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EFFECTS OF INFANTICIDE RISK AND TIMBER HARVEST ON AMERICAN
BLACK BEAR SPACE USE

By

D. Cody Norton

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EFFECTS OF INFANTICIDE RISK AND TIMBER HARVEST ON AMERICAN
BLACK BEAR SPACE USE

This thesis by D. Cody Norton is recommended for approval by the student's Thesis
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ABSTRACT

EFFECTS OF INFANTICIDE RISK AND TIMBER HARVEST ON AMERICAN
BLACK BEAR SPACE USE

By

D. Cody Norton

Space use is an important aspect of bear ecology that maybe influenced by infanticide risk and timber harvest. I used generalized linear mixed models (GLMM) to determine if female American black bear (*Ursus americanus*) space use was consistent with avoidance behavior to reduce infanticide risk in the Upper Peninsula of Michigan during the 2009–2011 and 2013–2014 breeding seasons. Females with cubs occupied core areas and home ranges of similar size and relative probability of male use to females without cubs. Additionally, females with cubs did not reduce movements during times of day when male movements were greatest. Female black bears may exhibit variation in avoidance behavior based on the occurrence of infanticide. I used GLMM to estimate black bear use of stands harvested for timber production in the Escanaba River State Forest in Michigan during May–October 2009–2011. In general, bears used stands $\leq$ 100 ha more than larger stands, with some gender and seasonal differences. Bears used even-aged stands more than uneven-aged stands and stands $\geq$ 6 years old more than younger stands. However, bear use did not differ between deciduous stands and coniferous stands, or among land cover types except that grass/pasture and open water were avoided. Bear use was greater in areas farther from roads. Managing the amount of black bear resources appears possible by considering the number, size, type, and rotation schedule of timber harvests in deciduous and coniferous forests. However, increased human access resulting from road creation during timber harvest activities may reduce associated benefits.

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D. CODY NORTON

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DEDICATION

This thesis is dedicated to my wife, Chelsea, and our daughters, Breanna and Claire.

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CHAPTER ONE: FEMALE AMERICAN BLACK BEARS DO NOT ALTER SPACE USE OR MOVEMENTS TO REDUCE INFANTICIDE RISK

Introduction

Infanticide occurs in a variety of animal species, and infanticide risk has large implications for the evolution of behavior in populations where infanticide is a significant mortality source [1,2]. Sexually-selected infanticide is the killing of dependent offspring by adult conspecifics to increase reproductive opportunities with the opposite sex [2,3]. The sex hypothesis of sexual segregation predicts that risk of infanticide can influence behavior and resource selection in animals, which can produce a despotic distribution as dependent offspring and their respective parents are displaced by potentially infanticidal adult conspecifics [2]. Strategies to reduce infanticide include dispersal, multi-male mating, female selection of a dominant male, male-female associations, intersexual aggression or territoriality, and sexual segregation [1–3]. Sexual segregation occurs when males and females of a species partition resources, which reduces competition and the likelihood of conflict [2,4], including risk of infanticide. Infanticide-avoidance behavior was first studied in social species. For example, female African lions (*Panthera leo*) and dependent young sometimes abandon their prides when a new male takes over to avoid risk of infanticide until the young are weaned [5]. Mountain gorilla (*Gorilla gorilla beringei*) groups may shift territories to avoid infanticide by encroaching males [6]. However, more recently, infanticide risk-avoidance behavior has been observed in solitary species, such as female cougars (*Puma concolor*) with dependent young, which may reduce risk of infanticide by occupying home ranges at lower elevations than males and females without dependent young [7].

Bears (*Ursus* spp.) are solitary species that sometimes commit infanticide [8–11] and exhibit behaviors to reduce this risk. For instance, female brown bears *(U. arctos)* select home ranges and habitat types with low male occupancy to reduce risk of sexually-selected infanticide [12]. Risk of sexually-selected infanticide also influenced seasonal range size of female brown bears in Scandinavia, with estrous females occupying larger home ranges during the breeding season than females with cubs [13]. In Sweden, female brown bears with cubs moved shorter distances from den emergence through the breeding season than females without cubs and exhibited differential habitat selection during diurnal periods than males and females without cubs [12,14]. In Alaska, female brown bears also denned earlier, left dens later, and denned at higher elevations than males [15]. Those behavioral changes likely reflected male avoidance strategies in order to reduce the risk of sexually-selected infanticide [15]. Female promiscuity, or multi-male mating, occurs in bear species, and may be employed by females as a counter-strategy to sexually-selected infanticide [17–19]. Female brown bears may mate with up to 8 males in a season [17] and multiple paternity occurs at levels of 14.5–28.0% in litters of 2–3 cubs [18]. Information about the effects of sexually-selected infanticide on black bear behavior and space use is limited despite the fact that in some cases, 45–50% of black bear cub mortality is from infanticide [8,16].

We evaluated whether space use and movements of female American black bears with dependent young were consistent with infanticide-risk-avoidance behavior as expected under the sex hypothesis of sexual segregation. We predicted that during the breeding season: (1) females with cubs would occupy areas with lesser relative probability of male use than core areas and home ranges of females without cubs, (2)

females with cubs would occupy smaller core areas and home ranges than females without cubs, and (3) movements of females with cubs would be inversely related to male movements during a given diel period.

Methods

Study areas

We conducted this study in 2 areas within the Upper Peninsula, Michigan, USA. The study area during 2009–2011 (hereafter Escanaba Study Area) included about 850 km^2 of Delta and Menominee counties (45.6°N, 87.4°E, Fig 1.1). Land ownership was 72% private and 28% public including the Escanaba River State Forest. Land covers were 52% lowland conifer forests (e.g., black spruce [*Picea mariana*], green ash [*Fraxinus pennsylvanica*], northern white cedar [*Thuja occidentalis*], speckled alder [*Alnus incana*]), 14% deciduous forests (e.g., sugar maple [*Acer saccharum*], quaking aspen [*Populus tremuloides*]), and 14% agriculture (e.g., row crops and pastures). The remaining 20% included upland conifer forests, mixed forests, developed areas, herbaceous wetlands, shrub, and open water [20]. Elevations ranged from 177 to 296 m. From May to September, the average monthly high occurred in July (24.3°C) and the average monthly low occurred in May (3.3°C [21]). Average monthly rainfall was 22.3 cm during May–September 2009–2011. Black bear densities were 14/100km^2 in 2009, 15/100km^2 in 2010, and 19/100km^2 in 2011 (unpublished data).

The study area during 2013–2014 (hereafter Crystal Falls Study Area) included about 1,830 km^2 of Baraga, Dickinson, Iron, and Marquette counties (46.3°N, 88.2°W,

Fig 1.1). Land ownership was 80% private and 20% public, including the Copper

Country and Escanaba River State Forests. Land covers were 36% deciduous forests

(e.g., sugar maple, quaking aspen), 31% lowland conifer forests (e.g., black spruce, green

ash, northern white cedar, speckled alder), and 12% mixed forests (e.g., sugar maple,

eastern hemlock [*Tsuga canadensis*], balsam fir [*Abies balsamea*]). The remaining 21%

included shrub, upland conifer forests, open water, developed areas, herbaceous

wetlands, and cultivated crops [20]. Elevations ranged from 396 to 579 m. Average

monthly high and low temperatures during May–September 2013–2014 were 18.6ºC

during July and 9.2ºC during May, respectively [22]. Average monthly rainfall was 9.4

cm during May–September 2013–2014. Black bear densities were 25/100km^2 in 2013

and 23/100km^2 in 2014 (unpublished data).

Animal capture and telemetry

We captured black bears using barrel traps [23] and modified Aldrich foot snares [24]

during May–July 2009–2011 and 2013–2014, which included the bear breeding season in

our study areas (1 June–15 July [25]). We immobilized captured bears estimated as ≥2

years old with 4–7 mg/kg Telazol [26]. For each bear, we determined sex and attached a

global positioning system (GPS) collar (Model GPS7000MU, Lotek Wireless Inc.,

Newmarket, Ontario, Canada) that collected and stored locations at 15-minute intervals.

We uploaded location data from GPS collars 1–2 times per week from a fixed-wing

aircraft. The mean GPS collar fix success rate during the breeding season was 94%. We

located bears that retained collars in winter and immobilized them in their dens to replace

collars and document number and age (cub or yearling) of offspring. Black bear capture

and den checks took place on both private and state lands. Permission to conduct research

on private land was granted by the respective landowners. As this was a cooperative study between the Michigan Department of Natural Resources and Mississippi State University, with the university acting as an extension of the state agency, specific permission was not needed to conduct research on state lands. All capturing and handling procedures were approved by the Mississippi State University Institutional Animal Care and Use Committee (protocols 09-004, 12-012).

Estimating male black bear space use

We estimated the relative male probability use for both study areas to facilitate testing our prediction that females with cubs would occupy core areas and home ranges with lesser probability of male use than females without cubs. We estimated male black bear space use in relation to roads and land cover using bear locations obtained during the breeding season (1 June–15 July [25]) because infanticide events after the breeding season would not increase male opportunities to breed [8]. We included distance to nearest road as roads can influence bear space use and resource selection [27,28]. We included land cover because the composition and abundance of bear foods is strongly related to land cover, and variation in food availability is a primary source of seasonal changes in black bear space use [29,30]. We included the interaction between land cover and distance to nearest road because bears may respond differently to road proximity in different land cover types due to differences in traffic, use for hunting, or other factors (31,32).

We identified roads classified as seasonal secondary or more highly-developed using Michigan Geographic Framework Transportation data [33]. We identified land covers (e.g., water, developed/barren, cultivated crops, grass/pasture, deciduous forest,

coniferous forest, mixed forest, and woody wetlands) using 2006 National Land Cover

Database grid data with 30-m resolution [20]. We combined the original barren land,

developed/open, developed/low intensity, developed/medium intensity, and

developed/high intensity into a developed/barren category. We combined shrub/scrub,

grassland/herbaceous, and pasture/hay and reclassified as grassland/pasture; we

combined and reclassified woody wetlands and emergent herbaceous wetlands as

wetlands.

We delineated final study areas by creating a 95% and 99% isopleth around all bear

locations in the Escanaba and Crystal Falls study areas, respectively, using a fixed kernel

density estimator with bandwidth selection [34]. We used different percentage isopleths

for each study area to account for differences in the distribution of locations and to ensure

relatively contiguous areas. We then generated a grid with 0.4-ha cells which we overlaid

on the isopleths and used ArcGIS (Environmental Systems Research Institute, Redlands,

California, USA) to determine the number of locations of each male bear in each cell. To

account for unoccupied areas, we calculated the number of locations in each cell in a

respective study area for each bear during the years it was collared. We calculated the

distance from the center of each grid cell to the nearest road using Patch Analyst 4.0 for

ArcGIS and determined the dominant land cover for each grid cell using the zonal

majority routine in ArcGIS [35].

We used generalized linear mixed models (GLMM) with zero-inflated Poisson

distributions (log link) to estimate relative probabilistic male black bear use for each

study area. Using the number of black bear locations within a given cell as the response

variable, we selected the appropriate random effect structure (bear ID, year, or bear ID

and year) by identifying the global model with the best fit using Likelihood Ratio Tests. We created a set of candidate models using the glmmTMB package [36] in R 3.5.0 [37]. Candidate models included the best-supported random effect structure, land cover, distance from nearest road, land cover and distance from nearest road, or the interaction between land cover and roads as fixed effects, and number of male locations as the response variable. Zero-inflated models included the intercept, because structural zeros were the result of the analysis design. We used Akaike's Information Criterion adjusted for small sample size (AIC_C [39]) to determine the best-supported model. For each study area, we used the best-supported model to estimate parameters with 95% confidence intervals (CI) and to predict the relative probability of use by males for each cell in the grid (Fig 1.1).

Home range and movements

To evaluate relationships between female reproductive status and space use, we used fixed kernel density estimators with bandwidth selection [34] to estimate core areas (50% isopleths) and home ranges (95% isopleths) of females with and without cubs during the breeding season. We then calculated median relative probability of male use in each female core area and home range to evaluate relationships between female reproductive status and male use of female core areas and home ranges. We selected the appropriate random effect structure by including all combinations of random effects (bear ID, year, study area) in global models and identifying the model with the best fit using Likelihood Ratio Tests. We then used GLMM with Gaussian (log link) distribution to compare median relative probabilistic male space use in core areas and home ranges of females with and without cubs. We created a set of candidate models using the lme4 package [38]

in R 3.5.0 [37] with the best-supported random effect structure, reproductive status, isopleth type (core area or home range), or reproductive status and isopleth type as fixed effects, and relative male probability of use as the response variable.

We also used generalized linear mixed models (GLMM) with Gaussian (log link) distribution to examine the relationship between reproductive status and the size of core areas and home ranges of females with and without cubs. We selected the appropriate random effect structure by including all combinations of random effect (bear ID, year, study area) in global models and identifying the model with the best fit using Likelihood Ratio Tests. We created a set of candidate models with the best-supported random effect structure, reproductive status (with or without cubs), isopleth type (core area or home range), or reproductive status and isopleth type as fixed effects, and area of core area or home range as the response variable.

To estimate whether females with cubs travel less at times males travel more, we divided each day into morning (0400–0800 hours), day (0801–1929 hours), evening (1930–2330 hours), and night (2331–0359 hours [40]). We calculated distances between consecutive 15-minute locations, summed the distances for each diel period per day, and then calculated the average distance travelled during each diel period. We selected the appropriate random effects structure by including all combinations of random effects (bear ID, year, study area) in global models and identifying the model with the best fit using Likelihood Ratio Tests. We then created a set of candidate models to compare the distance travelled by diel period for each level of sex/reproductive class using GLMM with Gamma (log link) distribution, the best-supported random effect structure, all combinations of sex/reproductive class, diel period, the interaction between

sex/reproductive class and diel period, and number of locations as fixed effects, and distance travelled per diel period as the response variable. We used AIC_C to evaluate support among candidate models for all female home range and movement analyses. We considered models with $\Delta AIC_C \leq 2$ to have equivalent support to the best-supported model [39]. However, if a competing model had a $\Delta AIC_C \leq 2$ of the top model, and the parameters in one model were a subset of the parameters in a competing model, we selected the simpler model in order to avoid inclusion of uninformative parameters [41].

Results

We captured and placed GPS collars on 18 male and 8 female black bears in the Escanaba study area and 8 males and 8 females in the Crystal Falls study area. Overall, we used 29 male, 12 female with cubs, and 10 female without cubs bear-season combinations for analyses, which provided 151,642 locations. During breeding season, the mean number of locations per individual was 2,346 (SD = 1,372) for males, which equates to about 24 days and 3,252 (SD = 1,465) for females, which equates to about 34 days.

The best-supported models for estimating relative probability of male use in both study areas included land cover, distance from nearest road, and their interaction as fixed effects. The model with the lowest AIC_C for estimating median relative probability of male use in female core areas and home ranges included isopleth type (core area or home range) as a fixed effect. However, we found similar support for the null model ($\Delta AICc = 0.43$) and the model that contained isopleth type and reproductive status ($\Delta AICc = 2.00$).

Because parameters in the null model were a subset of the competing models, we considered the null model best-supported. Because reproductive status was not included in the best-supported model, we concluded that females with cubs occupied core areas and home ranges with similar relative probability of male use as females without cubs (Fig 1.2, Table 1.1).

The best-supported model for examining the relationship between reproductive status and the size of core areas and home ranges of females included isopleth type (core area or home range) as a fixed effect. We found similar support (ΔAICc = 1.96) for the model that included isopleth type and reproductive status but because parameters in the top model were a subset of parameters in the competing model, we only considered the model containing isopleth type as best-supported. Because reproductive status was not included in the best-supported model, we concluded that females with cubs occupied core areas (mean = 4.64 km^2, SE = 1.28) and home ranges (mean = 19.46 km^2, SE = 5.10) of similar size to females without cubs (core area mean = 4.11 km^2, SE = 0.59; home range mean = 16.07 km^2, SE = 2.26). The best-supported model for estimating distance travelled per diel period included diel period, number of locations, and sex/reproductive status as fixed effects. We found less support (ΔAICc ≥ 4.88) for models that included the interaction between sex/reproductive status and diel period (Table 1.2, Fig 1.3).

Discussion

Observed space use and movements of female black bears were not consistent with the sex hypothesis of sexual segregation. Contrary to our predictions, females with cubs did not avoid males spatially or temporally during the breeding season. Rather, irrespective

of reproductive status, females used areas with similar relative probability of male use, occupied core areas and home ranges of similar size, and traveled similar distances including at times of day when males traveled more. An alternative to the sex hypothesis of sexual segregation predicts that females with cubs will have decreased space use and movements during spring due to limited mobility of cubs [42–44]. However, our results do not support this alternative hypothesis because we did not detect differences in space use and movements between females with and without cubs (e.g., [45]).

The lack of avoidance behavior by female black bears as demonstrated by space use and movements suggests the risk of sexually-selected infanticide is not great enough to cause strong behavioral changes in these populations. Therefore, sexually-selected infanticide may not occur, or may occur at lesser levels in our black bear population than has been observed in other bear species. Other species predicted to exhibit sexually-selected infanticide also have not demonstrated these behaviors. For example, male degus (*Octodon degus*) did not exhibit infanticidal behavior, even though it should be beneficial due to their social structure and breeding system [46]. Although infanticide is a large mortality source in some black bear populations, infanticide also may vary across populations within species, such as in some North American bear populations in which infanticide appears to be explained by nutritional gain or reduced competition rather than increased breeding opportunities [8,16,47–49].

The black bear populations we studied are hunted and we assume experience relatively high male turnover, as annual apparent hunting mortality was 25% to 44%, with males composing 61% of the harvest (unpublished data). There are two competing hypotheses to predict the impacts of the harvest of males of a species that exhibits

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sexually-selected infanticide. The immigrant male hypothesis predicts the harvest of

males will increase offspring mortality as immigrant males move in and resident males

spatially reorganize to replace harvested resident males and kill offspring in the new area

to breed with females sooner [7,11,47,50]. Conversely, the mate-recognition hypothesis

predicts that the harvest of males can actually decrease offspring mortality in populations,

since infanticide risk is likely to decrease as the number of males in the population

decreases [51,52]. The mate-recognition hypothesis suggests that males can recognize

females they have bred with and take advantage of any opportunity to commit sexually-

selected infanticide, whether they are new immigrants in an area or already established

residents [51,52]. Our results do not support the immigrant male hypothesis, as females

did not reduce core area and home range sizes, avoid areas with high relative probability

male use, or travel less distance at times of day males travel more to decrease sexually-

selected infanticide risk in these hunted populations. However, it is possible that females

with cubs in our study only avoid males with whom they did not mate during the previous

breeding season, so the mate-recognition hypothesis may explain the lack of spatial and

temporal sexual segregation (e.g., African lions [53]).

Though the causes of variation in rates of infanticide among black bear

populations remain unknown, infanticide can be a major source of cub mortality in some

populations, representing up to 50% of 46–48% overall annual mortalities [8,16].

Although infanticide has been documented in the Upper Peninsula of Michigan [54], it

does not appear to be an important source of mortality here or in surrounding areas. Cub

mortality in Minnesota was 25% with no infanticide detected [55]. Cub mortality in the

northern Lower Peninsula of Michigan also was 25%, but cause-specific mortality was

not estimated [56]. Similarly, annual cub mortality in our study areas averaged 22%

(unpublished data), which is less than populations in Arizona (48%) and Florida (46%)

that have relatively high rates of infanticide [8,16].

For an infanticidal male to increase breeding opportunities, he would have to kill

a female's entire litter. Brown bear populations in Alaska with lesser rates of complete

litter loss (14–26% [53]) experienced low infanticide rates and greater levels of harvest,

while brown bear populations in Alaska and Sweden with greater rates of complete litter

loss (35–59%) had greater infanticide rates and lesser harvest levels [10,53]. Though

cause-specific mortality of cubs in our study was not investigated, we observed only one

case of complete litter loss in 11 litters in our study areas (unpublished data), which also

suggests sexually-selected infanticide was not an important mortality source.

A limitation of our study is that we classified females as being with or without

cubs during a given breeding season based on whether or not they had cubs in the

previous den check and/or yearlings in the following den check. It is possible that a

female could have lost her litter before a breeding season and been incorrectly classified

as a female with cubs. However, our low cub mortality rate and low incidence of

complete litter loss suggest this is uncommon and should have had minimal impacts on

our results.

Infanticide-avoidance behavior and the sex hypothesis of sexual segregation

originated from studies of social species [2,3,5,6]. However, sexually-selected infanticide

can be an important source of mortality in solitary species [4,7,8,16]. Studies that

document cause-specific mortality of offspring at varying rates of harvest and population

densities are needed to better understand the role of infanticide in black bears.

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Additionally, quantifying the effects of proximity and relatedness between male and female black bears during the breeding season on infanticide could support or refute the immigrant male or mate-recognition hypotheses. Further research is needed to determine the pervasiveness of behavior consistent with the sex hypothesis of sexual segregation in solitary mammal species, and for other taxa (e.g., black rock skinks [*Egernia saxatilis*] [57]).

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CHAPTER TWO: EFFECTS OF TIMBER HARVEST ON AMERICAN BLACK

BEAR SPACE USE

1. Introduction

The American black bear (*Ursus americanus*) is considered a forest obligate

species (Maehr, 1997) and a generalist omnivore, with most of its overall range-wide diet

composed of plant material including herbaceous material, soft mast, and hard mast

(Eagle and Pelton, 1983; Graber and White, 1983; Clapp, 1990). Variation in food

availability is the primary source of seasonal changes in black bear space use (Landers et

al., 1979; Hellgren et al., 1991).

Timber harvest can influence the composition and abundance of black bear foods

by creating forest openings that facilitate understory plant growth. However, the species

and abundance of plants varies by timber harvest type and site characteristics (Mitchell

and Powell, 2003). For example, uneven-aged timber harvest typically results in some

herbaceous and soft mast plant species and creates openings for the regeneration of hard

mast species. In contrast, even-aged timber harvest usually results in a greater abundance

of herbaceous and soft mast plant species than uneven-aged harvest due to the increased

amount of light available for shade-intolerant species (Perala and Verry, 2011). The

amount of bear food resulting from timber harvest is also dependent on spatial extent,

with larger areas resulting in more food. The numbers and types of plant species, and

therefore plant foods, resulting from timber harvest also depend on the tree species

present before harvest (Coffman et al., 1984). Diversity and productivity of soft mast-

producing species are generally less in coniferous stands than in deciduous stands

following harvest (Jonkel and Cowan, 1971; Clark et al., 1994). The number of years

since timber harvest occurred in an area also can affect the abundance of plant foods. Young upland hardwood stands (1–10 years after harvest) typically provide abundant soft mast (Greenberg et al., 2011), but productivity of berry species tends to decline as stands age (Clark et al., 1994).

Timber harvest can alter resource selection, and consequently space use, by black bears but the effects can vary and are not well documented (Oli et al., 2002). In Idaho, black bears selected even-aged stands during all seasons, with the greatest selection occurring during summer, less during spring, and least during fall (Young and Beechum, 1986). Black bears in Arkansas generally avoided coniferous stands, which were associated with less food (Clark et al., 1994). In New York, black bears selected even-aged stands during spring and summer when associated food levels were high and did not exhibit selection for uneven-aged stands during any season (Costello and Sage, 1994). Black bears in Quebec selected areas 6–20 years post-harvest more than younger or older stands due to greater associated fruit density and biomass (Brodeur et al., 2008). However, few studies have simultaneously assessed the effects of multiple aspects of timber harvest on black bear space use. Our objective was to evaluate how black bear space use of available stands harvested for timber production was influenced by harvest type, harvest size, harvest age, land cover, sex, and season.

2. Methods

2.1. Study Area

The study area included about 211 km^2 of Escanaba River State Forest lands within Delta and Menominee counties in the Upper Peninsula, Michigan, USA (45.6°N,

87.4°E, Figure 2.1). Land covers were 69% conifer forests (e.g., black spruce [*Picea mariana*], green ash [*Fraxinus pennsylvanica*], northern white cedar [*Thuja occidentalis*], speckled alder [*Alnus incana*]), 14% developed/barren lands (e.g., roads, buildings, recent clear-cuts), 8% wetlands (herbaceous and woody), and 6% mixed forest (e.g., red maple [*Acer rubrum*], balsam fir [*Abies balsamea*], quaking aspen [*Populus tremuloides*], and white pine [*Pinus strobus*]). The remaining 3% included cultivated crops, deciduous forest, grass/pasture, and open water (Fry et al., 2011). From May to September, the month with the highest average temperature was July (24.3ºC) and the lowest was May (3.3ºC; National Weather Service, 2011). Average monthly rainfall was 22.3 cm during May–September 2009–2011. Black bear densities were $14/100km^2$ in 2009, $15/100km^2$ in 2010, and $19/100km^2$ in 2011 (Belant, unpublished results).

2.2. Animal Capture and Telemetry

We captured black bears using barrel traps (Kohn, 1982) and modified Aldrich foot snares (Johnson and Pelton, 1980) during May–July 2009–2011. We immobilized captured bears estimated as ≥ 2 years old with 4–7 mg/kg Telazol (Kreeger et al., 2002). For each bear, we determined sex and attached a global positioning system (GPS) collar (Model GPS7000MU, Lotek Wireless Inc., Newmarket, Ontario, Canada) that collected and stored locations at 15-minute intervals. We uploaded location data from GPS collars 1–2 times per week from a fixed-wing aircraft. We located bears that retained collars in winter and immobilized them in their dens to replace collars. The Mississippi State University Institutional Animal Care and Use Committee approved all capturing and handling procedures (protocol 09-004).

2.3. Study Design and Resource Attributes

To estimate seasonal black bear space use, we first delineated a study area by creating a 95% isopleth around all bear locations using a fixed kernel density estimator with bandwidth selection (Gitzen et al., 2006), then clipped the data to the boundary of the Escanaba River State Forest. We chose the Escanaba River State Forest as the study area due to the number of areas harvested for timber production and detailed records kept by the Michigan Department of Natural Resources (DNR) on all state-owned lands. For computational efficiency, we generated a grid with 0.4-ha grid cells, which included all cells within or intersecting the perimeter of the Escanaba River State Forest. We considered the grid to be the available area for all individual black bears. Because space use by black bears varies seasonally (Landers et al., 1979; Hellgren et al., 1991), we calculated the number of locations of each bear in each cell by season. We defined seasons as spring (1 May–15 July), summer (16 July–31 August), and fall (1 September–15 October) based on the phenology of herbaceous, soft-mast producing, and hard-mast producing plant species (DeBruyn, 1999).

We used ArcGIS (Environmental Systems Research Institute, Redlands, California, USA) to extract resource attributes and bear location data. We characterized areas harvested for timber production using Michigan DNR Forest Inventory Data (https://gis-michigan.opendata.arcgis.com/) and grouped them using type of harvest, spatial extent, and years since harvest. We determined dominant timber harvest characteristics for each grid cell using the zonal majority routine in ArcGIS (Belant et al., 2010). Roads influence bear space use and resource selection through vehicle collisions, hunting pressure, vegetation phenology, dispersal facilitation, and finding mates (Carter et al., 2010; Stillfried et al., 2015). We calculated the distance from the center of each

grid cell to the nearest road classified as either a seasonal secondary road or a more highly developed road using Michigan Geographic Framework Transportation data (MIGDL, 2013) and the near analysis tool for ArcGIS. Because sex influences bear space use and resource selection (Collins et al., 2002; Mitchell and Powell, 2003), we included the sex of each bear in subsequent analyses.

Land cover (i.e., water, developed, cultivated crops, grass/pasture, deciduous forest, coniferous forest, mixed forest, and wetlands) was identified using 2006 National Land Cover Database grid data with 30 m resolution (Fry et al., 2011; Table 2.1). We combined the original barren land, developed/open, developed/low intensity, developed/medium intensity, and developed/high intensity and reclassified as developed. Shrub/scrub, grassland/herbaceous, and pasture/hay were combined and reclassified as grassland/pasture; woody wetlands and emergent herbaceous wetlands were reclassified as wetlands. We determined the dominant land cover for each grid cell using the zonal majority routine in ArcGIS (Belant et al., 2010).

2.4. Model Development and Selection

We used generalized linear mixed models (GLMM) with zero-inflated Poisson distributions (log link) to estimate seasonal black bear resource use. Using the number of black bear locations within a given cell as the response variable, we selected the appropriate random effect structure (bear ID, year, or bear ID and year) by identifying the global model with the best fit using Likelihood Ratio Tests. We created our model set using the glmmTMB package (Brooks et al., 2017) in R 3.5.0 (R Development Core Team, 2018) by focusing on our 5 predictions: (1) bears use larger stands, especially during fall, (2) females use smaller stands than males, (3) bears use 6-20-year-old stands

more than stands of other ages overall, and these stands are used most during spring and summer, (4) bears use even-aged stands more than uneven-aged stands, and (5) bears use deciduous stands more than coniferous stands. We included distance to nearest road to control for its effect. We constructed 2 models, which consisted of the global model and the null model. Zero-inflated models included the intercept, because structural zeros were the result of the analysis design. Model term reference categories were Even-aged (harvest type), 1–5 years (harvest age), 0–40 ha (harvest size), Male (sex), Spring (season), and Open water (land cover). We used Akaike's Information Criterion adjusted for small samples (AIC_C) to evaluate support among candidate models. We considered models with $\Delta AIC_C \leq 2$ to have equivalent support to the best-supported model (Burnham and Anderson, 2002).

3. Results

During 2009–2011, we captured 19 male and 10 female black bears for analyses. As some bears were collared for multiple years, we obtained data for 38 bear-year combinations. Overall, we obtained 122,568 locations, including 32,337 male and 21,917 female locations during spring, 22,949 male and 26,110 female locations during summer, and 8,380 male and 10,875 female locations during fall. The number of locations per individual averaged 1,702 (SD = 1,588) for males and 2,739 (SD = 2,118) for females in spring, 1,912 (SD = 1,684) for males and 2,611 (SD = 1,036) for females in summer, and 1,197 (SD = 883) for males and 1,208 (SD = 880) for females in fall. The percentages of grid cells with no bear locations were 81.0 and 89.0% for male and female bears,

respectively, during spring, 87.5 and 87.0%, respectively, in summer, and 96.4 and 96.6%, respectively, in fall.

The best-supported random model structure included bear ID and year. The best-supported model was the global model (Table 2.2). There was no support ($\Delta AIC_c > 6919$) for the null model. In general, bears used smaller stands more than larger stands, but did use larger stands more during summer and fall than during spring (Table 2.3). Females generally used medium-sized stands. Bears used even-aged stands more than uneven-aged stands and stands 6 years old and older more than younger stands. However, bear use was not different between deciduous stands and coniferous stands. Bears used developed/barren, wetlands, mixed forest, coniferous forest, deciduous forest, and cultivated crops land covers similarly, and more than grass/pasture and open water. Bear use was positively related to distance from nearest road.

4. Discussion

Black bear use of stands harvested for timber production in our study area was likely related to the abundance of plants bears used as food. However, bears may have altered space use of harvested stands in relation to roads due to perceived risk from humans (e.g. Carter et al., 2010; Stillfried et al., 2015). Although variation in food availability is the primary source of seasonal changes in black bear space use (Landers et al., 1979; Hellgren et al., 1991), the relationship between resource availability and space use of bears is complex and likely extends beyond the abundance of food.

Overall, bears used stands $\leq$ 100 ha more than larger stands in our study, although we observed seasonal differences. Foraging efficiency is important for large mammals

that undergo winter lethargy and rely on relatively small, nutrient-poor food sources (Welch, 1997). Large stands may supply a greater concentration of available bear foods than smaller, dispersed stands with the same food sources. However, female black bears in Michigan, Missouri, and Mississippi exhibited behavioral trade-offs by selecting areas with decreased mortality risk at the expense of food acquisition, depending on vegetation productivity and risk associated with male conspecifics and vehicle collisions (Duquette et al., 2017). Bears in our study may have used stands $\leq$ 100 ha more due to reduced distance to cover. Additionally, females in our study used 40–100 ha stands more than smaller or larger stands. Female use of 40–100 ha stands may represent a behavioral trade-off between foraging efficiency and distance to nearest cover (Herrero, 1972; Lindzey and Meslow, 1977), especially for females with cubs that have greater energy demands and are more susceptible to predation.

Black bears in our study used large stands (> 100 ha) more than smaller stands during summer and fall, likely to increase foraging efficiency prior to denning. Additionally, use of stands > 100 ha was greatest in fall, less in summer, and least during spring. The amount of fat stored by bears during late summer and fall, prior to denning, can influence survival and reproduction (Costello et al. 2003). Thirty-nine percent of female and 44% of male black bears in Minnesota travelled long distances during late summer and fall to forage in large, mast-producing stands (Noyce and Garshelis, 2011).

Overall, bears used stands $\geq$ 6 years old more than younger stands in our study. Black bears in Quebec selected stands that were 6–20 years post-harvest more than younger stands due to greater associated fruit density and biomass (Brodeur et al., 2008). In New York, bears used deciduous stands ≥ 9 years old because they provide more

herbaceous vegetation and soft mast than younger stands (Costello and Sage, 1994). However, bears in our study used stands < 6 years old more than older stands in summer and stands < 6 or > 20 years old more during fall. Use of stands < 6 years old may result from peak mast-production of certain plant species in young stands. For example, pokeweed (*Phytolacca americana*) abundance can peak by around 2 to 3 years post-harvest and be virtually absent from stands at 5 years post-harvest (Perry et al., 1999; Greenberg et al., 2007). Use of stands > 20 years old during fall is likely the result of abundant hard-mast production in mature stands. Common hard mast-producing species in our study area were red oak (*Quercus rubra*), American beech (*Fagus grandifolia*), and hazelnut (*Corylus* spp.). Additionally, black cherry (*Prunus serotina*) is an important fall soft mast food associated with older deciduous stands. Older stands may also have more escape trees, concealment, and thermal cover; especially those with a coniferous component (Fecske et al., 2002). There could be a point at which bear use declined in older stands in our study area, as data limitations resulted in our grouping of stands > 20 years old.

Bears used even-aged stands more than uneven-aged stands in our study. Even-aged harvests result in greater regeneration of bear foods like herbaceous vegetation and soft mast (Costello and Sage, 1994). Bears in Washington selected home ranges that included recent clear-cuts, which were associated with greater concentrations of soft mast-producing shrubs and greater mast-production per plant (Lindzey and Meslow, 1977). During the non-denning period, young even-aged stands can provide denser cover and mature even-aged stands can provide more escape trees and a more intact canopy for thermal cover, which helps with thermoregulation in hot weather (Fecske et al., 2002).

Bear use of land cover types was similar in our study, except grass/pasture and open water were avoided. Although deciduous forests generally provide more food, coniferous forests can provide a variety of other resources for bears, such as escape trees, concealment, and cover. Bears in Arkansas used deciduous forests, as they provided greater abundances of foods than coniferous forests (Clark et al., 1994). In contrast, bears in Maryland used coniferous forests for escape, concealment, and thermal cover throughout the non-denning period (Fecske et al., 2002). Bears in Massachusetts and Minnesota used mature conifer trees to escape danger due to the ease with which they can be climbed by both adults and cubs (Elowe, 1984; Rogers and Lindquist, 1992). Mixed forests were used in Maryland due to the bear foods associated with deciduous species, as well as the additional cover provided by coniferous species (Fecske et al., 2002). Developed/barren lands include residential areas and roads. As a result, bears may use developed/barren lands for travel corridors, anthropogenic food sources, and early-successional vegetation and soft-mast (Hellgren et al., 1991; Costello and Sage, 1994; Hristienko and McDonald, 2007).

As expected, bear use was positively related to distance from nearest road. Although roads can facilitate dispersal and finding mates, particularly in spring, they are also associated with vehicle collisions and increased hunting pressure (Carter et al., 2020; Stillfried et al., 2015). Black bears in Virginia used areas near roads in spring due to the regeneration of early-successional vegetation and soft-mast along roadside margins (Hellgren et al., 1991). Female black bears in Michigan and Mississippi selected areas nearer to main roads and avoided riparian areas, while females in Missouri did the opposite, suggesting trade-offs between food acquisition and risk associated with

conspecifics and vehicle collisions (Duquette et al., 2017). Bears in Missouri generally selected areas farther from roads but may have selected areas near roads in unsuitable cover types as travel corridors, during breeding season, and dispersal routes, or due to roads acting as barriers (Hiller et al., 2015). Bear crossing of roads in North Carolina decreased as the number of vehicles traveling the roads increased (Beringer et al., 1990). Female black bears with cubs in Michigan, Missouri, and Mississippi denned closer to roads and used areas closer to roads in spring than females without cubs and males, suggesting a trade-off between risk of infanticide and vehicle collision (Gantchoff et al., 2019). Bears in Michigan avoided non-paved roads during summer hunting dog training and fall hunting seasons to decrease the risk of hunting-related mortality (Stillfried et al., 2015).

5. Conclusions

Bear use of stands harvested for timber production was influenced by harvest size, harvest age, harvest type, and distance to nearest road. Land cover was generally not important for determining overall bear use of harvested stands. Therefore, it may be possible to increase the amount of food, cover, and other resources for black bears by adjusting the number of timber harvests in an area of a given size, rotation schedule, and harvest type in virtually all forested land cover types. To manage spring and early summer habitat for black bears, land managers could prescribe ≤ 100 ha stands, or portions of stands associated with herbaceous vegetation and soft mast production for clearcutting. All candidate stands in that area could be scheduled for harvest based on rotation length to ensure an approximately equal proportion of ≤ 20-year-old stands are

available each year, and proximity to young, densely stocked coniferous stands. Late summer and fall habitat could be managed by prescribing > 100 ha stands, or multiple adjoining stands of hard mast-producing species to be selectively harvested. These stands could also be scheduled based on rotation length to ensure an approximately equal proportion of > 20-year-old stands are available each year, and mature coniferous trees and dense conifer inclusions could be retained.

However, increased road creation due to changes in timber harvest activity may reduce associated benefits to black bears. Hunting pressure, vehicle collisions, and other associated risk factors can make a habitat less suitable for bears (Carter et al., 2010; Stillfried et al., 2015). To maintain road densities at favorable levels in bear habitat, managers could require future logging operations to use pre-existing roads, require any new roads to be gated following completion of timber harvests, or defer harvests. We emphasize that attributes of timber harvesting, including roads, are not independent and should be considered collectively in relation to overall suitability for black bears.

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Table 1.1. Size and Male Use of Female Core Areas and Home Ranges.

| Study area | Reproductive status | Size | | | | Relative probability of male use | | | |
| | | Core area | | Home range | | Core area | | Home range | |
		Mean	SD	Mean	SD	Mean	SD	Mean	SD
Escanaba	Females with cubs	6.36	6.02	26.07	23.67	0.44	0.02	0.43	0.03
	Females without cubs	5.55	1.78	22.03	5.13	0.45	0.04	0.44	0.03
Crystal Falls	Females with cubs	2.92	0.67	12.85	4.68	0.54	0.06	0.52	0.02
	Females without cubs	2.97	0.64	11.32	2.99	0.52	0.02	0.52	0.02

Size (km^2) of female American black bear core areas and home ranges with and without cubs and relative probability of male use, Upper Peninsula of Michigan, 2009–2011 and 2013–2014.

Table 1.2. Distance Travelled per Diel Period.

Study area	Sex/reproductive status	Morning		Day		Evening		Night	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD
Escanaba	Males	1.71	0.89	4.55	1.85	2.63	1.16	1.51	1.10
	Females with cubs	0.86	0.68	2.19	1.20	1.44	1.12	0.90	0.79
	Females without cubs	0.93	0.61	3.55	0.44	2.29	0.91	0.77	0.72
Crystal Falls	Males	3.13	0.52	5.53	1.25	2.70	0.90	0.95	0.61
	Females with cubs	0.72	0.24	2.87	1.21	0.98	0.67	0.20	0.05
	Females without cubs	1.27	0.58	3.46	0.69	0.98	0.28	0.23	0.03

Distance (km) travelled per diel period (morning [0400–0800 hours], day [0801–1929 hours], evening [1930–2330 hours] and night [2331–0359 hours]) by male and female American black bears with and without cubs, Upper Peninsula of Michigan, 2009–2011 and 2013–2014.

Table 2.1
Land covers used to assess American black bear space use, Upper Peninsula of Michigan, 2009–2011. Land covers were reclassified from the 2006 National Land Cover Database.

Land cover	Definition
Water	Areas of open water, generally with <25% cover or vegetation or soil
Developed/barren	Areas with anthropogenic materials or structures, or <15% vegetative cover
Deciduous forest	Forest with >75% deciduous trees that are >5 m tall and >20 % vegetation cover
Coniferous forest	Forest with >75% coniferous trees that are >5 m tall and >20% vegetation cover
Mixed forest	Forest with a mix of deciduous and coniferous trees that individually comprise <75% tree cover
Grass/pasture	Vegetation >80% graminoid or herbaceous, or trees or shrubs <5 m tall, or grasses or legumes for livestock grazing or production of seed or hay crop
Cultivated crops	Area with >20% used for row crop production, including orchards and land actively tilled
Wetlands	Areas periodically saturated with water and >20% forest or shrub cover

Table 2.2

Candidate models used to assess American black bear space use, Upper Peninsula of Michigan, 2009–2011.

Prediction	Model	ΔAIC_C	w	log likelihood	K
Global	roads + land cover + season + sex + harvest type + harvest age + harvest size + harvest age * season + harvest size * season + harvest size * sex	0.0	1.0	-290706.3	28
Null	Null	6919.4	0.0	-294192.0	2

Table 2.3
Habitat selection parameter estimates for American black bears during spring
(1 June–15 July), summer (16 July–31 August), and fall (1 September–15 October)
in the Upper Peninsula of Michigan, 2009–2011. Model term reference categories
are Even-aged (harvest type), 1–5 years (harvest age), 0–40 ha (harvest size), Male
(sex), Spring (season), and Open water (land cover).

Model term	Parameter estimate	Standard error	95% Confidence limit	
			Lower	Upper
Intercept	-2.209	0.613	-3.411	-1.007
Roads	0.018	0.004	0.010	0.026
Uneven-aged	-0.446	0.024	-0.493	-0.399
Developed/barren	1.716	0.555	0.629	2.804
Wetlands	1.736	0.555	0.648	2.824
Mixed forest	1.744	0.555	0.657	2.832
Coniferous forest	1.898	0.555	0.811	2.985
Deciduous forest	1.550	0.557	0.458	2.643
Grass/pasture	-1.468	0.928	-3.288	0.351
Cultivated crops	1.109	0.556	0.019	2.199
6-20 years	0.341	0.041	0.261	0.420
>20 years	0.323	0.038	0.249	0.398
40-100 ha	-0.010	0.014	-0.037	0.018
>100 ha	-0.158	0.025	-0.207	-0.110
Summer	0.074	0.054	-0.031	0.179
Fall	-0.344	0.112	-0.564	-0.123
Female	1.134	0.431	0.289	1.979
6-20 years * Summer	-0.398	0.058	-0.512	-0.285
>20 years * Summer	-0.275	0.054	-0.381	-0.168
6-20 years * Fall	-0.250	0.121	-0.487	-0.013

>20 years * Fall	0.217	0.113	-0.005	0.439
40-100 ha * Summer	0.015	0.017	-0.020	0.049
>100 ha * Summer	0.468	0.029	0.411	0.525
40-100 ha * Fall	-0.044	0.033	-0.109	0.020
>100 ha * Fall	1.168	0.033	1.103	1.233
40-100 ha * Female	0.147	0.017	0.114	0.180
>100 ha * Female	0.021	0.023	-0.024	0.066
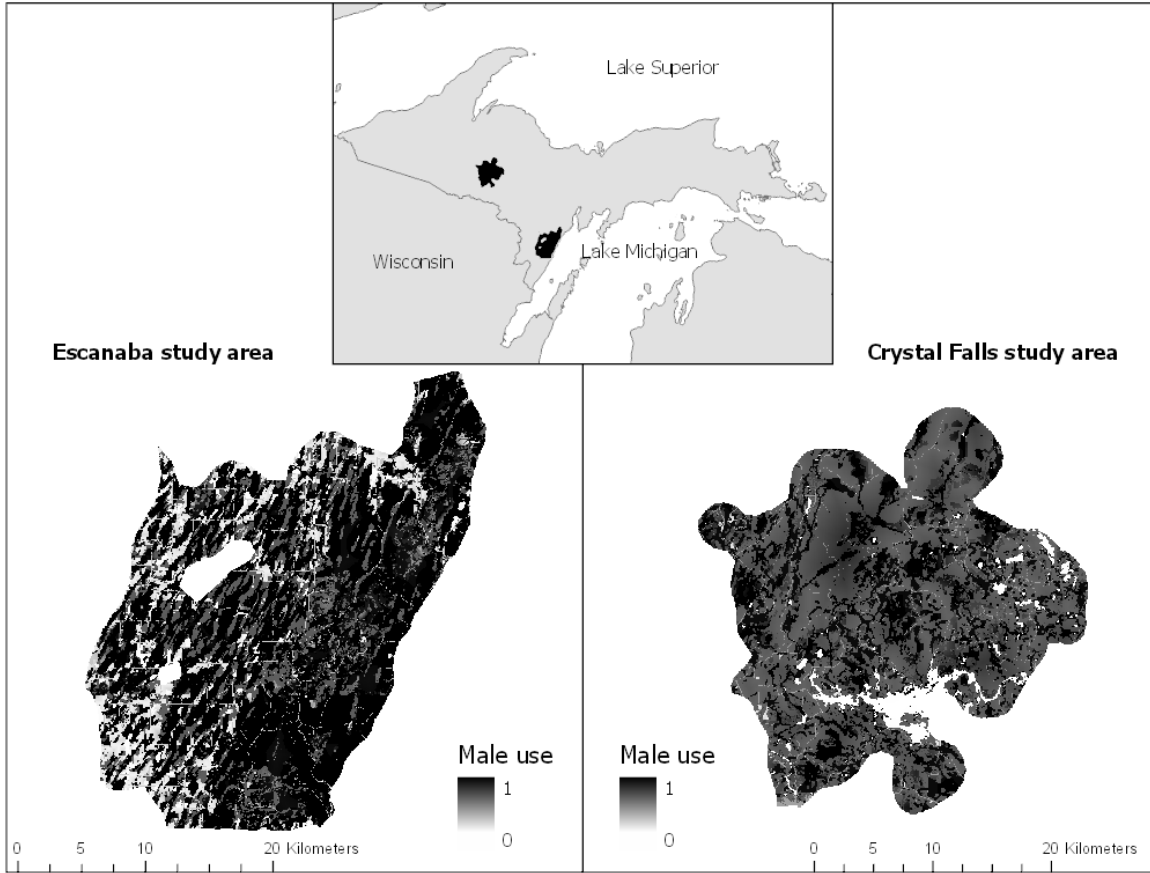
Figure 1.1. Male Use of Available Area. Relative probability of male American black bear space use in Escanaba (2009–2011, 45.6ºN, 87.4ºW) and Crystal Falls (2013–2014, 46.3ºN, 88.2ºW) study areas during the breeding season, Upper Peninsula of Michigan.
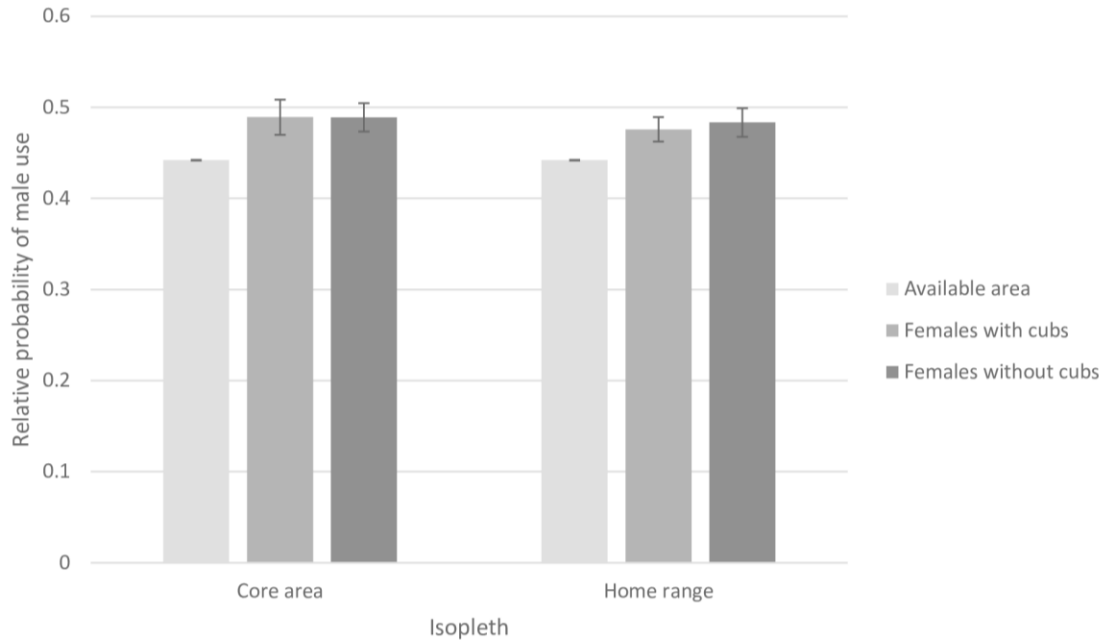
Figure 1.2. Male Use in Female Core Areas and Home Ranges. Relative probability of male American black bear use in core areas (50% kernel) and home ranges (95% kernel) of females with and without cubs, Upper Peninsula of Michigan, 2009–2011 and 2013–2014. Error bars represent 1 standard error.
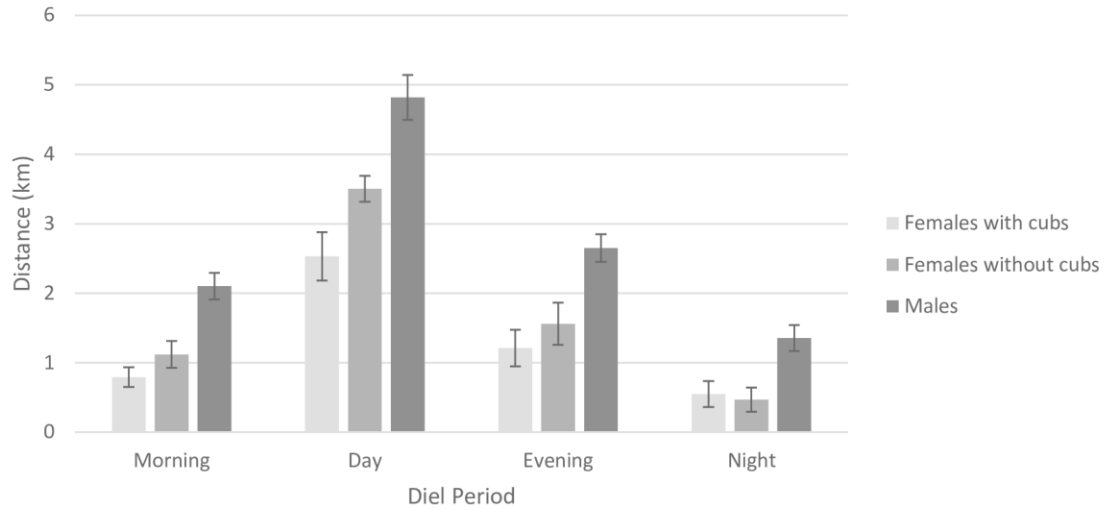
Figure 1.3. Distance Travelled During Diel Periods. Distance travelled during diel periods (morning [0400–0800 hours], day [0801–1929 hours], evening [1930–2330 hours] and night [2331–0359 hours]) by male and female American black bears with and without cubs, Upper Peninsula of Michigan, 2009–2011 and 2013–2014. Error bars represent 1 standard error.
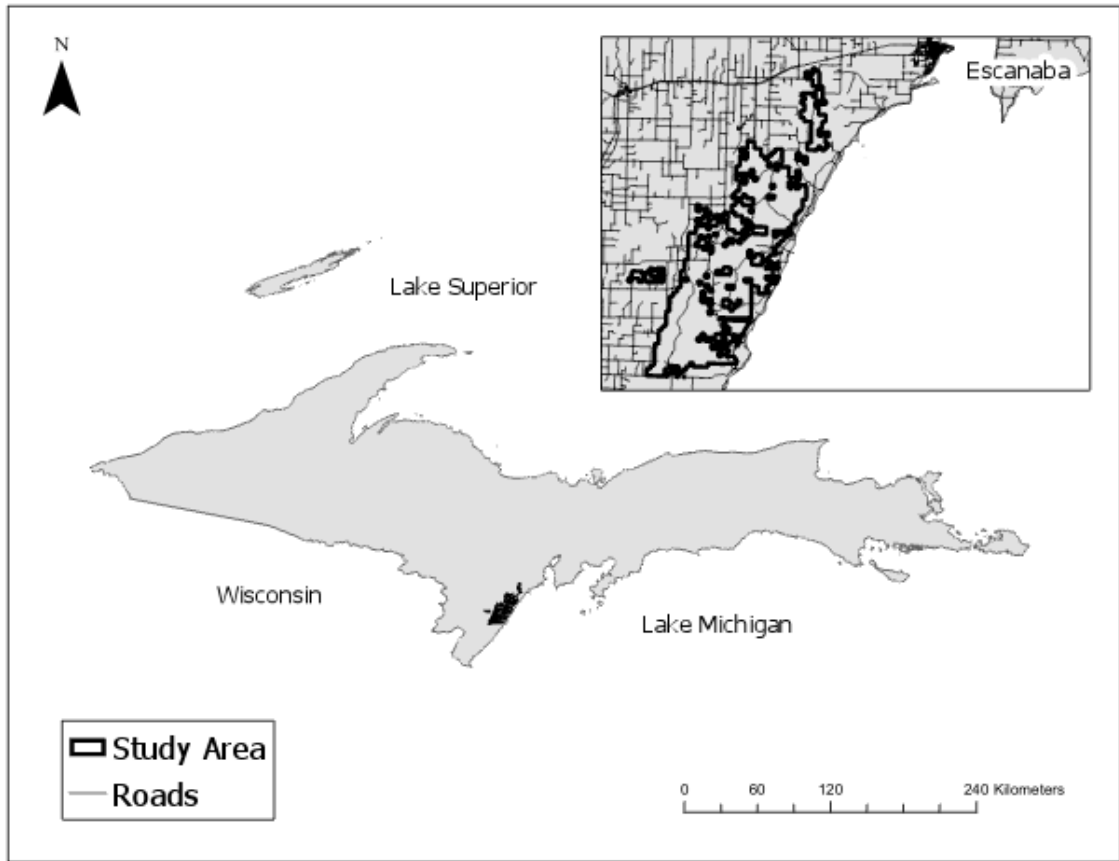
Fig. 2.1. Location of study area (45.6$^{\mathrm{o}}$N, 87.4$^{\mathrm{o}}$W) with inset showing roads, Upper Peninsula of Michigan, 2009–2011.