the daytime HR of female bears showed the strongest response to FRAG (Table 2, Figure 6). Our post-hoc analysis suggests that females' unexpected HR response to FRAG, after accounting for movement rate (MOVEHR) and Julian date (JULIAN), may be due to a drop in activity (ACT) during daytime (n=5, $\hat{\beta}$ = -0.042, SE = 0.010, p = < 0.001) in fragmented areas Activity levels for male bears (n=2) did not show a significant relationship with our indices for habitat fragmentation ($\hat{\beta}$ = -0.019, SE = 0.017, p = 0.258).

We found evidence that bears moved more quickly when at the periphery of their home ranges (ISO) during spring and fall ($\hat{\beta}$ = 0.301, 0.380, SE = 0.138, 0.135, p = 0.029, 0.005 for spring and fall respectively) relative to movements near the home range center. Conversely, when near the center of their home ranges, they had significantly higher HR than would be expected given their movement rate (Table 2, Figure 6).

During spring, higher ambient temperatures were associated with faster movements ($\hat{\beta} = 0.044$, SE = 0.004, $p \leq 0.001$) and higher than expected HR (Figure 8A). In fall, HR was negatively associated with ambient daily temperatures (Figure 8B) despite faster movement rates ($\hat{\beta} = 0.050$, SE = 0.004, $p \leq 0.001$)

*Indirect effects on bear heart rates*

In all seasons, when bears crossed roads, their rate of movement increased ($\hat{\beta}$ = 1.10, 1.03, 1.14, SE = 0.044, 0.056. 0.066, $p \leq 0.001$ for spring, summer, fall respectively) but HR did not change beyond what was expected given the increased movement. Road crossings were a common occurrence in northwestern Minnesota: our nine bear-years of data contained 1923 road crossings and 1243 (7% of total) movement steps with at least one crossing. Males crossed roads more frequently than females in the spring ($\bar{x}_m$ = 17.1 % of movement steps; SE = 1.5%; $\bar{x}_f$ = 2.2 %; SE = 1.1%) and summer ($\bar{x}_m$ = 16.8%; SE = 3.6%; $\bar{x}_f$ = 2.1%; SE = 0.57%), but neither sex crossed roads very frequently in the fall ($\bar{x}_m$ = 3.9%; SE = 1.23%; $\bar{x}_f$ = 3.4%; SE = 1.5%).

Several habitat types appeared to indirectly influence HR by influencing movement rates (Figure 6). Bears moved most slowly in marshy habitats in spring, a habitat they used infrequently ($\bar{x}$ = 4.5%, SE = 3.5%; Figure 6A), perhaps because it physically impeded travel. During fall, bears moved slowly through lowland deciduous shrub and marsh habitats, whereas they moved quickly in open habitats, such as grasslands, oak forest, and agricultural areas (Figure 6C). Bears reduced movements on windy days throughout the year ($\hat{\beta}$ = -0.046, -0.028, -0.036, SE = 0.009, 0.012, 0.009, p < 0.001, = 0.004, < 0.001 in spring, summer, and fall respectively).

*Model validation*

The heart rate data from three female bears (two with cubs, one solitary) that were used to validate our models post-hoc spanned an entire year of activity (den emergence to den entry); mean number of monitored days was 187 (SE = 31.0, range = 126 - 208) and mean number of useable HR intervals was 349 (SE = 63, range = 223 – 419). The average number of movement steps per individual annually was 2,296 (SE = 613, range = 1436 – 3,482), 562 (SE = 328, range = 62 – 1,180) in the spring, 817 (SE = 141, range = 574 – 1,062) in the summer and 917 (SE = 197, range = 559 – 1,240) in the fall.

These females responded to natural and anthropogenic landscape features similarly to the other bears (2009-2012 data). Movement rate (MOVEHR) was positively related to HR ($\hat{\beta}$= 2.81, SE = 0.51, p < 0.001) and night time movement and HR data showed the same divergence during the fall (Figure 3I-3K). Agricultural areas induced a strong positive association with HR (AGFIELD: $\hat{\beta}$= 11.46, SE = 2.21, p < 0.001) while bears' HR was slower than expected, after accounting for movement, at the periphery of their respective home ranges (ISO: $\hat{\beta}$= - 3.33, SE = 1.67, p < 0.047). The updated model estimates (Table 3), utilizing all 12 bear-years (2009-2013), were similar to the original estimates (Table 2).

Road crossings were again the strongest positive influence on bear movement rates in all seasons (six of seven individuals) but road crossings were not common for these individuals (1.9% of movement steps). During spring and summer all three moved significantly faster near the periphery of their home ranges (ISO) than in the center, but only one bear displayed significantly faster movement rates during fall. During summer, two of the three bears moved through agricultural fields regularly ($\bar{x}$=15.1% of movement steps potentially included an agricultural crossing) and they displayed a pattern of increased rates of movement (although not significantly) in these fields. In the fall, all three bears significantly increased movement when located in agricultural fields and two bears which used crop fields (60.6% and 40.0% of fall locations) had significantly reduced movement rates when located in these fields.

## 3.4 DISCUSSION

The addition of HR monitoring to already common methods of movement monitoring, provided novel insights into a bear's view of its world. As black bear populations continue their resurgence into agricultural and other human-dominated landscapes, it is important to understand not only how, but why bears react in certain ways, and also appreciate that not all bears react the same. Our unique ability to simultaneously capture bears' physiological status in conjunction with their locations has uniquely enabled us to control for movement when interpreting HR. We identified direct physiological responses to crop fields and other anthropogenic landscape features, ambient temperature, and location of the bear within its home range, beyond the effects of their influences on movement.

### *Temporal effects*

American black bears are known to alter their activity and movements among seasons (Amstrup and Beecham 1976, Garshelis and Pelton 1981, Garshelis et al. 1983, Bridges et al. 2004, Noyce and Garshelis 2010). We also observed seasonal changes in daily activity rhythms, but the patterns we observed were different than previously reported. Most previous studies of bears, especially American black bears, show that they are most active during the day (summarized by Paisley and Garshelis 2006). It was previously reported that black bears usually only deviate from this pattern in fall, when they increase their level of nocturnal activity (Garshelis and Pelton 1980, Bridges et al. 2004). We observed here, when looking at movements, that in northwestern Minnesota, bears were also more nocturnally active in spring. We also observed seasonal changes in HR, indicative of metabolic changes (Green 2011). However, the bears exhibited a temporal misalignment between HR and movement during the fall: metabolism decreased earlier and more rapidly than their movements. This may explain how bears are able to rapidly accumulate fat during hyperphagia (Hilderbrand et al. 1999). They feed on calorically rich food (Brody and Pelton 1988, Ditmer 2014, chapter 4), reduce activity during the day to avoid overheating, and slow their metabolism while not sacrificing rate of food intake, all to maximize weight gain. This strategy fits with Florant and Healy's (2012) described general hibernation model, which suggests a temporal lag between reductions in metabolic rate and food consumption to maximize fat accumulation.

### *Human disturbance effects*

Agricultural fields and crops had dramatic effects on bear behavior. We anticipated that as bears quickly traversed agricultural fields, their HR would increase not only commensurate with their hastened movement, but also due to the stresses of being in an open environment with potential exposure to humans. In fact, bear HR's were higher than would be predicted by movement rate alone, which we consider indicative of an acute stress response. Bears of both sexes were not commonly found in these areas, but due to the pervasiveness of agricultural land, they were forced to traverse them routinely. Metabolic costs increase for bears with the need to move greater distances between areas of habitat (Ellis 2011) than in forested areas. In our study, female bears in agricultural areas during the summer did demonstrate faster movement rates relative to other land cover types, indicating that there is also an indirect cost associated with home ranges that incorporate more agricultural areas. We found that weekly home range size in this area was positively linked with the percentage of agricultural lands (Ditmer 2014, chapter 4), yielding the largest reported annual home ranges for the species (Ditmer 2014, chapter 4).

Whereas traversing agricultural fields where they did not forage increased energy expenditure for bears, the edible crops available in some fields provided tremendous energy gain for those bears that took advantage of this food source. Bears that fed on corn, oats, or sunflowers had slower movement rates, access to abundant calories, and several individuals had lower than expected HRs. Unlike foraging in natural areas, where intense activity foraging could cause HR to increase above what is expected given movement (movement is likely to be slow when foraging), bears saved energy by feeding on densely-packed crops, and their HR showed no indication of being on alert. These crops also reduced weekly home range size (Ditmer 2014, chapter 4). We observed (Ditmer 2014, chapter 1) that the benefits of these crops seem to be accrued disproportionately by large males and females without cubs, suggesting that some bears were being socially excluded from crop fields or exhibiting risk-aversion by staying away (e.g. females with cubs and juvenile bears). Bear foraging in corn and other crops has been well documented throughout North America (Landers et al. 1979, Elowe and Dodge 1989, Mattson 1990, Maddrey 1995); our findings demonstrate that bears not only have access to plentiful calories, but that they are able to forage more easily and do not seem to incur acute stress while doing so. The highly-predictable availability of edible crops also likely reduces chronic stresses associated with periods of reduced natural foods (Hellgren et al. 1993).

Many species show indications of elevated stress in fragmented habitats (MacArthur et al. 1979, Newcomb et al. 2003, Johnstone et al. 2012). However, Wasser et al. (2004) reported lower levels of cortisol, a stress-related hormone, in bears living in areas with high levels of human activity. Bourbonnais et al. (2013) found higher stress levels in male bears in areas with higher human disturbance, but found the opposite to be true in females. Our results were also mixed: whereas bears exhibited heightened HRs in agricultural areas, females had slower HRs during the daytime hours in areas with high habitat fragmentation. One explanation is that the reduced HRs exhibited by females were a result of reduced activity in response to human activities. Bears have been observed to limit diurnal foraging activity to avoid competitors (Schwartz et al. 2010) or in response to human presence (Ayres et al. 1986, Baruch-Mordo et al. 2014). Alternatively, what we observed may have been complicated by road crossing. The extensive road network in our study area created small habitat patches with high ratios of edge to habitat, thus creating high levels of FRAG (Spellerberg 1998, Trombulak and Frissell 2000). Roads are often associated with higher rates of movement (Coffin 2007, Dussault et al. 2007), just as we found. Female bears may view roads as “barriers of fear” (Eftestøl et al. 2014); they approached and crossed quickly, then slowed way down after reaching some safe distance.

### *Home range effects*

The periphery of an animal’s home range is typically in flux, changing position from one year to the next (Powell 2000). We expected HR to increase at the edges of the bear’s home range, where they would presumably feel less comfortable, and encounter other bears more often. Instead, bears located at the periphery of their home ranges exhibited high rates of movement but lower than expected HRs. We interpret this novel finding to suggest movements at the home range periphery were more exploratory in nature, due to less familiarity with resources and possibly less preferred habitat. In contrast, we would expect movement and activity in the core of a home range to be focused on foraging in areas with better-known resources; this foraging activity would increase HR above what is predicted from the bears’ relatively slow rates associated with travel. Accordingly, Samson and Huot (1998) found that the core of female black bear home ranges in Ontario, Canada, contained better producing food resources than the periphery.

### *Weather effects*

Temperature had a direct influence on HR, but the most notable effects occurred only early and late in the year. Previously, Tøien et al. (2011) reported that bears returned to normal body temperatures after den emergence, but they maintained reduced metabolic rates for up to an additional three weeks. Our results show that after den emergence, bears exhibited higher HR on days with higher ambient temperature. We hypothesize that this relationship was related to phenology of early season vegetation; as temperatures in early spring increased, more green vegetation became available for consumption and this in turn promoted foraging, resulting in increased metabolism. During the fall, the relationship was reversed; HR decreased with rising temperatures. While preparing for hibernation, bears may increase weight by 50-100%, largely in the form of fat, and also grow a dense coat of underfur. In an effort to conserve energy and prevent overheating, they reduce activity during periods of warm temperatures and appear to become lethargic. Craighead and Craighead (1972) first described this pre-hibernation lethargic state, and noted that grizzly bears (*U. arctos*) exhibited higher levels of activity on cooler fall days.

### *Improvements and future research*

The use of biologger technology in the fields of ecology and conservation biology is rapidly expanding and being used in a wide variety of species to better understand a given animal's physiological response to its environment (Ropert-Coudert and Wilson 2005, Cooke et al. 2014). Whereas the devices that we employed enhanced our interpretation of American black bear behavior, they were not without some noteworthy limitations. To date, the ones we utilized need be implanted and only stored two average HR values for each 24 hours (daytime and nighttime), with eight hours not measured. Thus, we could not match fine-scale (sometimes hourly) locations from the GPS units with corresponding HR. Instead, we relied on a sophisticated modeling approach that compared a bear’s suite of activities during the course of one 8-hour daytime and a 4-hour nighttime interval each day with its average HR for that interval. It should be noted, that we are currently employing and developing methodologies to utilize biologgers that record HR at much shorter intervals to overcome this limitation. Second, about half the implanted HR devices were rejected (expelled from their subcutaneous placements) by these bears, so our sample was reduced accordingly (Echols et al. 2004, Laske et al 2005, Iaizzo et al. 2012). Despite a small sample size, however, we were encouraged that three post-hoc datasets supported our model results. Large datasets of physiological data from a few individuals tend to contain highly autocorrelated data and must be analyzed and interpreted cautiously (Fieberg and Ditmer 2012). We expect that as biologger technology becomes more widely used, comparative and collaborative research efforts will provide even more reliable inferences and insights.

Developing a deeper understanding of the ecology and biology of species living in human-dominated landscapes is becoming increasingly important because of the expanding human footprint and recovery of native species to these geographies. Anthropogenic features on the landscape increased both the metabolic costs and the caloric rewards for a population of bears in northwestern Minnesota. The novel uses of biologger technologies will open new doors in ecology and biology by enabling physiological research to move from the lab to the field and thus from the conceptual to the quantifiable. Future research should also increase collaboration with the medical community to best incorporate and utilize the latest remote technology to capture meaningful physiological changes in free-roaming organisms at fine temporal and spatial scales.

### *Acknowledgements*

We thank Medtronic, Inc. for donation of the Reveal cardiac monitors and funding towards GPS collars. We thank Stephen Howard, Tinen Iles, Douglas Page, Thomas Enright, Andrew Tri, Marta Lyons, Morgan Elfelt and S. Rettler for assistance in data collection. We thank Sarah Thompson and Elizabeth Wallace for helpful suggestions on previous drafts.

Table 1: Response and explanatory variables included in individual bear-year models after other variables were removed due to collinearity.

| Variable | Type | Analysis | Description |
|---|---|---|---|
| HR | Response | Heart | Average heart rate in beats per minute (bpm) during heart rate recording interval |
| MOVEALL | Response | Move | Estimated movement rate between successive GPS locations - log(m/hr) |
| MOVEHR | Movement | Heart | Estimated rate of movement during heart rate recording interval - log(m/hr) |
| SEX | Individual | Both | Sex of bear (male or female) |
| JULIAN | Temporal | Heart | Julian date of year |
| DAYNITE | Temporal | Heart | Categorical -day/night heart rate sampling period |
| SUN | Temporal | Move | Categorical – daylight or dark during hour of the day? |
| HOUR | Temporal | Move | Hour of the day |
| OAK | Habitat | Heart | Bur oak (*Quercus macrocarpa)* |
| LLS | Habitat | Heart | Alder (*Alnus spp.*), willow (*Salix spp.*), dogwood (*Cornus spp.*), black spruce (*Picea mariana*) |
| GRASS | Habitat | Heart | Conservation Reserve Program lands, remnant prairie patches, fallow fields |
| MARSH | Habitat | Heart | Various wetland classifications |
| HABITAT | Habitat | Move | Habitat type of end location of a movement step (categorical) |
| AGFIELD | Human | Heart | All agricultural fields: Primarily soy, wheat, sunflowers, corn, canola, sugarbeets |
| CROP | Human | Both | Frequently consumed crop types only: corn, sunflowers and oats |
| FRAG | Human | Both | First loading PCA using distance to road, natural patch size, and distance to edge of natural patch |
| ROADX | Human | Both | Rate of road crossings (# of road crossings per hour) |
| ISO | Home range | Both | Corresponds to average isopleth within an individual's annual home |
| TEMP | Weather | Both | Mean daily ambient temperature (Fahrenheit) |
| WIND | Weather | Both | Mean daily wind speed (miles per hour) |
| PRECIP | Weather | Both | Total daily precipitation |
| CLOUD | Weather | Both | Average daily degree of cloud cover (0-10) |
| TSTORM | Weather | Both | Occurrence of a thunderstorm event (0-1) |

Table 2. Beta estimates, standard errors, t-statistics and p-values for the covariates included in the top linear mixed (population) model assessing factors influencing heart rate in beats per minute for American black bears in northwestern Minnesota (2009-2012, excluding time spent in the den).

| Type | Covariates†‡ | β | SE(β) | t-value | p-value |
|---|---|---|---|---|---|
| | Intercept | 32.130 | 5.816 | 5.525 | < 0.001 |
| Movement | MOVEHR | 1.866 | 0.350 | 5.334 | < 0.001 |
| Individual | SEX: Male | -9.113 | 2.707 | -3.366 | 0.012 |
| Temporal | JULIAN – S1 | 45.057 | 9.088 | 4.958 | < 0.001 |
| | JULIAN – S2 | 12.586 | 7.126 | 1.766 | 0.078 |
| | JULIAN – S3 | 80.900 | 14.090 | 5.742 | < 0.001 |
| | JULIAN – S4 | 9.627 | 8.162 | 1.180 | 0.238 |
| | DAYNIGHT:Night | 3.700 | 1.356 | 2.728 | 0.006 |
| Human | FRAG | -0.994 | 0.273 | -3.640 | 0.000 |
| Human | AGFIELD | 4.796 | 0.840 | 5.712 | < 0.001 |
| Home Range | ISO | -3.709 | 0.933 | -3.975 | < 0.001 |
| Weather | TEMP | 0.248 | 0.103 | 2.407 | 0.016 |
| Interaction 1 | DAYNIGHT:Night × JULIAN – S1 | -15.344 | 1.421 | -10.800 | < 0.001 |
| | DAYNIGHT:Night × JULIAN – S2 | 10.075 | 1.676 | 6.011 | < 0.001 |
| | DAYNIGHT:Night × JULIAN – S3 | -1.644 | 3.412 | -0.482 | 0.630 |
| | DAYNIGHT:Night × JULIAN – S4 | 5.112 | 2.113 | 2.419 | 0.016 |
| Interaction 2 | FRAG × DAYNIGHT:Night × Sex:Male | 0.961 | 0.463 | 2.075 | 0.038 |
| | FRAG × Sex:Male | 0.100 | 0.384 | 0.261 | 0.794 |
| | FRAG × DAYNIGHT:Night | 0.408 | 0.328 | 1.244 | 0.214 |
| | DAYNIGHT:Night × Sex:Male | 10.207 | 0.734 | 13.915 | < 0.001 |
| Interaction 3 | TEMP × JULIAN – S1 | -0.305 | 0.150 | -2.037 | 0.042 |
| | TEMP × JULIAN – S2 | 0.240 | 0.128 | 1.877 | 0.061 |
| | TEMP × JULIAN – S3 | -1.019 | 0.270 | -3.774 | < 0.001 |
| | TEMP × JULIAN – S4 | -1.000 | 0.184 | -5.446 | < 0.001 |

†Explanations for abbreviations can be found in Table 1.

‡ “S” stands for spline

Table 3). Updated beta estimates, standard errors, t-statistics and p-values for the covariates included in the top linear mixed (population) model assessing factors influencing heart rate in beats per minute for American black bears in northwestern Minnesota excluding time spent in the den (2009-2013).

| Type | Covariates†‡ | β | SE(β) | t-value | p-value |
|---|---|---|---|---|---|
| | Intercept | 28.377 | 5.380 | 5.275 | < 0.001 |
| Movement | MOVEHR | 2.291 | 0.519 | 4.410 | < 0.001 |
| Individual | SEX: Male | -10.484 | 2.921 | -3.590 | 0.005 |
| Temporal | JULIAN – S1 | 73.919 | 7.417 | 9.966 | < 0.001 |
| | JULIAN – S2 | 9.454 | 6.070 | 1.557 | 0.120 |
| | JULIAN – S3 | 61.209 | 12.524 | 4.887 | < 0.001 |
| | JULIAN – S4 | 3.291 | 5.453 | 0.604 | 0.546 |
| | DAYNIGHT:Night | -1.089 | 1.250 | -0.871 | 0.384 |
| Human | FRAG | -1.025 | 0.242 | -4.241 | < 0.001 |
| Human | AGFIELD | 5.822 | 0.812 | 7.168 | < 0.001 |
| Home Range | ISO | -3.369 | 0.847 | -3.978 | < 0.001 |
| Weather | TEMP | 0.287 | 0.093 | 3.091 | 0.002 |
| Interaction 1 | DAYNIGHT:Night × JULIAN – S1 | -16.368 | 1.289 | -12.694 | < 0.001 |
| | DAYNIGHT:Night × JULIAN – S2 | 13.786 | 1.478 | 9.327 | < 0.001 |
| | DAYNIGHT:Night × JULIAN – S3 | 6.468 | 3.184 | 2.031 | 0.042 |
| | DAYNIGHT:Night × JULIAN – S4 | 2.233 | 2.244 | 0.995 | 0.320 |
| Interaction 2 | FRAG × DAYNIGHT:Night × Sex:Male | 0.211 | 0.421 | 0.501 | 0.617 |
| | FRAG × Sex:Male | 0.037 | 0.371 | 0.098 | 0.922 |
| | FRAG × DAYNIGHT:Night | 1.132 | 0.260 | 4.359 | < 0.001 |
| | DAYNIGHT:Night × Sex:Male | 13.059 | 0.668 | 19.547 | < 0.001 |
| Interaction 3 | TEMP × JULIAN – S1 | -0.682 | 0.125 | -5.446 | < 0.001 |
| | TEMP × JULIAN – S2 | 0.188 | 0.106 | 1.774 | 0.076 |
| | TEMP × JULIAN – S3 | -0.851 | 0.245 | -3.467 | 0.001 |
| | TEMP × JULIAN – S4 | -1.015 | 0.141 | -7.191 | < 0.001 |

†Explanations for abbreviations can be found in Table 1.

‡ “S” stands for spline

Figure 1) Influence of hour of day on log movement rate (MOVEALL, mean and 95% CI) during (A) spring, (B), summer, and (C) fall of American black bears in northwestern Minnesota, 2009–2012. Gray shaded areas represent the approximate range of sunrise and sunset. Original data were in meters per hour.

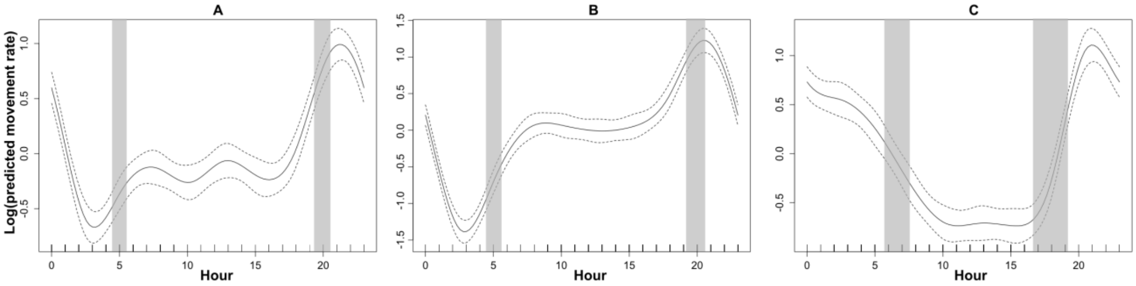


Figure 2) Estimates of mean (A) daytime and (B) nighttime heart rate (bpm, mean and 95% CI) versus mean log movement rate (m/hour, mean and 95% CI) for black bears over the course of a year, 2009–2012. Original movement rate data were in meters per hour.

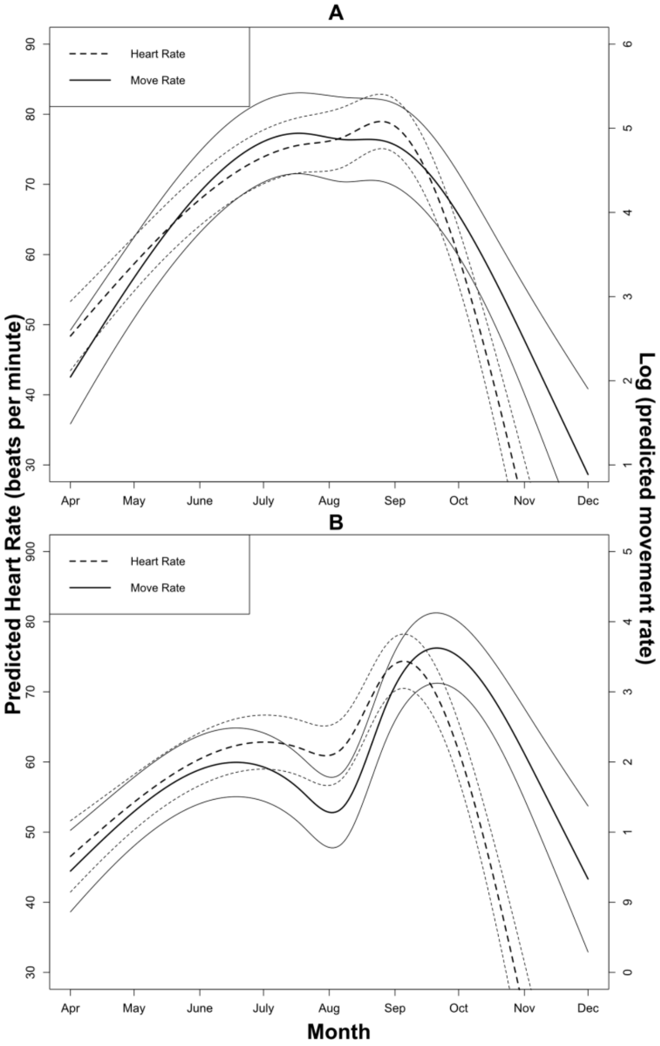


Figure 3) Loess smoothed data of nighttime heart rate (bpm, first y-axis) and movement rate (log, second y-axis) data over time (August – den). 3A – 3H were produced with data obtained from 2009-2012 and used as the primary data for our analysis. Figures 3I-3K were produced from 2013 data as part of model validation. All bear-years exhibit the pattern of a reduced average daily nighttime heart rate prior to reduced daily nighttime movement rates except for the largest bear in the study (3C). Original movement rate data were in meters per hour.

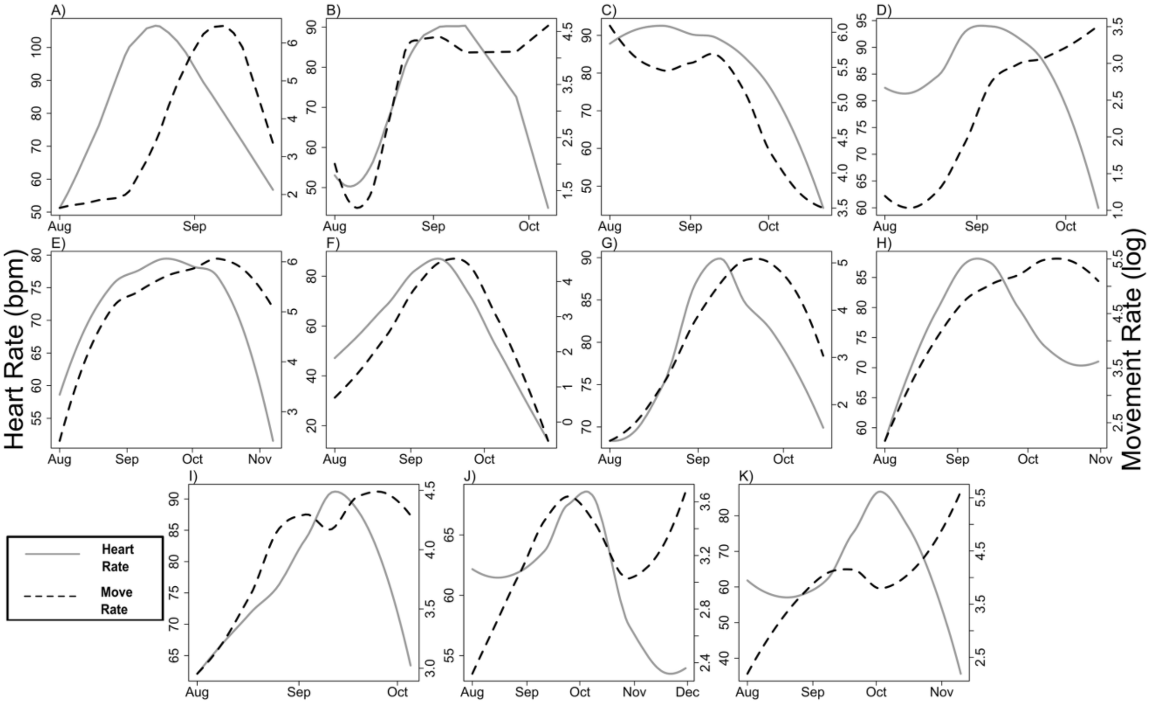


Figure 4) (A) Influence of movement rate (MOVEHR, log(m/hour)) on heart rate (bpm, mean and 95% CI) of free-roaming black bears, based on the best-approximating population model with all other covariates held constant at their mean values. (B) Percent increase in mean estimated heart rate with quantile change in log movement rate. Original movement rate data were in meters per hour.

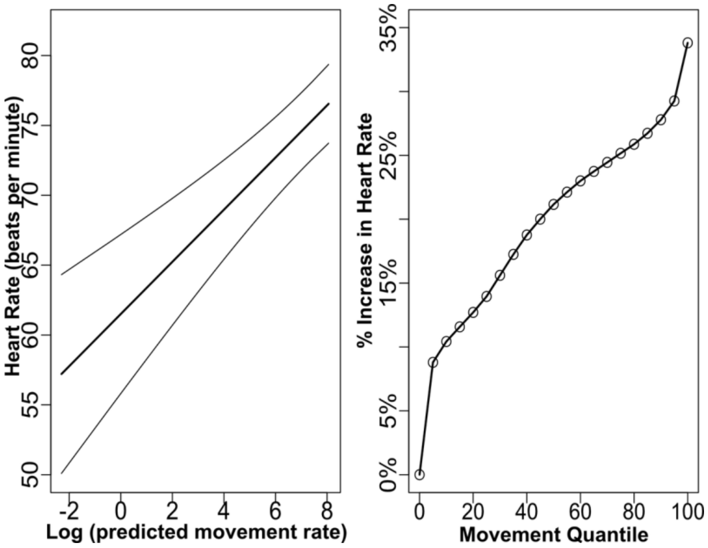
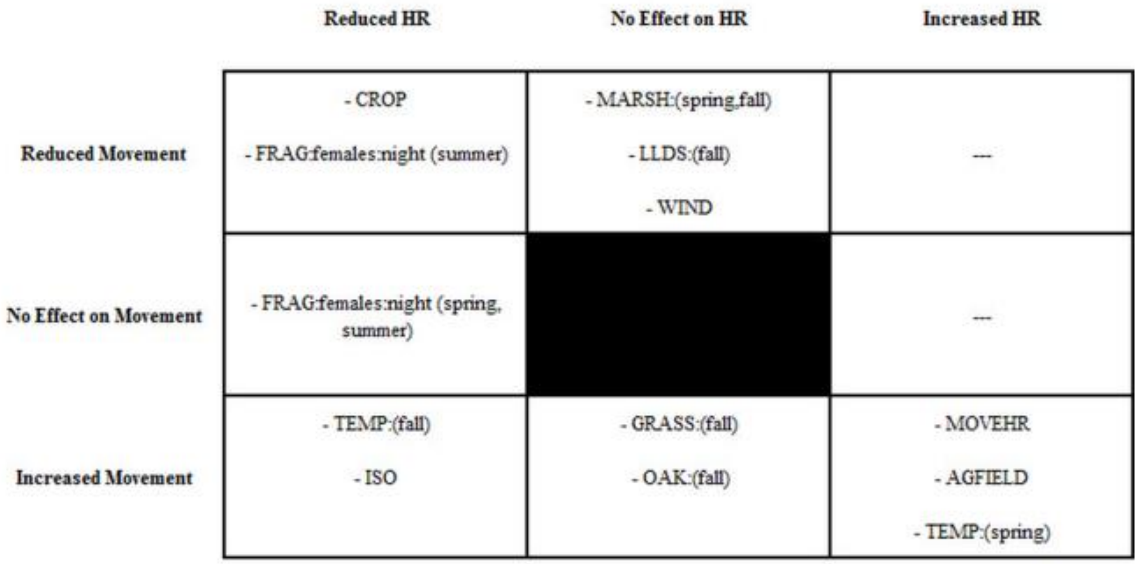


Figure 5) Summary of the influences of covariates on bear movement and heart rate (HR) based on the best fitting movement and heart rate models. Categories reflect how increasing values of the specified covariate influenced HR and movement rate. Squares from top-to-bottom and left-to-right indicate a significant negative response, no significant response and a positive significant response for movement and heart rate models respectively. Covariate descriptions can be found in Table 1.



| | **Reduced HR** | **No Effect on HR** | **Increased HR** |
|---|---|---|---|
| **Reduced Movement** | - CROP<br>- FRAG:females:night (summer) | - MARSH:(spring,fall)<br>- LLDS:(fall)<br>- WIND | — |
| **No Effect on Movement** | - FRAG:females:night (spring, summer) | ■ | — |
| **Increased Movement** | - TEMP:(fall)<br>- ISO | - GRASS:(fall)<br>- OAK:(fall) | - MOVEHR<br>- AGFIELD<br>- TEMP:(spring) |

Figure 6) Influence of habitat type on log movement rate (MOVEALL, mean and 95% CI) during (A) spring, (B) female bears during summer, (C) male bears during summer and (D) all bears during fall in northwestern Minnesota, 2009–2012. Original data were in meters per hour.

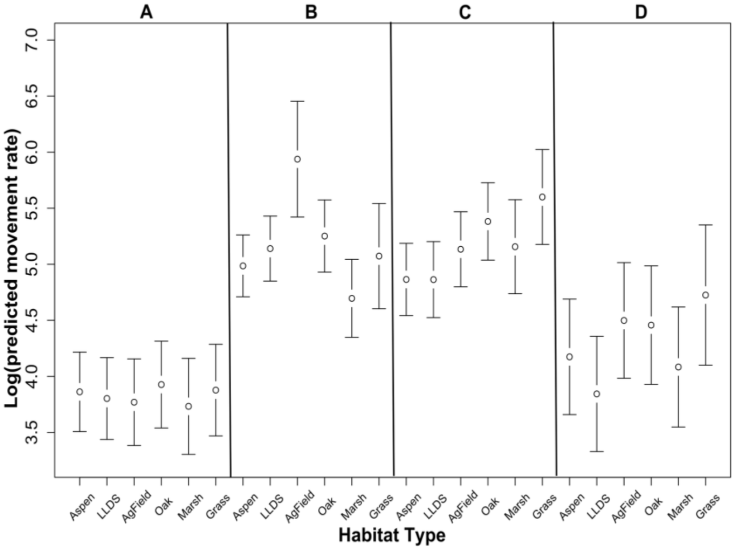


Figure 7) Influence of landscape fragmentation (FRAG) on movement rate (MOVEALL, mean and 95% CI) of (A) male and (B) female American black bears in northwestern Minnesota, 2009–2012. We used the values for each quantile of the covariate FRAG, which was derived from a principal components analysis of habitat patch size, distance to natural habitat edge, and distance to nearest road from GPS-collared bears. Estimates at high levels of FRAG appear to bend the trends due to bears only responding to the highest (and highly skewed) FRAG values. We loess smoothed all values to create cleaner lines. Original data were in meters per hour.

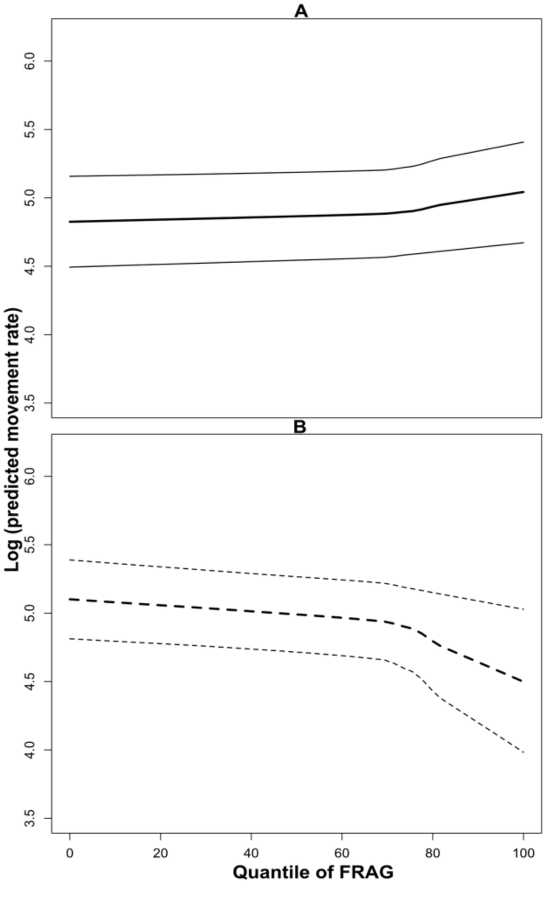
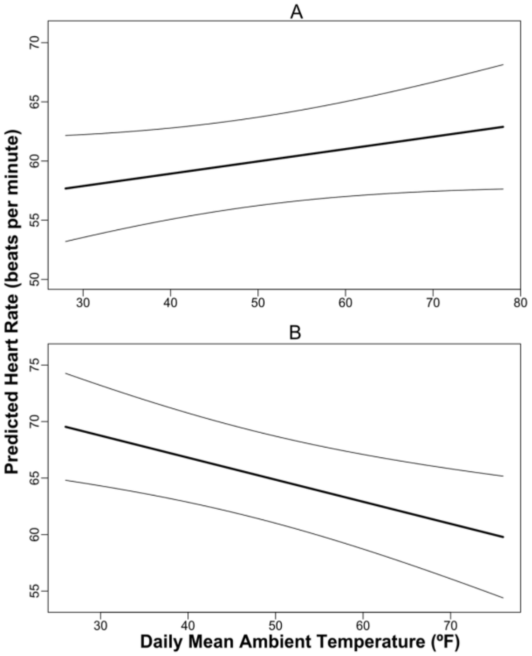


Figure 8) Influence of mean daily ambient temperature (Fº) on heart rates (bpm, mean and 95% CI) of American black bears near the time of (A) den emergence (predicted values for 29 April the 10% quantile of JULIAN), and (B) den entrance (predicted values for 3 October the 90% quantile of JULIAN). Values of mean daily temperature included represent temperatures recorded during the first quartile of Julian dates for (A) and last quartile for (B).



# CHAPTER 4

# DELINEATING THE ECOLOGICAL AND GEOGRAPHIC EDGE OF AN OPPORTUNIST: THE AMERICAN BLACK BEAR THRIVING IN AN AGRICULTURAL LANDSCAPE

## 4.1 INTRODUCTION

Understanding species range limits is critical to conservation planning and management. Range limits are fluid and may expand or contract with changes in demography (Swensen et al. 1998), behavior (Bullock et al. 2000; Holt and Barfield 2009), weather and climate (Parmesan 2006), human tolerance (Oakleaf et al. 2006), mobility (Tinner and Lotter 2006) and habitat quality (Proctor et al. 2005). Animals living at the edge of their range can yield important insights into the requisites for species persistence (Pe’er et al. 2014). It was previously assumed that animals living at the periphery of their range must suffer reduced fitness. However, new research suggests that even where the margins of primary range recede into fragmented habitat patches, individuals can thrive if habitat quality remains high (Sexton et al. 2009).

One way of assessing an animal’s response to habitat is through home range analysis. A home range is generally defined as the space an animal uses in order to meet basic needs such as food, shelter, and breeding opportunities (Burt 1943). There is still debate about the best methodology for delineating home range areas (see Börger et al. 2008; Kie et al. 2010), but ecologists recognize the range of insights home range analysis can provide (Powell 2000; Powell and Mitchell 2012). Well defined home range studies can identify links between species range limits, habitat quality and use, movement, breeding strategies and foraging behavior (Fieberg and Börger 2012; Mitchell and Powell 2012).

If animals follow an ideal-free distribution (Fretwell and Calver 1969), then intraspecific differences in home range size should be largely driven by habitat quality, with individuals inhabiting the smallest area required to maximize fitness (Ford 1983; Mitchell and Powell 2007; Bjørneraas et al. 2012). Therefore areas with lower quality habitat should result in larger home ranges. However, studies have found that social factors (Boydston et al. 2003; Murray et al. 2007), population density (Kilpatrick et al. 2001, Dahle and Swenson 2003), and anthropogenic influences such as habitat fragmentation (Kie et al. 2002; Crooks 2002; Saïd and Servanty 2005; Saïd et al. 2009) also influence home range sizes within a species.

The American black bear (*Ursus americanus*) inhabits a variety of landscapes from swamps of Louisiana, to the boreal forests of Alaska, and numerous forest types and human-modified landscapes in between (Garshelis and Hristienko 2006; Don Carlos et al. 2009). Reported home range sizes vary dramatically across bear range (Tri et al. 2014). Bear home range size generally increases with higher latitudes and comparative studies report smaller home ranges in areas with higher vegetative diversity and caloric availability (Smith and Pelton 1990; Gompper and Gittleman 1991; Moyer et al. 2007). However, within a population, fluctuations in phenology, weather, and mast availability can have large effects on habitat use and effect bear home ranges at shorter time scales (Garshelis and Pelton 1981; Noyce and Garshelis 2010). Demographics also play a role in most populations; male bears have larger home ranges than females, and males also exhibit a weaker relationship between home range size and habitat productivity (Koehler and Pierce 2003). Female bears with cubs of the year often have reduced home range sizes compared to females without cubs, likely due to the immobility of cubs and time spent caring for the cubs (Alt et al 1980; Blanchard and Knight 1991). Behavioral differences between demographic groups may also affect home range size because males are known to dominate areas of highly valued food resources (Garshelis and Pelton 1981; Powell et al. 1997) and exhibit higher risk tolerance such as crossing roads and seeking out human-related forage opportunities (Beckmann and Berger 2003; Baruch-Mordo et al. 2014).

Anthropogenic influences on the landscape can alter movement and activity patterns of bears (Beringer et al. 1990; Lewis et al. 2011; Van Manen et al. 2012). Urban areas, roads, and agricultural fields reduce natural habitat cover and fragment remaining habitat into smaller areas requiring animals to increase travel distances to obtain necessary resources, ultimately increasing home range sizes. Conversely, these areas can offer highly concentrated, calorically abundant food resources in the forms of increased natural forage around habitat edges (Hellgren et al. 1991; Romain 1996), human garbage (Baruch-Mordo 2008; Thiemann 2008), birdfeeders (Merkle et al. 2011), orchards (Garner and Vaughan 1987), apiaries (Jonker 1998) and crops (Maddrey 1995). Thus in some situations, human-altered landscapes can reduce the area an animal requires to obtain necessary caloric resources (Beckmann and Berger 2003; Ditmer 2014, chapter 1).

Our study area provided an optimal opportunity to examine the influences of habitat fragmentation and varying forage availability on both the home range size and the location of home ranges with respect to the edge of a bear population. In northwestern Minnesota, the forests of the upper Midwest fade into extensive areas agricultural production. This landscape shift from forest to agriculture marks the western edge of the American black bear's eastern population (Scheick and McCown 2014). Bears in this area are the largest and most fecund bears in the state (Garshelis and Noyce 2009; Garshelis et al. 2010), which is enabling the population to continue to creep further into more intensely-agricultural lands with less natural habitat cover.

We sought to identify biotic and abiotic factors that influenced black bear home range size. We examined annual and weekly home range sizes, and their relationship to landscape metrics, habitat types, weather, and temporal and individual covariates. We specifically tested the hypothesis that higher caloric density of bear foods leads to smaller home ranges; equivalently, we predicted that low caloric density necessitates increasingly larger home ranges, with growing gaps between patches of food and cover — eventually food density would become too low, or the spaces between food patches too great to support a bear because it would need to expend too much energy travelling. We used these results to assess the edge of habitable landscape, or the ecological limit of this gradually expanding population. Documenting the minimal habitat requirements necessary for persistence is key to conserving and managing large mammals living in increasingly human-dominated landscapes, yet despite innumerable home range and habitat use studies, remarkably little empirical information exists that defines what species need. Our novel approach used empirical results of home range requirements to delineate the edge of the population's geographic range. To our knowledge, this is the first attempt to do so with black bears.

## 4.2 STUDY AREA

Our primary study area was located in northwestern Minnesota, centered near the town of Middle River (48.43°N, 96.16°W). The study area was approximately 10,000 $km^2$ and included Marshall, Kittson, Roseau, Polk, Beltrami, Red Lake, and Pennington Counties. We included additional areas outside the primary study area when forecasting bear range. Additional Minnesota counties included Norman, Mahnomen, Clearwater, and Lake of the Woods, and four counties in eastern North Dakota: Pembina, Walsh, Grand Forks, and Traill.

Typical weather conditions in the region range from humid and warm summers (warmest month July: $\bar{x}$ = 21 ºC, min = 15 ºC, max = 27 ºC) to cold winters (coolest month January $\bar{x}$ = -14 ºC, min = -20 ºC, max = -9 ºC). Precipitation peaks in June ($\bar{x}$ = 101.9 mm) and the region receives abundant snowfall over the winter (Dec–Mar monthly precipitation $\bar{x}$ = 15.8 mm, www.weather.com). Windy conditions are a common occurrence due to the open, flat landscape and average wind speeds were 17.8 mph (www.usa.com/middle-river-mn-weather.htm).

This area marks a transition between the deciduous forest biome to the east and the tall grass prairie biome to the west. The landscape was largely devoted to agricultural production (areal coverage ~ 52.5%); common crops included soybeans, wheat, corn, sugar beets, alfalfa, sunflowers and oats. Corn, sunflower, oats and barley were known to be consumed by black bears in this study and other regions (Mattson 1990; Ditmer 2014, chapter 1). Field corn for animal feed accounts for most corn grown in the region but sweet corn production and corn production in general is increasing. Disease has reduced the popularity of sunflowers in the region and oats and barley are uncommon. Overall, these four crop varieties covered 2.3% of the land area of the study area, but with recent increases (2009 = 1.4%, 2013 = 3.9%).

Despite the large agricultural footprint, only ~ 4% of the landscape is classified as "developed". Road density in the region is 0.6 km of road per km$^2$, but most roads had low traffic volume (≤5 vehicles per day) with some heavily used county roads and highways (max traffic volume = 22,500 vehicles per day, Minnesota Department of Transportation 2014).

Forest cover (~17%) is dominated by aspen-parklands (typically aspen/white birch (*Populus tremuloides/Betula papyrifera*, areal coverage =12.9%) and bur oak forests (Quercus macrocarpa, 3.6% areal coverage). Common bear foods in both forest types include soft mast (some ripening in early July) from juneberry (*Amelanchier humilis*), chokecherry (*Prunus virginiana*), gray and red dogwood (*Cornus racemosa*, *Cornus sericea*), and hard mast from American and beaked hazel (*Corylus americana*, *Corylus cornuta*). Aspen-parklands also commonly contain raspberry (*Rubus strigosus*), arrowwood (*Viburnum dentatum*), and sarsaparilla (*Aralia nudicaulis*) in the herbaceous layer. Bur oak forests also provide abundant forage from hawthorn (*Crataegus spp.*), wild plum (*Prunus americana*) and acorns starting in early September.

Lowland deciduous shrub (LLDS, 11.5% areal coverage) is primarily composed of willow (*Salix spp.*), and alder (*Alnus spp.*). Bear forage in LLDS is composed of red-osier dogwood (*Cornus sericea*), high-bush cranberry (*Viburnum trilobum*) and alder-leaved buckthorn (*Rhamnus alnifolia*). Wetlands (11.2% areal coverage, emergent and woody) contain some spring vegetation consumed by bears such as sedges (*Cyperaceae*) and horsetail (*Equisetem*). Grasslands (7.4% areal coverage) are a mix of Conservation

Reserve Program land, temporarily fallow fields, or remnant prairie. Estimates of areal coverage for non-crop layers were derived from the Minnesota Department of Natural Resources (2013) and crop coverage estimates were obtained through the U.S. Department of Agriculture, National Agricultural (USDA 2013).

Prior to the mid-1990s, the Minnesota Department of Natural Resources considered the area “secondary bear range” due to the lack of natural bear habitat and low bear density relative to the more forested parts of the state (Garshelis and Noyce 2011). In 1995, bear abundance in the region increased when bears moved into the area while seeking alternative foods during a statewide natural food failure. Since this initial influx, northwestern Minnesota has supported a high and growing bear population (Garshelis and Noyce 2008).

## 4.3 MATRERIALS AND METHODS

From May to July, 2007– 2011 we captured black bears in northwestern Minnesota using baited barrel traps. Bears were immobilized with a combination of ketamine hydrochloride and xylazine, or premixed tiletamine hydrochloride and zolazepam (Telazol®, Elkins-Sinn, Cherry Hill, NJ, USA). We fit all adult bears with either VHF radio-collars (Telonics Inc., Mesa, AZ, USA), GPS store-on-board collars (Telemetry Solutions Concord, CA, USA; Lotek Wireless Inc., Newmarket, Ontario, Canada**;** Advanced Telemetry Systems, Isanti, MN, USA) or GPS Iridium satellite collars (Vectronic Aerospace, Berlin, Germany). We programmed GPS collars to attempt fixes once every 1–6 h during the non-denning seasons dependent on the collar type and remaining battery life. We increased the sampling rate during fall on some collars to capture agricultural foraging at a finer scale.

We assigned each bear a unique identification number and attached numbered plastic ear tags. We downloaded GPS data each winter (Dec–Mar, 2007–2013) after anesthetizing collared bears in winter dens using Telazol. We classified females as being with cubs if cubs were present in the den in March (cubs were born in January). All animal handling was approved by the University of Minnesota’s Institutional Animal Care and Use Committees (permit no. 1002A77516).

### *Annual and weekly home range size*

We estimated annual home range size by first removing locations that were less than four hours from each previous fix starting for the first fix from a bear-year. We also excluded individuals with <120 days of data. We delineated home ranges and reported the 50% and 95% area estimates using: 1) minimum convex polygons (we also reported the 100% estimate for comparative purposes); 2) kernel density estimators using the reference bandwidth; 3) kernel density estimators with the rule-based approach using the ad-hoc method for selecting a bandwith as suggested by Kie (2013). The ad-hoc method iteratively uses decreasing scaling values (1.0, 0.95, 0.9 decreasing by 0.1 thereafter) multiplied by the estimated href value determined by the reference bandwidth method. The home range is taken to be the area of the isopleth having the lowest scaling value that did not cause it to fracture into non-contiguous polygons. If the home range fractured during the first iteration, we used a scaling value of 1.0, which is equal to the reference bandwidth method. We also used 4) the fixed k LoCoH (or k-NNCH) method of home range estimation where a convex hull is created for every fix using k-1 nearest neighbors to the focal fix (Getz and Wilmers 2004). We set “k” for each bear-year by taking the square root of the number of fixes per bear-year. We used program R (R Core Team

2013) with package adehabitatHR (Calenge 2006) to create the first three home range estimates and package ‘rhr’ (Reproducible Home Range Analysis; Signer 2013) for LoCoH estimates.

To estimate weekly home ranges, we used all available GPS fixes and assigned each location a week of the year and excluded locations that were associated with weeks: 1) during which the bear was denning; 2) occurring before May 1 or after Dec 1; 3) that did not include fixes covering at least 6 of the 7 days; or 4) with <21 successful fixes. We delineated weekly home ranges using the same rule-based approach of the ad hoc method for selecting a bandwith as for annual home ranges (Kie 2013). The choice of isopleth for analyzing weekly home ranges involves a bias-variance tradeoff (Fieberg 2007). Smaller isopleths produce more biased estimates of the area actually used, and they may fail to capture many of the landscape features responsible for changes in home range size. Yet, smaller isopleths should be less variable. We used a 90% isopleth because Börger et al. (2006) found it resulted in increased precision and statistical power, relative to a 95% isopleth, when evaluating relative comparisons (e.g., estimating changes in home range size over time or differences among bears). These comparisons are critical for determining why animals use certain areas on the landscape.

### *Landscape covariates*

Within each weekly home range we calculated the proportion of major habitat types classified in a GIS land-cover layer created by the U.S. Geological Survey Upper Midwest Gap Analysis Program (Minnesota Department of Natural Resources 2012) using Geospatial Modeling Environment (Beyer 2012). We grouped land-cover classes into eight composite cover types: ASP (aspen-dominated forest, white birch, black ash:

*Fraxinus nigra*), OAK (bur oak, upland shrub), WET (aquatic and marsh), SHRUB (lowland deciduous and coniferous shrubs), CON (conifer shrub and forest, pine, spruce, cedar, tamarack, spruce), GRASS (grassland), DEV (developed) or AGLAND (agricultural lands). We added a covariate for the cumulative percentage of agricultural crops consumed by bears in this region (CROP, e.g. corn, sunflowers, oats, barley; see Garshelis et al. 2013; Ditmer 2014, chapter 1) within each home range using a cover map created by the U.S. Department of Agriculture, National Agricultural Statistics Service (2014).

We used a GIS shapefile created by the Minnesota Department of Transportation (Minnesota Department of Natural Resources 2012) to calculate road density within each home range (road length km/home range area $km^2$). The road layer also provided information from which we could estimate mean traffic volume of roads within each weekly home range. We created a covariate, ROAD, by multiplying road density by the average traffic volume within each home range.

*Weather and temporal conditions*

We calculated weekly averages for ambient temperature (Cº, TEMP), dew point (Cº, DEW), wind speed (mph, WIND), and precipitation (cm, PREC) using Weather Underground (http://www.wunderground.com/) weather station data from a site near the center of the study area (Gatzke — Agassiz National Wildlife Refuge station).

We created a covariate for day length (DAYLEN) using package ‘geosphere’ (Hijmans 2014) in program R (R Core Team 2013). We used the latitude for Middle River in this function and provided the Julian day of the first day of each week for the temporal requirement of the calculation. We created a categorical covariate for season

(SEAS) for use in testing seasonal interactions with other covariates. We classified weeks < 26 as spring (~May 1 – July 1), 26-36 as summer (~July 1 – Sept. 1), and >37 (~Sep 1 – Dec 1) as fall.

### *Individual covariates*

Bear age (AGE) was estimated from annuli in the root of a first upper premolar (Coy and Garshelis 1992), or was known for bears first observed as cubs. We created a categorical variable for gender (SEX) and a binary variable to distinguish adult females with cubs of the year (COY =1) from those with yearlings or no offspring (COY=0).

### *Calories available to bears*

We measured abundance of the principal summer and fall bear foods during 2007 – 2011 (Table 1). We conducted 253 surveys, averaging 51 surveys per year (min: 2011 = 28, max: 2007 = 75) allocated to four habitat types: aspen/ash/birch (62%), oak (29%), LLDS (5%) and coniferous habitats (4%). Each survey was composed of 15 plots, spaced along transects. We ran three parallel transects, one along the open edges of habitat stands (along roadways or clearings), one 15-m deep into the stand, and one 30-m into the stand. We sampled five 3-m diameter circular plots every 15m along each transect. In each plot we estimated the percent cover of each type of food-producing plant, and then converted this to area ($m^2$). We also assigned a subjective fruit production score, 0–5 (0 = no fruit or nuts, 5= highest production of fruit) to each fruiting species in the plot. We converted these production scores to biomass by collecting, counting, and weighing fruits from smaller subplots (0.25 – $1m^2$). We obtained year-specific relationships between fruit production scores and biomass for sets of years with different observers. We combined estimates of productivity and areal coverage to obtain an estimate of biomass of each food per area in each survey.

Acorns were sampled differently, since they are the only tree-borne bear food. During 2007 – 2011 we sampled at least 10 oak forest stands per year to estimate acorn abundance. We established sampling plots at the same spacing and pattern as our other fruiting surveys. We counted fallen acorns and capules in 1-m$^2$ plots, after clearing away fallen leaves. We used the number of caps to help estimate the number of acorns that had been there before consumption by insects and small mammals. We multiplied acorn number by average acorn weight (2.5g; Tecklin and McCreary 1991) to obtain biomass per area.

We used bomb calorimetry to estimate caloric content of 13 common species of wild fruit and nuts and the 2 most commonly consumed agricultural crops by bears in the region, corn and sunflowers (Table 1). We did not estimate the caloric content of 4 less common natural fruits so we assigned them caloric values from similar species (as noted in Table 1). We estimated the percentage of refuse per species sample by weighing samples before and after removing stems, cupules, shells, and sizeable pits. We removed moisture by freeze-drying or baking (at 100ºC) for at least 24 hours (Table 1). We crushed the dried samples and used a Parr Calorimetric Thermometer (Model#:1672, Parr Instrument Company, Moline, Illinois USA) to obtain caloric content per gram dry weight (Table 1). We typically ran two replicates of each sample and calculated the standard deviation to ensure samples did not produce significantly different caloric values.

We multiplied estimates of biomass per $m^2$ for each species in each food survey (including acorns) by the respective percent consumable dry content and calories per gram dry weight to produce estimates of calories per area. We separated species by their seasonal availability (Table 1), and summed foods within each season to derive caloric availability per $m^2$ for each habitat patch that we surveyed. Different fruits ripened and decayed in different time windows and each survey captured availability at a point in time; since surveys were conducted throughout the fruiting period, they encompassed a majority of the changing biomass of each fruiting species. We averaged results of surveyed patches of each habitat type to estimate average calories/$m^2$ for aspen/ash forest, oak forest, conifer, and LLDS habitats in summer and fall during each year of our study (2007 – 2011). We did not sample conifer and LLDS in all years, so we used an average value for unsampled years. We did not sample wetlands, grasslands or developed areas; we assigned these areas zero caloric availability for summer and fall.

For agricultural crops, we used yields from northwestern Minnesota for each crop type during 2011 and 2012 as reported by the United States Department of Agrcilture's (USDA) National Agricultural Statistics Service (Table 2; http://www.nass.usda.gov), and converted these to grams per $m^2$. We converted this to calories per $m^2$ using our calorimetry data for corn and sunflowers and values provided by the USDA's National Nutrient Database for Standard Reference (http://ndb.nal.usda.gov/) for barley and oats (Table 2). We had no evidence of bears eating other crops, so assigned them a caloric value of zero.

We obtained the total caloric availability within each weekly home range by multiplying the percent of each habitat and crop type within the corresponding weekly home range and the average caloric values for each in that specific year. We took the log of the total caloric availability divided by the size of the weekly home range to obtain average log caloric availability per $m^2$ (logCAL).

*Model selection and analyses*

We used linear mixed models with function 'lme' in package nlme of program R (R Core Team 2013; Pinheiro et al. 2013) to relate the log of weekly home range size (WHR) to covariates, while allowing for repeated measures and within-individual temporal autocorrelation. Specifically, we included random intercepts for each bear-year combination and specified an AR1correlation structure based on the week number of the year, assuming errors within each bear-year followed a pattern. This assumption implies that observations collected from the same bear, but collected in different years, are independent. We felt comfortable making this assumption because food availability, landscape, and individual information varied annually. We scaled and centered all numeric covariates (Schielzeth 2010). We excluded the covariates ASP, CON and DEV to reduce the collinearity associated with all proportions of habitat types adding up to one within each WHR. Our full model considered main effects associated with ROAD, AGFIELD, WET, LLDS, DEW, DAY, COY, CROP, SEAS, OAK, WIND, AGE, TEMP, PRECIP and interactions between SEX and CROP and season (SEAS) with CUB, OAK, and CROP each separately.

We began with the global model and used backwards elimination to remove the least significant covariates based on the lowest p-value until we reached a model with only the intercept included. We ranked models by taking the difference in Akaike Information Criterion adjusted for small sample sizes (AICc) from the model with the smallest AICc value to obtain ΔAICc and determined the relative likelihood using Akaike model weights (Burnham and Anderson 2002) and reported all models within 2 AIC units of the top model (Arnold 2010). We used the top model to generate model-based predictions of WHR (and 95% confidence intervals) based on the range of values from a single covariate or interaction while holding all other covariates at their mean values using the 'effects' package in Program R (Fox 2003, R Core Team 2013).

We used the same linear mixed model structure and functions to test the relationship between WHR and the log of caloric density (scaled and centered as well). We created a model using only logCAL as the independent variable and WHR as the dependent due to the correlation between habitat types and caloric availability. We tested support for an interaction between logCAL and SEAS. Support for this interaction would indicate the relationship between WHR and logCAL is significantly different between seasons.

### *Geographic range delineation*

We incorporated results from our analysis of factors that influence WHRs to better delineate suitable bear range and classify habitat quality for male and female bears on a seasonal basis. Spring maps used the compositional percentages of natural cover available to bears and the amount of road density and traffic volume. Summer and fall also required a minimum amount of natural cover, accounted for roads and traffic, but also utilized our surveys of estimated and natural food abundance and crop availability.

We started by creating a GIS layer for natural cover that classified all cover types as either natural (ASPEN, OAK, SHRUB, WET, GRASS and CON) or not (DEVELOPED, AGFIELD, CROP). We created a buffer around our GIS road layer by multiplying 0.5 × the associated traffic volume (average count of vehicles per day). We chose 0.5 because buffering by the traffic volume created road buffers that we believed were too large to be biologically influential. If a section of road did not have a value for traffic volume (e.g, in North Dakota), we assigned a buffer of 15m. We combined all road sections to create a map for the influence of road density and volume.

To create caloric availability maps, we used the caloric estimates from our habitat surveys and created three layers based on the minimum, mean, and maximum values associated with each habitat type sampled (i.e., lowest value from 2007–2011 sampling of aspen and oak; Table 3). We used the crop GIS cover layer from the U.S. Department of Agriculture, National Agricultural Statistics Service (NASS) to determine the minimum, median and maximum areal coverage of CROP from 2007 – 2013 (min = 1.4%, med. = 1.8%, max. = 3.9%). We assumed the spatial configuration of CROP was the same as the year included and assigned each raster cell associated with the field a caloric value (Table 2). Finally, we combined the natural calorie layers with the corresponding edible crop layers (e.g., highest natural calorie year combined with year with most available CROP) to create total caloric availability layers based on the lowest, average, and highest amounts of availability.

We used the ‘Focal Statistics’ tool in ArcGIS to slide across each GIS raster cover map (natural cover, roads, calories) and calculate a metric (mean or sum) for a user-defined area (window). We used a circular moving window that matched the area of the median WHR of each sex for each season (Table 4). The “moving window” assigns the metric to the focal raster cell in each layer until all cells have been assigned a value based on the focal cells and the surrounding cells within the moving window. The resulting layer is a smoothed raster where values associated with each cell were considered to represent the same spatial scale as the corresponding median WHR.

For spring maps, we subtracted road influence values from natural cover values. We classified the resulting cell values by the distribution of natural cover found within spring WHRs by sex (Table 4). Cells with percentages of natural cover that fell below the 5th quantile of the distribution were considered “Very Low” quality spring habitat or non-suitable for bears. Because we did not survey for available forage, we assumed areas with higher levels of natural land cover will provide more available spring forage in the form of early green vegetation and ants. The classifications of remaining cells were based on the following quantile levels within spring natural cover distributions (by sex): 5-25% = Low, 25-50% = Medium, 50-75% High, 75-100 = Very High (Table 4).

Summer and fall maps used the same methods as spring mapping, but also incorporated caloric values from within WHR’s and the total caloric availability layers. Cells that met the minimum 5th quantile natural cover requirement based on summer and fall natural cover distributions of percentages by sex (Table 4) were then classified based on caloric availability (otherwise categorized “Very Low”). The remaining cell classifications were based on the following quantile levels of caloric availability within WHR by sex and season: 5-25% = Low, 25-50% = Medium, 50-75% High, 75-100 = Very High (Table 5). We used three caloric availability scenarios in the summer and fall to test the sensitivity of bear ranges and habitat suitability categories to changes in forage availability (Table 9). We used the areas considered habitable (>5% quantile in habitat cover for all seasons; >5% quantile in caloric availability in summer and fall) during scenarios with maximum natural forage and crops to explore how far west bears can persist during each season given maximum resources. We then overlaid GPS locations of bears with their corresponding seasonal range map and reported the percentage of locations found either inside or outside of suitable habitat.

## 4.4 RESULTS

### *Annual and weekly home range size*

We used 42,552 locations to create annual home range estimates of 60 bear-years (33 female, 27 male) from 29 individual bears (14 female, 15 male). The MCP, Ad-Hoc and H-Ref methods resulted in similar estimates (broadly overlapping 95% CIs), while the LoCoH estimates were significantly smaller (Table 6). Male home ranges were 2.9 (LoCoH 50%) to 9.7 (AdHoc 95%) times larger than females, depending on estimation method. Variation among home range sizes within each sex was large. Three males had annual home ranges <250 km$^2$ (min = 174 km$^2$, h-ref KDE) whereas three had home ranges >1,600 km$^2$ (max = 2,760 km$^2$, h-ref KDE; maximum for 100% MCP = 2,923 km$^2$). Five females had home ranges <30 km$^2$ (min = 17 km$^2$), whereas three exceeded 200km$^2$ (max = 620 km$^2$). All extreme values were from different individuals, not different bear-years from the same individual.

We utilized 80,441 locations from 38 individual animals (17 female, 21 male) over 75 bear-years (37 female, 38 male) to create 1,453 bear-week home range estimates. The mean male WHR (averaged across weekly averages) was 129 ±18.0 (SE) km$^2$ with the minimum occurring in November (week 45; $\bar{x}$ = 41.5 ± 24.1 km$^2$) and maximum in mid-August (week 33; $\bar{x}$ = 221.5 ± 83.2 km$^2$, Figure 1A). The average weekly female WHR was 23.5 ± 4.0 km2 with the minimum during the end of September (week 38; $\bar{x}$ = 8.39 ± 1.6 km$^2$) and maximum during mid-June (week 24; $\bar{x}$= 46.5 ± 10.1 km$^2$; Figure

1B). Male average WHR exceeded female WHR for all weeks, by an average of 105.5 ± 17.2 km$^2$; most male WHRs exceeded the maximum observed female WHR (Figure 1).

The top three models of WHR accounted for 88% of model weights and no other models were within 2 AIC of the top models (Table 7). The variable representing crops consumed by bears (CROP) was supported in all models and had the strongest negative influence on home range size (Table 8). All top models indicated that edible crops had a larger impact on home range size during summer and fall relative to spring (Figure 2) and more so for males than females (Figure 3). In contrast, agricultural areas without consumable crops (AGFIELD) caused expansion of WHR during all seasons (Table 8). Among natural cover types, WET had a strong positive association, LLDS had a negative association, and OAK had a positive association with WHR during the spring but had a negative influence during summer and fall (Table 8, Figure 4,). The presence of COY had a strong seasonal influence on females' home ranges (Table 8). Females with COY had smaller WHR during spring (when cubs were smallest) compared to summer and fall (Figure 5). Higher road densities and traffic volumes (ROAD) resulted in larger WHR's (Table 8). Weeks with longer average day length (DAY) and higher average dew points (DEW) were associated with increased WHR (Table 8). Wind speed (WIND) was included in two of the top models and was associated with smaller home ranges but the effect size was the smallest of all covariates in the top models (Table 8).

WHRs during summer and fall (n = 645) were smaller when they contained higher caloric density of wild foods and crops (Tables 2, 3) ($\beta$ =-1.00, SE=0.07, $t$ = -14.8, $p \leq 0.001$). We did not find support for including an interaction with season (AIC $\Delta$ +1.9) indicating the relationship was similar in summer and fall. Although logCAL was the only covariate in the model, the resulting β suggests it has a larger influence than any individual covariate in the top models.

### *Geographic range*

Relative to females, male bears had larger median home ranges (86 km$^2$ vs. 12 km$^2$) but required half as much natural cover in their WHR during the spring (10% vs. 5%, Table 4). The smaller natural habitat requirement resulted in 8% more area of northwestern Minnesota considered habitable during spring (above “Very Low” classification, Table 9) for males (53.9% habitable, Figure 6B) than females (46%, Figure 6A). However, because spring range was only delineated by natural cover (no caloric estimates) both spring maps contained similar levels of “High” or “Very High” habitat categories (~27%, Table 9).

Median WHRs for females increased from spring to summer resulting in larger moving windows (12 km$^2$ vs. 17 km$^2$); the opposite was true for males (86 km$^2$ vs. 64 km$^2$). The minimal suitable natural cover in summer was slightly less than in spring for both sexes (Table 4), which increased the estimated habitable range by 6% from spring to summer (Figures 7 and 8). Male bears had, on average, 10 times more total calories (Table 5) within their WHRs relative to females, and variation among males was 7 times greater than for females. A ten-fold greater caloric availability within a 3.7 times larger moving window meant that males had 2.7 (10/3.7) times greater density of calories within their summer moving window. As a result, males had 20% more habitable area (i.e., better than “Very Low”; Figure 8B) than females (Figure 7B) in the low caloric scenario (Table 9). The minimal suitable summer range for males varied less with changes in food availability than did the range for females. In the high caloric scenario, total suitable range increased by 13% for females but only 1.2% for males (Table 9, Figures 7A and 8A). With low wildland calories and no crop availability, female range declined 4.0% (compared to the low calorie scenario) versus only 0.1% for males. However, the total percentage of "High" and "Very High" habitat categories increased by 29.2% for females and 47.4% for males between the extreme scenarios (high calorie scenario versus low calorie with no crops; Table 9; Figures 7C and 8C) suggesting that summer crop availability may be required to provide enough calories for females in parts of their range while the extent of suitable male range was not altered by crop availability. However, male ranges showed greater changes in percentages of habitat quality across the scenarios (Table 9). The male summer habitat suitability map with minimum wildland calories and corn as the only crop available highlighted the importance of corn among crop types;  only 3% of  "Medium" habitat changed to "Low" and 0.1% of "High" went to "Very Low" compared to minimum wildland calories – all available crop scenario (Figures 8B and 8C; Table 8).

Fall WHRs were the lowest of any season for both sexes but natural cover requirements were the highest for females and the lowest for males of any season (Table 4). The caloric availability of primary natural habitats (ASP and OAK) was greater than during summer (Table 2). The lower natural cover requirement led to an small increase for males but larger increases for females in the total suitable habitat area (high calorie scenarios: females −  summer: 51%, fall: 56%, males − summer: 60%, fall: 61%; Table 9; Figures 9A and 10A). Significant portions of very western Minnesota within the Red River Valley (marking the border with North Dakota), and even several spots in North Dakota appeared suitable in fall, mainly for males, having adequate-sized patches of natural cover near consumable crops (Figures 11). However, we are unaware of any bears that have occupied these areas, which are separated by a large gap (~ 20−35 km wide) from the suitable Minnesota bear range.

Areas with the highest ranked habitat suitability increased in area by 20−30% during good fall food conditions (Table 9; Figures 9A and 10A). Scenario maps clearly show the tradeoff of crop availability and natural food forage; suitable habitat quality decreased (e.g. “Very High” to “Low”) in the west when crop availability was removed (Figures 9C and 10C) or reduced (Figures 7C and 8C). In contrast, eastern regions of the study area show marked changes from higher ranked suitability categories to lower when changes natural food availability is reduced while areas further west with crop availability remain in the higher suitability categories (Figures 8−11, compare panel A to B). However, in scenarios when crop availability is reduced or removed, the region still contained a high percentage of suitable habitat suggesting natural forage in the area could sustain a bear population even in the absence of crops (Figures 9−11, panel C).

Bears were located in areas designated as suitable habitat in 96.9% of all GPS locations (n = 80,230). This varied little in spring and summer. During fall, only 29 of 16,016 (0.02%) locations of female bears were located in the “Very Low” habitat designation, while male bears were found there more often (5.2% of 15,712 locations). However, 51% of fall male locations that occurred outside of suitable habitat were from one 2 year-old individual (Figures 12 and 13).

## 4.5 DISCUSSION

Black bears living in northwestern Minnesota responded to the fragmented and agricultural landscape as we predicted: non-consumable crops were perceived as gaps that increased the space between patches of resources, forcing bears to expand their home ranges. By examining home ranges at a weekly time scale, we were able to determine which attributes led to an increase (e.g., non-consumable crops and roads) or decrease (e.g., corn, care of cubs) in space use. We used these insights to generate maps of suitable habitat. These maps delineated the ecological and geographical limits for the species, and have potential applications in forecasting range shifts under different future landscape changes (e.g., acreage of crops planted).

Tri (2014) compiled estimates of annual home ranges from 187 studies of black bears and reported within-study averages for males that spanned two orders of magnitude (6 – 606 km$^2$). The largest reported average annual male home range occurred in a region composed of 15% agriculture in the lower peninsula of Michigan (Carter et al. 2010). That estimate of 606 km$^2$ was generated using the fixed kernel approach; based on a comparable approach, our average estimate of 834 km$^2$ was 38% larger (H-Ref; Table 5). Only two previous studies reported average areas >500 km$^2$ (Unger 2007; Hechtel 1991). We caution that perceived home range area varies with different estimators (e.g., Table 5) and with sampling intensity (e.g., from VHF vs. GPS collars; Hebblewhite and Haydon 2010). Carter et al.'s (2010) sampling rate was much lower than ours (134 vs. 609 average fixes per home range) and the use of a fixed kernel estimator may inflate home range sizes for individuals with locations sampled at a lower rate (Fieberg and Börger 2012). Tri's (2014) compilation indicated a general trend of smaller home ranges in lower latitudes or when bounded by geographic features (e.g. islands), but previous studies have not reported the profound effects of agriculture. Indeed, no previous study that we are aware of measured home ranges of resident bears in a region where the ratio of agriculture to forest was as large as in northwestern Minnesota (3:1).

Female bears in northwestern Minnesota exhibited home range sizes that were not of record size, but were on average ~2.5x larger (95% MCP: $\bar{x}$= 72.5 $km^2$) than other studies (180 studies compiled by Tri et al. 2014: $\bar{x}$ = 28.2 $km^2$). Pacas and Paquet (1994) reported the largest average female home range (295 $km^2$) from a study area that was similar to ours, on the edge between the boreal forest and an extensive agricultural area of Manitoba, Canada. Carter et al. (2010), in Michigan, reported the second largest average female home range (227$km^2$) resulting in a male to female home range size ratio of ~2.7. In contrast, males in northwestern Minnesota had 5.7 – 9.7x larger ranges than females (depending on method used).

Nearly all home range studies of bears have found that males occupy larger areas, due to their larger body size and polygynous mating system. This difference in range size may be exacerbated in strongly human-influenced landscapes. Male bears exhibit less risk-averse behavior and thus are more prone to exploit areas of strongly human-altered environments, tolerating larger gaps between patches of food and cover. Males have been shown to traverse and forage at the edges of ranges (Swenson et al. 1998; Kovach and Powell 2003; Kojola and Heikkinen 2006), urban areas (Beckmann and Berger 2003; Baruch-Mordo et al. 2014), agricultural fields (Maddrey 1995; Ditmer 2014, chapter 1), near roadways (McCown et al. 2004), and may be more innately inclined to test human food sources (Ditmer 2014, chapter 2).

Behaviorally, males in northwestern Minnesota may have taken the “easy road” by seeking out crop fields. These fields offer a greatly condensed source of calories during hyperphagia, when bears are attempting to rapidly gain mass. Crop fields are often adjacent to small woodlots and are typically far from high levels of human activity. In the northwestern Minnesota landscape, though, consumable crops constitute a small portion of the agricultural matrix (1-4% of areal cover), so finding them may require extensive traveling; but once there, a bear could settle down and eat, and travel a short distance to some nearby cover to sleep. We found that the size and variance of male weekly home ranges expanded in late summer (mid-August – September) as they searched for crop fields, possibly trying to avoid those already occupied by another bear, and then contracted sharply if they found one. Moreover, in a companion study where we used implanted heart monitors to gauge energy expenditure, we found that crop feeding bears showed little indication of being stressed in this non-natural environment (Ditmer 2014, chapter 3). Despite their exceedingly large home ranges, males appear to be “energy maximizers,” using natural forage when and where it is abundant, but seeking out calorically-dense consumable crops as soon as they are available. This behavior explains the strong negative correlation between crop use and weekly home range size (Schoener 1971). In essence, male bears appear to be “high-grading” the landscape, just as they apparently do within the smaller scale of a berry patch (Welch et al. 1997).

In contrast, female bears consumed fewer crops (corn, sunflowers, potentially oats and barley; Ditmer 2014, chapter 1), and instead must find areas with sufficient natural forage. They were less likely to traverse across an expanse of agriculture or forage in crop fields due to the risks associated with encountering humans and large males. This “safer” strategy yields female home ranges that are generally smaller with less dense but also far less variable food resources. Likewise, Mitchell and Powell (2007) reported that female black bear home ranges contained higher average food availability than adjacent areas but did not maximize forage availability. These authors suggested that social exclusion of high quality forage may influence home range placement and size.

Our results show that home range size is not always a good measure of habitat quality, at least not at commonly used temporal scales (e.g., annual ). Some studies have linked home range size with habitat quality or caloric availability (Samson and Huot 1998; Koehler and Pierce 2003; Dahle and Swenson 2003; Moyer et al. 2007) but without GPS collars they could only view the ranges annually or seasonally. Our ability to examine home ranges on a weekly scale enabled us to perceive how bears honed in on areas of high caloric availability, thus reducing space-use requirements on short time scales. However, because these patches of high calorie abundance are spread out in northwestern Minnesota, home range sizes increased dramatically when viewed over longer periods of time.

Bear home range size exhibited strong seasonal associations with habitats that varied in forage availability throughout the year. For example, oak forests produced little food in spring so caused weekly ranges in those seasons to inflate, whereas a good acorn crop in the fall enabled bears with more available oak habitat to use smaller areas. We had not anticipated the strong negative association between WHRs and lowland deciduous shrubs. Our food surveys indicated that these areas were highly variable in terms of bear food production, so it appears that bears employed their keen sense of smell to efficiently find dense, patch-level resources when they ripened.

The nature of the foods that bears eat creates an environment that is ever-changing and uncertain: different combinations and concentrations of fruit are available at any given time during a year and from year to year, and the location of highest resource availability is constantly shifting within a bear's home range. Black bears exploit this variability through a diverse and adaptable diet, so they are not too reliant on any one food type (Garshelis and Noyce 2008). However, populations that rely on anthropogenic food sources face additional long-term sources of variability. Bears subjected to radical changes in the availability of anthropogenic food sources have exhibited dramatic changes in demography and space use (Baruch-Mordo et al. 2011; Hopkins et al. 2014). Recent changes in agricultural technology coupled with climate change have enabled farmers to plant corn at higher latitudes, coinciding with more abundant bear populations (Malcom et al. 2012). Stowell and Willging (1992) associated an expansion in the Wisconsin bear range with the arrival of corn to areas of the state where it had previously not been climatically or economically suited. Our results showed that anthropogenic food sources in northwestern Minnesota altered bear space use and enhanced habitat suitability. Importantly, though, we found that even without the crops, this area had sufficient natural foods to support a bear population. This finding, based on our habitat modeling, is consistent with our observations that females in this area had the highest reproductive rate in Minnesota (Garshelis et al. 2012), even if they did not consume crops. The fragmented forest at this edge of the range is clearly productive in terms of natural bear foods.

Our habitat modeling showed that the edge of suitable bear range in northwestern Minnesota expands westward from spring to summer to fall. The extent of suitable habitat for female bears was closely linked to changes in caloric availability. Males, in contrast, could subsist for short periods below the resource threshold exhibited by females (Table 5). As such, they had a much farther potential reach westward, where there are widely separated pockets of suitable habitat. Females would not only be unlikely to cross vast expanses of agriculture, they would be less likely to settle in an area where they had to rely on crops for food.

Despite the potentially suitable habitat farther west than the current edge of the bear range in Minnesota, there is an extensive gap that bears would have to cross to get there, and we cannot tell from our data whether they are likely to make this leap. We observed one sub-adult male who moved into a continuous area of seemingly unsuitable habitat (Fig. 13B). In this case, closer inspection of the habitat that this bear occupied revealed a narrow corridor of trees and some isolated pockets of woodland that were not discernible with current remote sensing technology. Hence, there may in fact be stepping stones that bears can use to reach farther into the agricultural zone, drawn by the bounty of calories in fall. In spring and summer, though, these bears would need to retreat eastward. Vagrant bears who visit this area are likely to be young male bears, who exhibit a greater willingness for risk-taking (Nellemann et al. 2007) and may use the most marginal habitats because they have been excluded elsewhere by larger bears (Mattson 1990).

We utilized remotely sensed data and combined it with biological information to understand how bears are able to thrive in a region that was once considered secondary or poor bear habitat. GPS-collar technology allowed us to sample the locations of bears at high enough frequency to discern the compositional requirements of short-term home ranges. This in turn provided the basis for grading habitat suitability, which enabled us to demarcate the western edge of the eastern population of American black bears under different resource availability scenarios. Given the changing nature of today's climate and landscape, understanding how and why a species' range may expand or contract is important for both management and conservation.

TABLE 1

Abundance and caloric content of bear foods assessed in wild food surveys in natural habitats (2007-2011) or crop samples from northwestern Minnesota (2007 – 2011).

| **Common Name** | **Scientific Name** | **Season Available** | **% of Fruit Sampling Biomass[¥]** | **% Consumable Dry Component** | **Calories per Gram** | **# calorimetry samples** | **Standard Deviation of Cal. Per Gram** |
|---|---|---|---|---|---|---|---|
| Pagoda Dogwood | *Cornus alternifolia* | Summer | 0.10% | 38.86% | 5.43[*1] | 2 | 0.089 |
| Arrowwood | *Viburnum dentatum* | Summer | 2.45% | 15.09% | 5.03[*2] | 2 | 0.007 |
| Chokecherry | *Prunus virginiana* | Summer | 18.88% | 13.16% | 4.64 | 2 | 0.008 |
| Pin Cherry | *Prunus pensylvanica* | Summer | 1.00% | 16.95% | 4.64[*3] | 2 | 0.008 |
| Sarsaparilla | *Aralia nudicaulis* | Summer | 2.45% | 25.42% | 4.52 | 2 | 0.002 |
| Raspberry | *Rubus strigosus* | Summer | 4.23% | 13.07% | 4.50 | 2 | 0.059 |
| Juneberry | *Amelanchier humilis* | Summer | 5.43% | 25.12% | 3.98 | 2 | 0.002 |
| Alder-leaved Buckthorn | *Rhamnus alnifolia* | Summer | 0.23% | 17.79% | 3.98[*4] | 2 | 0.002 |
| Gooseberry | *Ribes hirtellum* | Summer | 0.23% | 12.97% | 2.75 | 1 | NA |
| Red-osier dogwood | *Cornus sericea* | Summer & Fall | 7.63% | 38.86% | 5.43 | 2 | 0.089 |
| Beaked Hazel | *Corylus cornuta* | Fall | 8.02% | 10.20% | 6.66 | 3 | 0.173 |
| American Hazel | *Corylus americana* | Fall | 31.34% | 10.20% | 6.66 | 3 | 0.173 |
| Oil sunflower seeds | *Helianthus annuus* | Fall | NA - CROP | 70.89% | 6.60 | 2 | 0.012 |
| Gray Dogwood | *Cornus racemosa* | Fall | 5.27% | 38.86% | 5.43[*5] | 2 | 0.089 |
| Nannyberry | *Viburnum lentago* | Fall | 1.99% | 15.35% | 4.50 | 2 | 0.056 |
| Acorn | *Quercus macrocarpa* | Fall | NA - Fall Survey | 28.27% | 4.43 | 4 | 0.089 |
| Cranberry | *Viburnum trilobum* | Fall | 1.96% | 15.09% | 4.24 | 2 | 0.095 |
| Corn | *Zea mays* | Fall | NA - CROP | 66.29% | 4.23 | 2 | 0.041 |
| Hawthorn | *Crataegus*spp. | Fall | 4.00% | 22.61% | 4.10 | 2 | 0.015 |
| Plum | *Prunus americana* | Fall | 5.81% | 24.89% | 3.74 | 2 | 0.087 |

[¥] Raw % of estimated weight for each bear food in 4 natural habitat types in northwestern Minnesota (2007 – 2011)
[*1] assigned caloric values of red-osier dogwood
[*2] assigned caloric values of high-bush cranberry
[*3] assigned caloric values of chokecherry
[*4] assigned caloric values of juneberry
[*5] assigned caloric values of red-osier dogwood

TABLE 2

Values used to estimate calories per m$^2$ for agricultural crops in northwestern Minnesota. Corn and sunflowers are commonly consumed by bears, and bears have been documented to consume oats and barley.

| **Crop Type** | ***Ave. yield per acre** | **¥Grams per m$^2$** | **Dry consumable %** | **Calories per gram** | **+Source** | **Calories per m$^2$** |
|---|---|---|---|---|---|---|
| Barley | 57 bushels | 306.1 | 91 | 3.5 | USDA | 981 |
| Corn (grain) | 125 bushels | 785.2 | 90 | 4.2 | calorimetry | 2,974 |
| Oats | 57 bushels | 203.5 | 92 | 3.9 | USDA | 727 |
| Sun (oil) | 1475 lbs | 165.3 | 73 | 6.6 | caloirmetry | 797 |

* Average yields were obtained using United States Department of Agriculture's (USDA) National Agricultural Statistics Service estimates for northwestern MN in 2011 and 2012 (http://www.nass.usda.gov)

¥We used yield estimates from the region to obtain grams per m$^2$. We then multiplied grams per m$^2$ by our estimates of dry consumable % for each crop type. We then obtained calories per gram for each crop using either bomb calorimetry or published values as noted in the Source column. The calories per m$^2$ value was assigned to the areas of our GIS layer for crop types when estimating calories within weekly home ranges or forecasting bear habitat quality.

+Calories per gram and Dry consumable % for barley and oats were obtained from: USDA National Nutrient Database for Standard Reference (http://ndb.nal.usda.gov/)

TABLE 3

Average calories of bear foods produced per $m^2$ (standard error) in four habitats and two seasons (summer: ~ late June–Aug., fall: Sept. – Oct.) in northwestern, Minnesota, 2007–2011. Values for oak habitat include calories from acorns.

| Season | Year | Aspen | Conifer | LLDS | Oak |
|---|---|---|---|---|---|
| **Summer** | 2007 | 46.9 (12.0) | 9.2 (3.7) | | 165.7 (50.1) |
| | 2008 | 40.7 (7.4) | | | 113.1 (22.2) |
| | 2009 | 98.6 (27.8) | | | 96.1 (20.8) |
| | 2010 | 202.0 (40.7) | | 173.3 (118.8) | 90.0 (23.8) |
| | 2011 | 98.4 (31.4) | | 213.4 (88.9) | 36.6 (11.1) |
| **Fall** | 2007 | 104.7 (26.5) | 0.2 (0.1) | | 223.4 (50.4) |
| | 2008 | 107.6 (22.7) | | | 176.2 (38.3) |
| | 2009 | 148.1 (31.2) | | | 46.1 (13.5) |
| | 2010 | 242.8 (52.8) | | 175.8 (115.4) | 222.3 (29.9) |
| | 2011 | 143.6 (52.2) | | 202.9 (86.9) | 229.4 (28.3) |

TABLE 4

Seasonal km$^2$ used for the moving window analysis and percent of natural cover required within a moving window for habitat area to be considered above "Very Low" habitat suitability.

| | **Females** | | | **Males** | | |
|---|---|---|---|---|---|---|
| Season | **Spring** | **Summer** | **Fall** | **Spring** | **Summer** | **Fall** |
| Moving window km$^2$ (median WHR) | 12.4 | 16.8 | 3.9 | 86.0 | 63.7 | 35.8 |
| Min. natural cover values (5th quantile nat. cover) | 9.9% | 9.0% | 10.1% | 5.0% | 4.1% | 2.8% |

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TABLE 5

Caloric values used to classify summer and fall habitat suitability for female and male bears in northwestern, Minneosta. Total calories < $5^{th}$ quantile were considered “Very Low”, $5^{th}$ to $25^{th}$ quantile = “Low”, $25^{th}$ – $50^{th}$ = “Medium”, $50^{th}$ to $75^{th}$ = “High”, and > $75^{th}$ = “Very High

| **Quantile of WHR caloric availability** | **Females** | | **Males** | |
|---|---|---|---|---|
| | Summer | Fall | Summer | Fall |
| **5th** | 9,968 | 278,000 | 175,200 | 90,430 |
| **25th** | 213,500 | 907,700 | 984,800 | 811,700 |
| **50th** | 547,900 | 1,616,000 | 4,384,000 | 2,446,000 |
| **75th** | 1,143,000 | 2,623,000 | 9,645,000 | 8,143,000 |

TABLE 6

Average annual home range size (km$^2$) (95% CI) of GPS-collared bears in northwestern Minnesota based on 33 female and 27 male bear-years, 2007 – 2013. Only fixes separated by four hours or more were included.

| Sex | [a]Method | 50% Isopleth | 95% Isopleth | 100% Isopleth |
|---|---|---|---|---|
| Female | MCP | 21.6 (8.3 - 34.9) | 72.5 (45.5 - 99.5) | 115.9 (80.5 - 151.2) |
| | Rule Based | 18.1 (10.4 - 25.8) | 77.8 (51.7 - 103.8) | --- |
| | H-Ref | 19.1 (11.5 - 26.7) | 91.4 (54.5 - 128.3) | --- |
| | k LoCoH | 2.6 (1.6 - 3.6) | 30.3 (18.5 - 42.1) | --- |
| Male | MCP | 172.8 (107.3 - 238.3) | 616.9 (466.1 - 767.7) | 861.4 (639.0 - 1083.8) |
| | Rule Based | 168.6 (114.4 - 222.7) | 754.0 (550.7 - 957.3) | --- |
| | H-Ref | 172.6 (118.7 - 226.6) | 834.1 (596.3 - 1071.9) | --- |
| | k LoCoH | 7.6 (4.8 - 10.4) | 172.9 (129.8 - 215.9) | --- |

[a] MCP = minimum convex polygon, Ad-hoc = rule-based approach using the ad-hoc method for selecting a bandwith (Kie 2013), H-ref = kernel density estimator with reference bandwidth for H, k LoCoH = fixed k nearest neighbor convex hull

TABLE 7

Top models describing variation in weekly home range size of black bears living in northwestern, Minnesota from 2007-2013. Starting with the full model, we performed backward stepwise selection using AICc (Akaike's Information Criterion for small sample sizes) to determine top models. We list all models with ΔAICc < 2, and the global and null models.

| **Model** | **K** | **$\Delta AIC_c$** | **Model weight** |
|---|---|---|---|
| ROAD+AGFIELD+WET+LLDS+DEW+DAY+(COY×SEAS)+(CROP×SEAS)+(CROP×SEX)+(OAK×SEAS)+WIND | 21 | 0.00 | 0.35 |
| ROAD+AGFIELD+WET+LLDS+DEW+DAY+(COY×SEAS)+(CROP×SEAS)+(CROP×SEX)+(OAK×SEAS) | 20 | 0.24 | 0.31 |
| ROAD+AGFIELD+WET+LLDS+DEW+DAY+(COY×SEAS)+(CROP×SEAS)+(CROP×SEX)+(OAK×SEAS)+WIND+AGE | 22 | 0.98 | 0.22 |
| ROAD+AGFIELD+WET+LLDS+DEW+DAY+(COY×SEAS)+(CROP×SEAS)+(CROP×SEX)+(OAK×SEAS)+WIND+AGE + TEMP + PRECIP | 24 | 4.79 | 0.03 |
| Null | 1 | 567.35 | 0.00 |

TABLE 8

Beta estimates, standard errors, t-statistics, p-values and 95% confidence intervals scaled and centered covariates included in the top model assessing influences of weekly home range size (log) for American black bears in northwestern Minnesota, 2007-2013.

| **Covariates†‡** | **β** | **SE(β)** | **t-value** | **p-value** | **LOCI** | **UPCI** |
|---|---|---|---|---|---|---|
| (Intercept) | 2.800 | 0.181 | 15.430 | 0.000 | 2.444 | 3.155 |
| CROP | 0.747 | 0.275 | 2.716 | 0.007 | 0.208 | 1.285 |
| COY | -0.462 | 0.135 | -3.421 | 0.001 | -0.726 | -0.197 |
| DAY | 0.228 | 0.114 | 1.997 | 0.046 | 0.004 | 0.452 |
| DEW | 0.230 | 0.072 | 3.204 | 0.001 | 0.090 | 0.371 |
| LLDS | -0.303 | 0.079 | -3.831 | 0.000 | -0.458 | -0.148 |
| AGFIELD | 0.721 | 0.094 | 7.676 | 0.000 | 0.537 | 0.905 |
| OAK | 0.230 | 0.097 | 2.356 | 0.019 | 0.039 | 0.421 |
| ROAD | 0.274 | 0.046 | 5.985 | 0.000 | 0.184 | 0.364 |
| Season:Fall | 0.089 | 0.244 | 0.363 | 0.716 | -0.389 | 0.567 |
| Season:Summer | -0.088 | 0.149 | -0.589 | 0.556 | -0.379 | 0.204 |
| SEX:Males | 0.616 | 0.217 | 2.842 | 0.006 | 0.191 | 1.041 |
| WET | 0.540 | 0.066 | 8.163 | 0.000 | 0.410 | 0.670 |
| WIND | -0.071 | 0.046 | -1.544 | 0.123 | -0.162 | 0.019 |
| CROP × Season:Summer | -1.108 | 0.282 | -3.935 | 0.000 | -1.660 | -0.556 |
| CROP × Season:Fall | -0.937 | 0.281 | -3.334 | 0.001 | -1.487 | -0.386 |
| CROP × Sex:Male | -0.356 | 0.090 | -3.954 | 0.000 | -0.532 | -0.179 |
| COY × Season:Summer | 0.569 | 0.114 | 5.005 | 0.000 | 0.346 | 0.791 |
| COY × Season:Fall | 0.516 | 0.127 | 4.052 | 0.000 | 0.267 | 0.766 |
| OAK × Season:Summer | -0.376 | 0.112 | -3.373 | 0.001 | -0.595 | -0.158 |
| OAK × Season:Fall | -0.364 | 0.111 | -3.290 | 0.001 | -0.580 | -0.147 |

TABLE 9

Estimated percent coverage of habitat suitability classes with different caloric availability scenarios for the seasons and between males and females. Spring (~May 1 – July 1) habitat suitability classes incorporate the % of natural habitat coverage (Table 4), road density and traffic volume associated with weekly home ranges of male and female bears in northwestern Minnesota. Summer (~July 1 – Sept. 1) and fall (~Sep 1 – Dec 1) habitat suitability classes are based on % of natural habitat coverage (Table 4), road density and traffic volume and caloric availability (Table 5) associated with weekly home ranges of male and female bears in northwestern Minnesota.

| | | **Females** | | | | | **Males** | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **Season** | **[a]Scenario** | **Very Low** | **Low** | **Medium** | **High** | **Very High** | **Very Low** | **Low** | **Medium** | **High** | **Very High** |
| Spring | Basic Spring Range (usable spring habitats - influence of roads) | 54.1% | 9.8% | 9.5% | 8.9% | 17.7% | 46.1% | 16.4% | 11.1% | 12.4% | 14.1% |
| Summer | Low Wildland Calories, Low CROP availability | 61.1% | 30.3% | 5.7% | 1.4% | 1.5% | 41.6% | 14.1% | 42.6% | 1.6% | 0.2% |
| Summer | Low Wildland Calories, Lowest Corn availability - no other crops | 65.1% | 32.2% | 2.0% | 0.5% | 0.2% | 41.6% | 17.2% | 39.5% | 1.5% | 0.2% |
| Summer | High Wildland Calories, High CROP availability | 48.7% | 6.7% | 14.8% | 17.6% | 12.2% | 40.4% | 1.3% | 9.2% | 33.3% | 15.7% |
| Fall | Low Wildland Calories, Low CROP availability | 45.2% | 40.1% | 13.9% | 0.7% | 0.1% | 40.3% | 11.4% | 34.7% | 11.3% | 2.3% |
| Fall | Average Wildland Calories, No CROP Available | 51.1% | 25.6% | 21.1% | 2.2% | 0.0% | 39.9% | 19.6% | 20.6% | 19.9% | 0.0% |
| Fall | High Wildland Calories, High CROP availability | 43.7% | 11.1% | 22.7% | 16.8% | 5.7% | 39.3% | 2.4% | 7.3% | 42.6% | 8.3% |

[a] CROP is based on the availability of corn, sunflowers, oats and barley. CROP's areal coverage is 1.4-3.9% of the study area with corn and sunflowers making up the majority CROP's composition (~ 80-90%).

FIGURE 1

Average weekly home range (WHR) estimates and 95% confidence intervals (km$^2$) of GPS-collared **A)** male and **B)** female black bears in northwestern Minnesota, 2007-2013. Seventy-five bear-years (37 female, 38 male) were used to construct 1,453 weekly home range estimates using the 95% isopleth with the rule based method of kernel estimation (Kie 2013). Averages and the corresponding confidence intervals were calculated using the point estimates of WHRs for each week. The gray horizontal line in the males' figure (A) represents the maximum value of the females' y-axis (70 km$^2$).

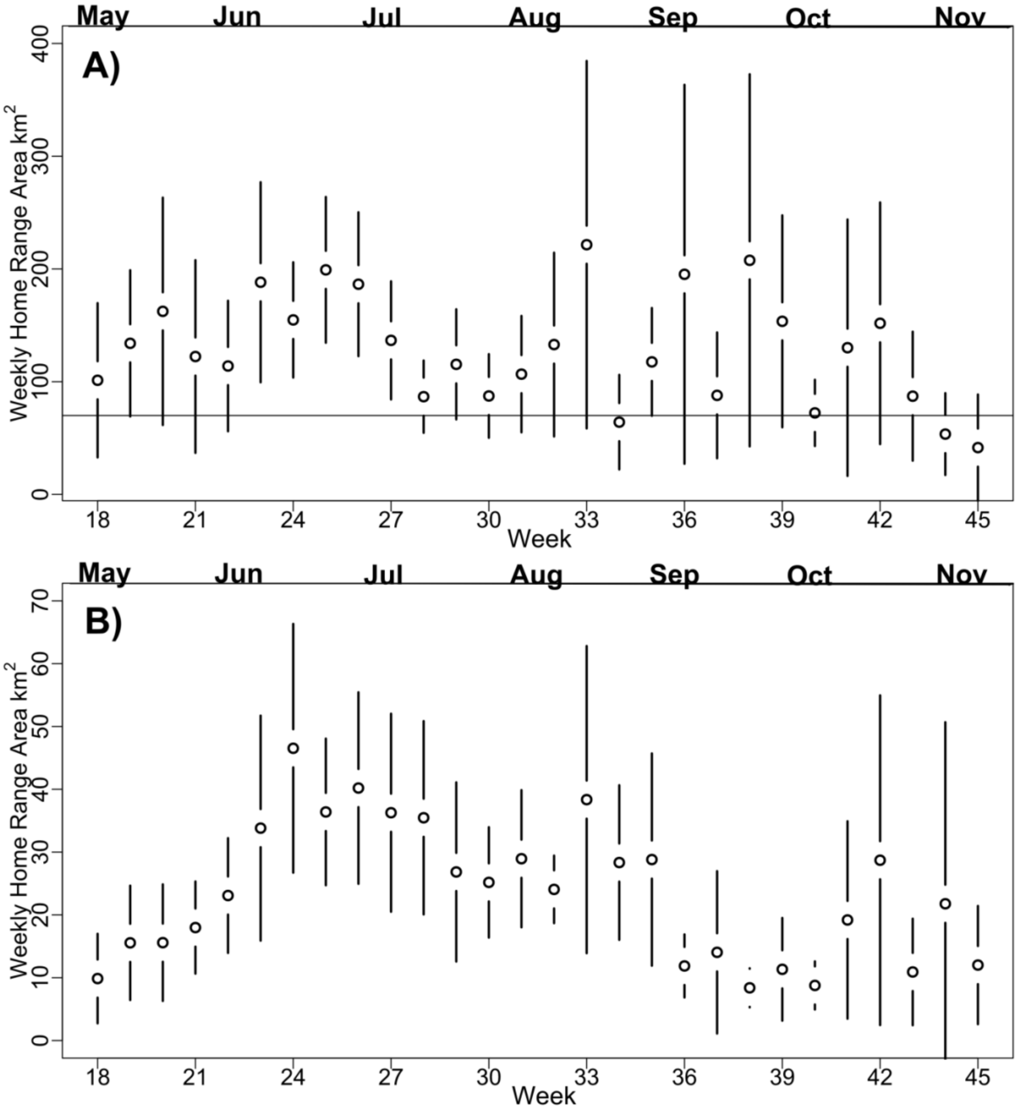


FIGURE 2

Predicted changes in weekly home range size (log km$^2$) in response to changes in the proportion of edible crops within the home range during spring (left, weeks < 26, ~May 1 – July 1), summer (middle, weeks 26-36, ~July 1 – Sept. 1) and fall (right, weeks > 37, ~Sep 1 – Dec 1) for bears in northwestern Minnesota. All covariates were scaled and centered.  We derived estimates from the best-approximating model and held all other covariates constant at their mean values.

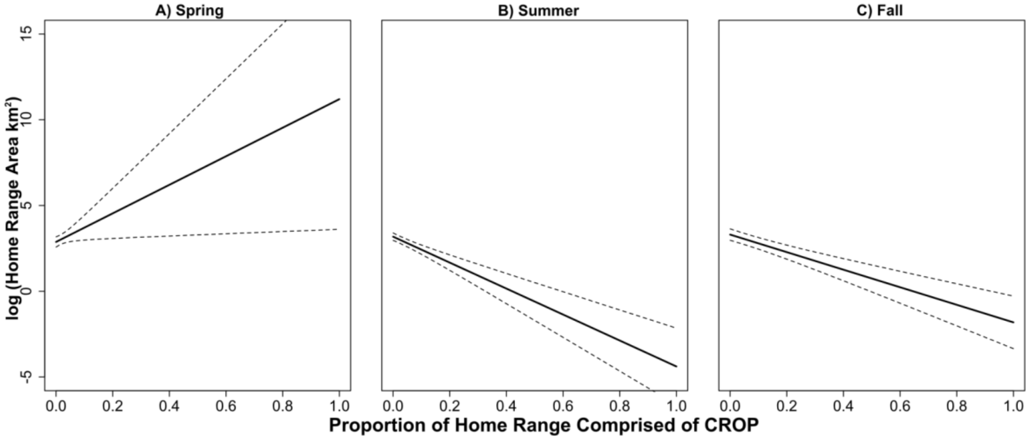


FIGURE 3

Predicted changes in weekly home range size (log km$^2$) in response to changes in the proportion of edible crop fields (CROP) for male (top) and female (bottom) bears in northwestern Minnesota. All covariates were scaled and centered. We derived estimates from the best-approximating model and held all other covariates constant at their mean values.

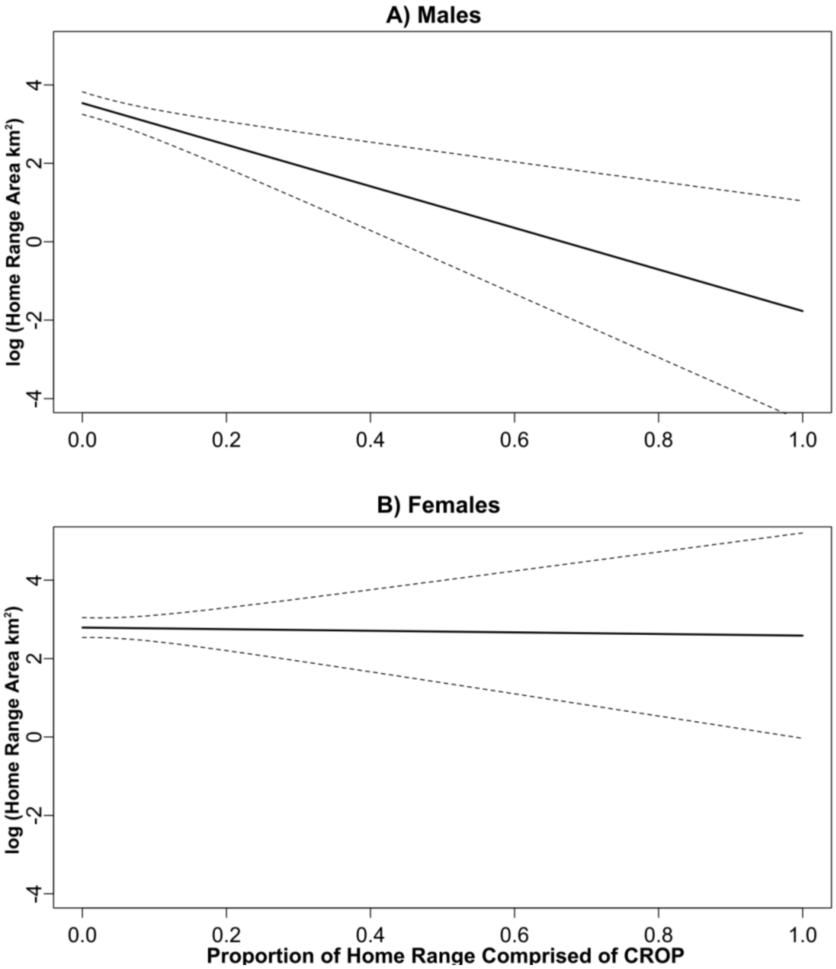


FIGURE 4

Predicted changes in weekly home range size (log km$^2$) in response to changes in the proportion of oak habitat within the home range during spring (left, weeks < 26, ~May 1 – July 1), summer (middle, weeks 26-36, ~July 1 – Sept. 1) and fall (right, weeks > 37, ~Sep 1 – Dec 1) for bears in northwestern Minnesota. All covariates were scaled and centered. We derived estimates from the best-approximating model and held all other covariates constant at their mean values.

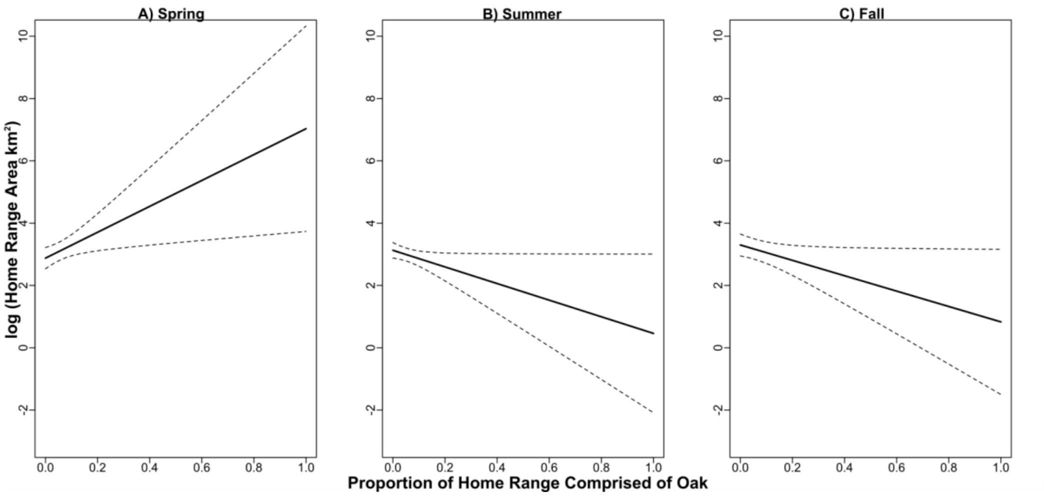


FIGURE 5

Predicted seasonal changes in weekly home range size (log km2) in response to caring for cubs of the year during spring (left, weeks < 26, ~May 1 – July 1), summer (middle, weeks 26-36, ~July 1 – Sept. 1) and fall (right, weeks > 37, ~Sep 1 – Dec 1) for bears in northwestern Minnesota. All covariates were scaled and centered. We derived estimates from the best-approximating model and held all other covariates constant at their mean values.

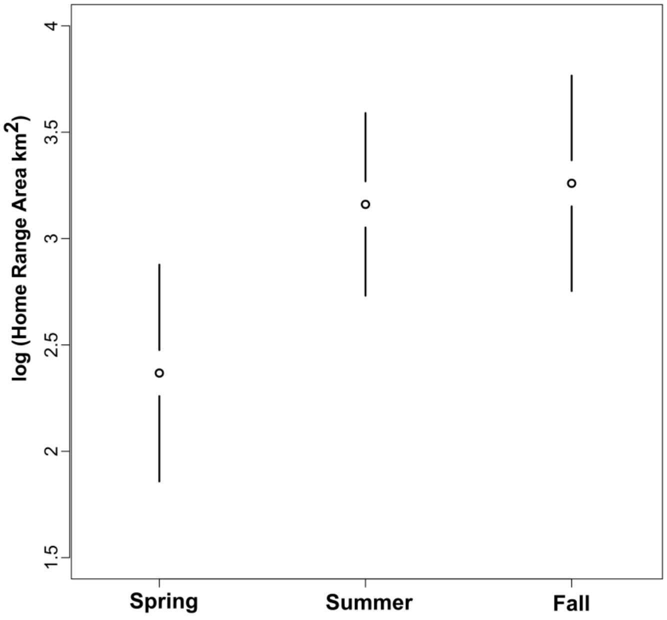


FIGURE 6

Projected habitat suitability during spring (May 1 – July 1) for females (left – 6A) and male (right – 6B) bears in northwestern Minnesota and eastern counties of North Dakota. Maps incorporate natural cover requirements and the influence of roads based on weekly home ranges of GPS-collared bears.

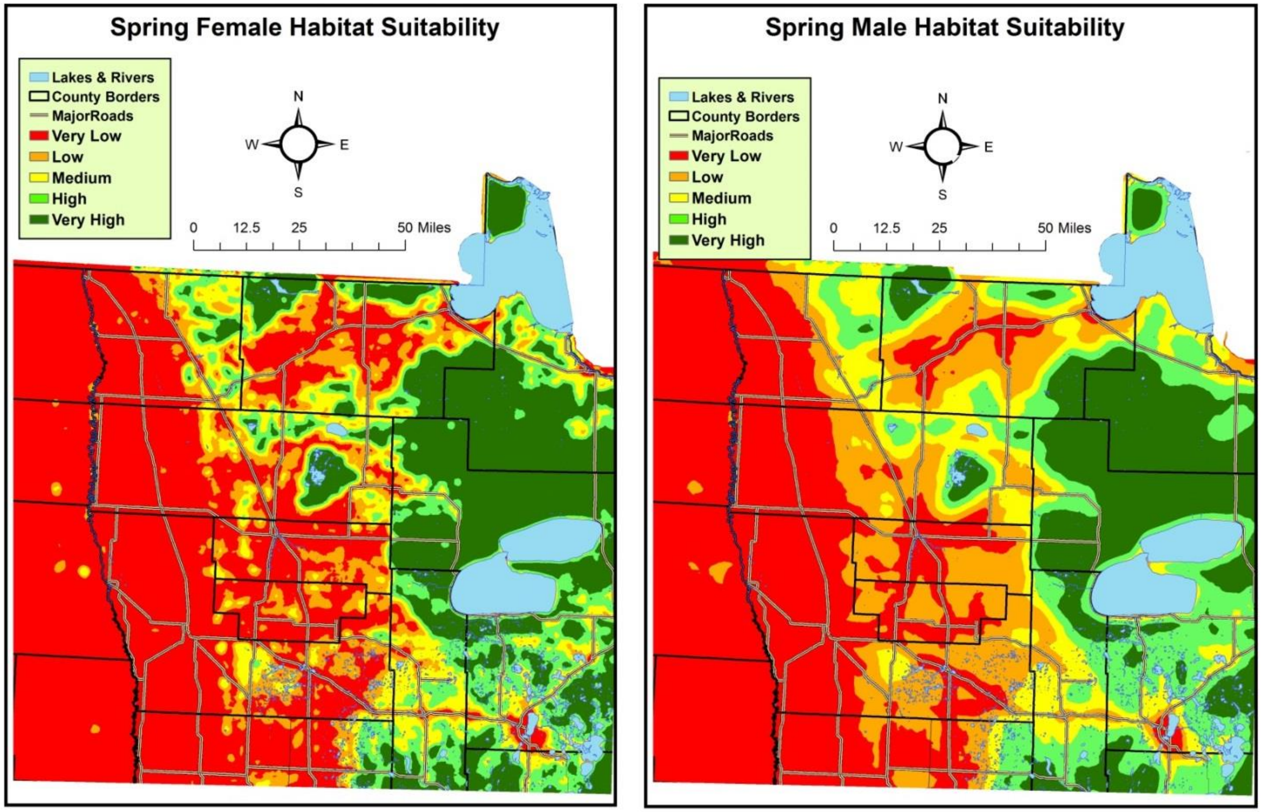
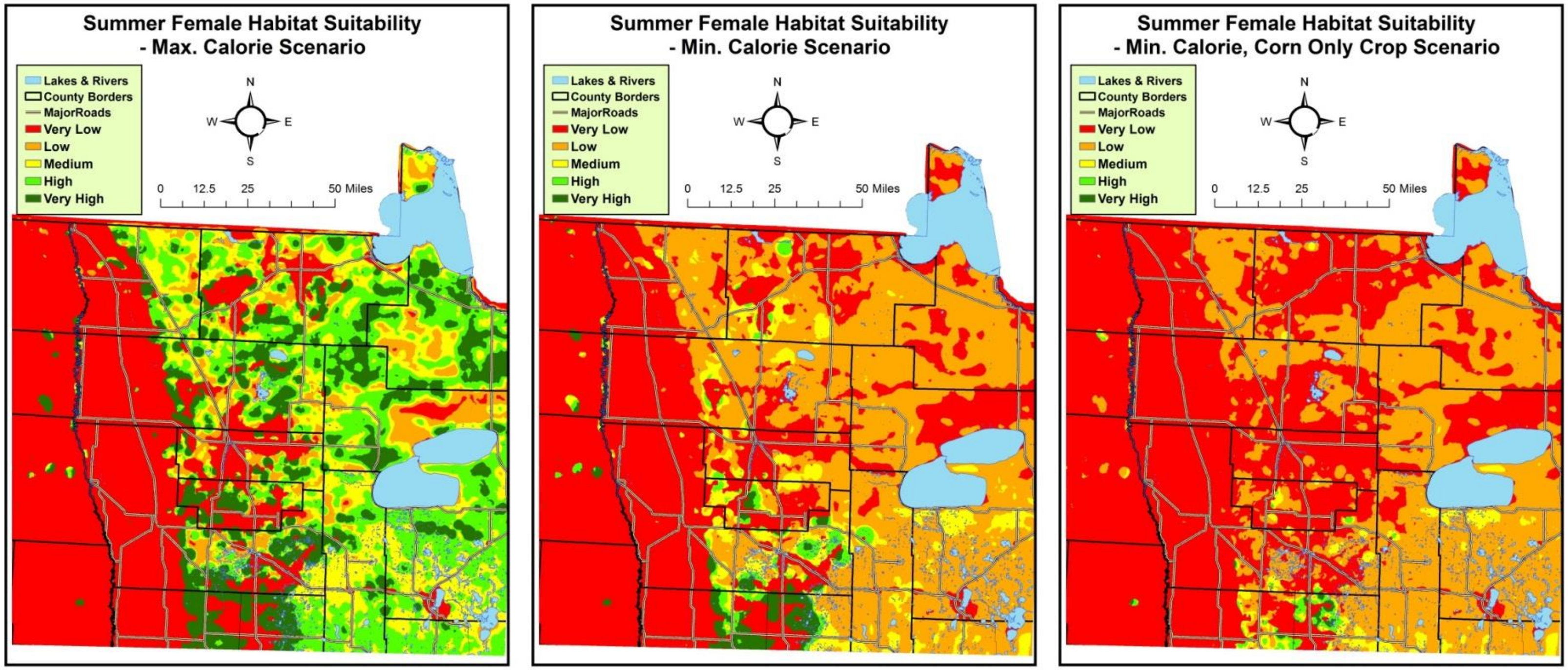


FIGURE 7

Projected habitat suitability during summer (July 1 – Sept. 1) for females bears living in northwestern Minnesota and eastern counties of North Dakota for natural food calories – most crop availability (left – 7A), minimum/low natural calories – all available crops (center – 7B), and low natural calories -corn the only available crop (right - 7C) caloric scenarios. Maps incorporate natural cover requirements, the influence of roads, and caloric values based on weekly home ranges of GPS-collared bears.



Summer Female Habitat Suitability - Max. Calorie Scenario

Summer Female Habitat Suitability - Min. Calorie Scenario

Summer Female Habitat Suitability - Min. Calorie, Corn Only Crop Scenario

FIGURE 8

Projected habitat suitability during summer (July 1 – Sept. 1) for males bears living in northwestern Minnesota and eastern counties of North Dakota for natural food calories – most crop availability (left – 8A), minimum/low natural calories – all available crops (center – 8B), and low natural calories -corn the only available crop (right – 8C) caloric scenarios. Maps incorporate natural cover requirements, the influence of roads, and caloric values based on weekly home ranges of GPS-collared bears.

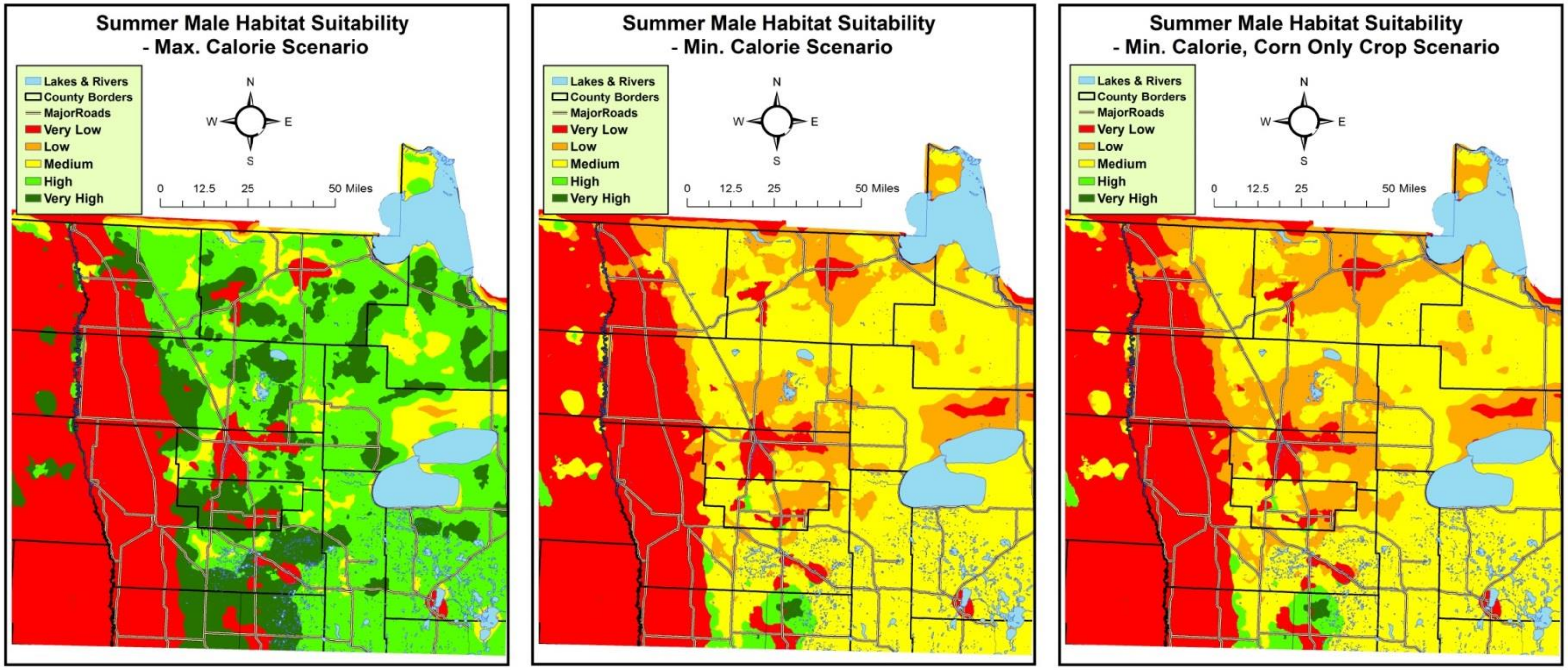


FIGURE 9

Projected habitat suitability during fall (Sep 1 – Dec 1) for females bears living in northwestern Minnesota and eastern counties of North Dakota for high natural food calories – most crop availability (left – 9A), minimum/low natural food calories (center – 9B), and minimum/low natural food calories – corn only crop available (right – 9C) caloric scenarios. Maps incorporate natural cover requirements, the influence of roads, and caloric values based on weekly home ranges of GPS-collared bears.

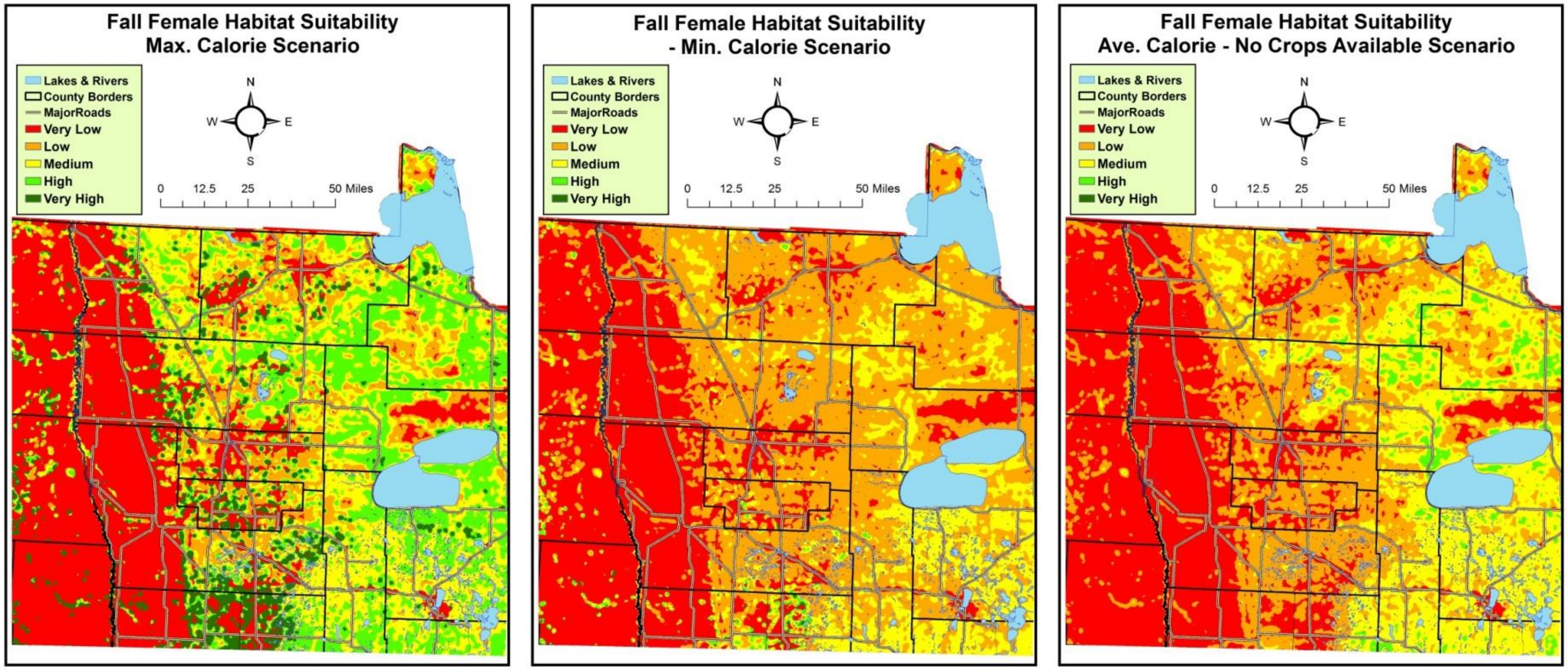


FIGURE 10
Projected habitat suitability during fall (Sep 1 – Dec 1) for females bears living in northwestern Minnesota and eastern counties of North Dakota for high natural food calories – most crop availability (left – 10A), minimum/low natural food calories (center – 10B), and minimum/low natural food calories – corn only crop available (right – 10C) caloric scenarios. Maps incorporate natural cover requirements, the influence of roads, and caloric values based on weekly home ranges of GPS-collared bears.

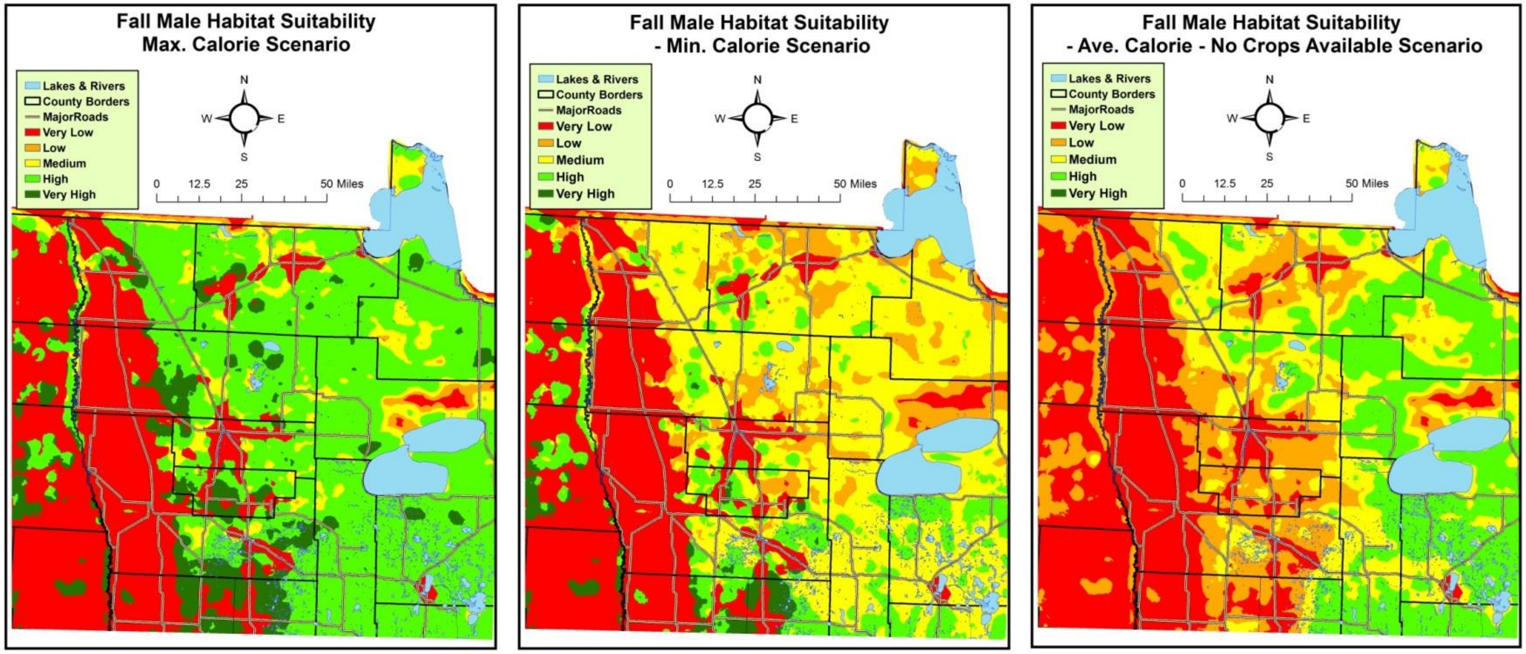
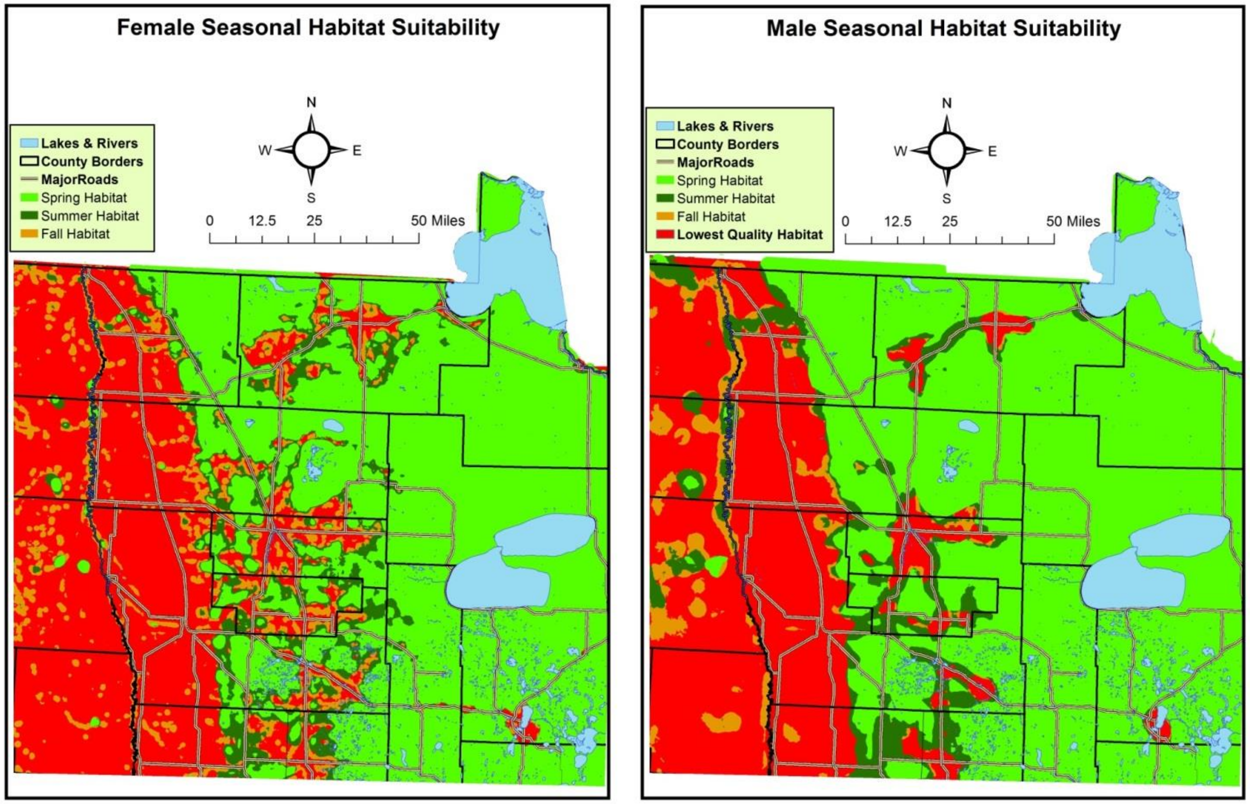


FIGURE 11

Projected maximum habitat suitability extent during spring (May 1 – July. 1), summer (July 1 – Sept. 1), and fall (Sep 1 – Dec 1) for female (11A) and male bears (11B) living in northwestern Minnesota and eastern counties of North Dakota. The map illustrates the expansion of usable habitat throughout the year. Spring had the least overall coverage so is shown as the top layer with summer and fall maps below. Any areas showing fall habitat are only available during fall but all spring area is available during summer and fall. Spring extent was based on maps 6A and 6B, summer based on 7A and 8A, fall on 9A and 10A.



Female Seasonal Habitat Suitability

Male Seasonal Habitat Suitability

FIGURE 12
Projected female fall habitat suitability in the region of the study area where bears were primarily collared displaying without (12A) and with all (12B) GPS fall locations from GPS-collared female bears. 99.8% of locations (16,016) were in our projected suitable habitat (anything above “Very Low” designation – red).

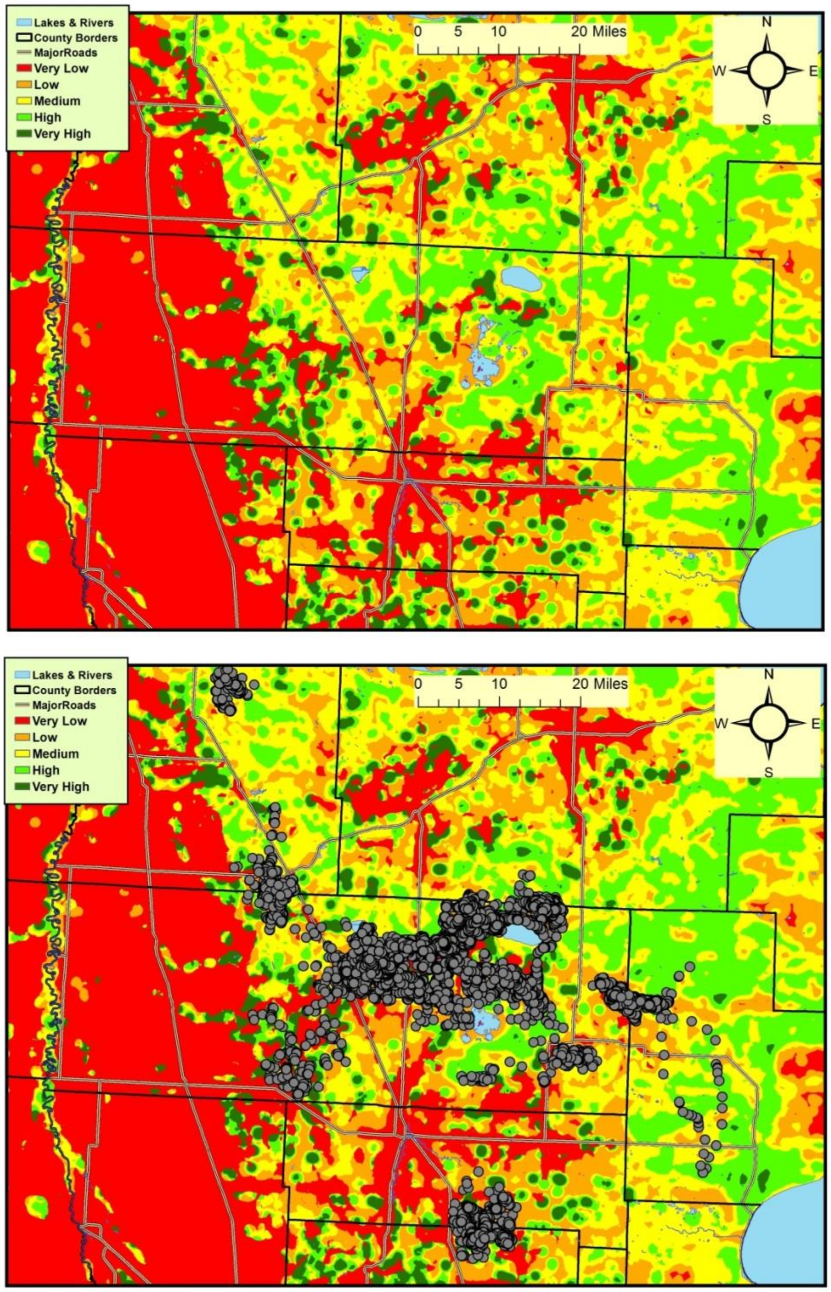
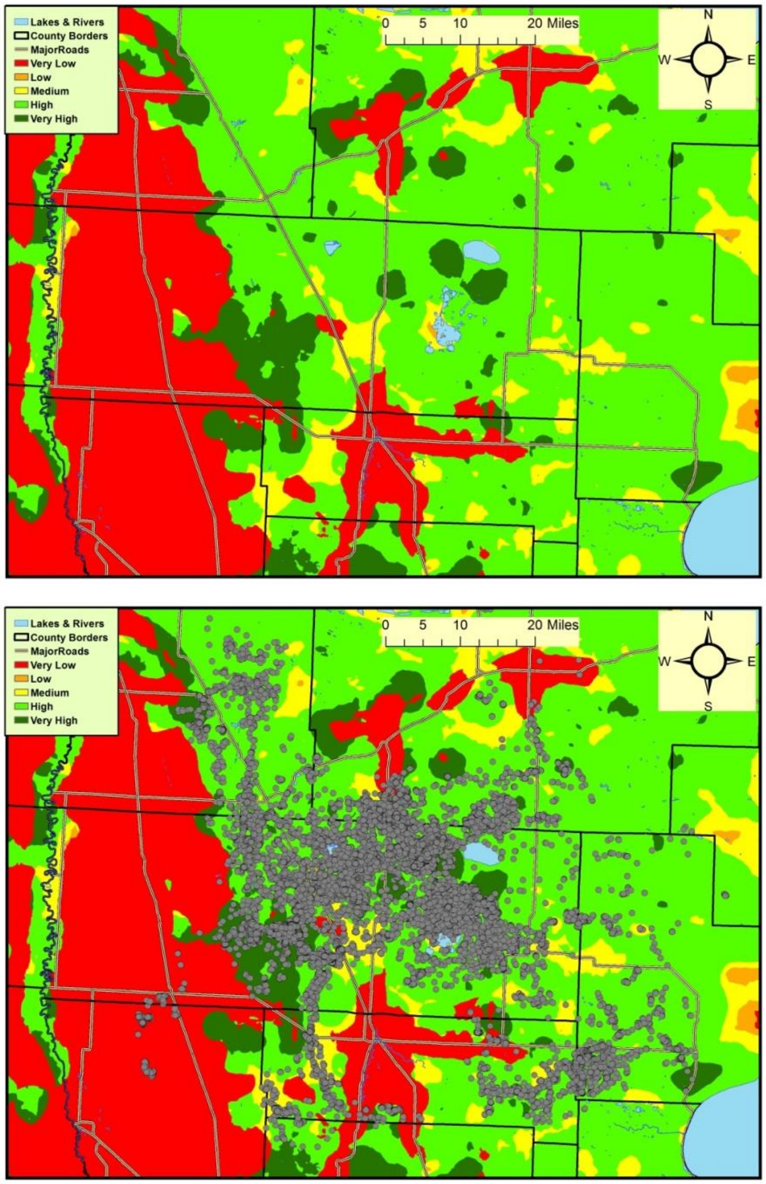


FIGURE 13

Figures 13A and 13B) Projected male fall habitat suitability in the region of the study area where bears were primarily collared displaying without (13A) and with all (13B) GPS fall locations from GPS-collared male bears. 94.8% of locations (15,712) were in our projected suitable habitat (anything above “Very Low” designation – red). The locations of a two-year-old male bear into the “Very Low” habitat at the western periphery show some bears are willing to move through or use these areas for at least a brief time.



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## APPENDIX I

## CROP DAMAGE BY BEARS AND RESULTING ATTIDUES OF FARMERS IN NORTHWESTERN MINNESOTA

### Appendix 1.1 METHODS

We interviewed farmers in northwestern Minnesota to gauge the amount and types of crops damaged by wildlife (with a focus on bear damage) and how farmer attitudes toward bears changed accordingly. Growers were asked to subjectively rate levels of bear damage to their crops based on a scale of 0–5, where 0=No Damage and 5=Major Damage. We asked how tolerant the grower was of bear-related damage to crops and asked if they would prefer less, the same, or more bears in the region. We also inquired about any attempted hunting of bears on the property either as a direct response to nuisance activity or a means to reduce the general number of bears near the crop land. Growers that did not experience wildlife-related crop damage or seemed reluctant to be interviewed were asked only a subset of the questions.

Initial interviews were conducted with growers who had reported damage to local Minnesota Department of Natural Resources offices, as well as growers who owned fields in which GPS-collared bears were known to have visited. After these growers were interviewed, all growers within the study area were considered potential interview subjects.

### Appendix 1.2 RESULTS

During 2009 – 2012, we conducted 38 interviews with growers (36) and apiarists (2) in the region. We conducted 9 interviews in person and 29 over the telephone. The average grower had been in the region for ~30 years (range 11–56 years). They owned or planted an average of 1,374 acres (range 30–4000 acres) or equivalently 556 ha (range

12–1619 ha). In addition to bears, growers reported crop damage from white-tailed deer *(Odocoileus virginianus)*, raccoons (*Procyon lotor)*, moose (in years past; *Alces alces*), waterfowl (unspecified species), elk (*Cervus canadensis)*, and sandhill cranes (*Grus canadensis)*.

Of the 38 growers and apiarists sampled, 24 (63.2%) reported some level of bear damage. Growers reported different levels of bear damage for different crops and crop varieties. Of the 25 survey participants who grew corn in recent years (65.8% of those surveyed), 91.3% reported damage from bears. The 13 survey participants who grew hybrid/grain corn reported a significantly higher mean level of damage ($\bar{x}$ = 3.61, 95% CI: 2.71 – 4.51) than those who grew field corn for silage ($\bar{x}$ = 1.83, 95% CI: 1.30 – 2.68).

Of 19 interviewed sunflower growers, 16 had grown oil sunflowers (used for cosmetics, cooking, birdseed), 9 confection sunflower growers (used for human consumption, birdseed) and 6 had experience growing both varieties of sunflowers. The mean score for amount of damage to oil sunflower fields was significantly higher ($\bar{x}$ = 2.20, 95% CI: 1.17 – 3.23) than for confectionary sunflower fields ($\bar{x}$ = 0.28, 95% CI: 0.04 – 0.52).

Apiarists (2 out of 2, but highly dependent on year) and oat growers (9 of 9, $\bar{x}$ = 2.94, 95% CI: 1.96 – 3.93) also reported significant amounts of bear damage. The crop with the most areal coverage, soybeans, had only 1 report of “minor” bear damage out of 25 growers. Those who grew wheat, canola, barley, alfalfa, sugar beets, and rye grass, grains, or hay either reported low or no amounts of distinguishable bear damage.

Unsurprisingly tolerance towards bear damage was largely determined by the perceived level of damage incurred. All 5 growers who had experienced no bear damage to crops considered themselves to be “tolerant”. Of the 18 respondents that had incurred bear damage, only 5 (27.8%) classified themselves as “tolerant” while 7 (38.9%) said that their level of tolerance was “contingent on level of damage” and 6 (33.3%) said they had “no tolerance” for bear damage.

Two of 7 (28.6%) growers who did not report any damage from bears did not kill or attempt to kill bears in the past and 57% (4 of 7) said they would prefer the “same number” or “more” bears in the region. However, among growers who reported crop losses to bears, 57.1% (8 of 14) said they had attempted to kill the bear and 79% (11 of 14) indicated that they would prefer “less” or “no bears” in the region.