BEHAVIORAL RESPONSES OF AMERICAN BLACK BEARS TO REDUCED NATURAL FOODS: HOME RANGE SIZE AND SEASONAL MIGRATIONS

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SUMMARY OF FINDINGS

American black bears (*Ursus americanus*) in the Chippewa National Forest demonstrated appreciable fat reserves and stable reproduction despite a substantial decline in natural food availability over a 30-year period. Here we investigated potential strategies that bears may have employed to adapt to this reduction in food. We hypothesized that bears increased their home range sizes to encompass more food and/or increased the frequency, duration and distance of large seasonal migrations to seek out more abundant food resources. We estimated home range sizes using both Minimum Convex Polygon and Kernel Density Estimate approaches and developed a method to identify seasonal migrations. Male home range sizes in the 2010s were approximately twice the size of those in the 1980s; whereas, female home ranges tripled in size from the 1980s to the 2010s. We found little difference in migration patterns with only slight changes to duration. Our results supported our hypothesis that home range size increased in response to declining foods, which may explain why body condition and reproduction has not changed. However, these increased movements, in conjunction with bears potentially consuming more human-related foods in the fall, may alter harvest vulnerability, and should be considered when managing the bear hunt.

INTRODUCTION

As a large generalist omnivore, American black bears (*Ursus americanus*; henceforth black bear or bear) demonstrate exceptional plasticity in response to changes in food availability. One way in which black bears cope with changing resources is through their mobility. Summer and fall natural bear foods (e.g., fruits, nuts) in Minnesota often fluctuate substantially on a seasonal and yearly basis (Noyce and Coy 1990). Bears have adapted to these vagaries in food availability by moving around their home range and using their keen sense of smell to find local patches of food. In a largely agricultural region of northwestern Minnesota, for example, some black bears exhibited the largest home ranges (>2700 km^2) ever reported for the species (Ditmer et al. 2018) because patches of food are widely spaced. In northcentral Minnesota, Noyce and Garshelis (2011) reported that in any given year, ~40% of black bears make large seasonal migrations in fall, and ~10% migrate in spring, to seek out patches of more abundant foods, such as acorns (*Quercus spp.*), which may be lacking in their home ranges. While these movement patterns were in response to short-term changes in food, few studies have explored how black bear populations respond to diminishing natural food availability over multiple decades.

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We documented a ~70% decline in natural food abundance for bears over the course of 3 decades (1980s – 2010s) on a study area in northcentral Minnesota, likely attributable to landscape-level changes in forest management practices and climate change (Rettler 2018). During this time, the bear population also drastically declined in this area (Garshelis and Tri 2018). It is unclear whether this decline in the population was attributable solely to over-hunting, or if the reduction in food availability also played a role. Contrary to our expectations, we have found little or no changes in weights, reproduction, or cub survival across the decades (Garshelis et al. 2020). These preliminary results leave us with many questions, and new hypotheses about how this bear population has responded to changes in food availability.

One possible reason for the lack of physical or biological changes in the bears is that they managed to obtain sufficient food by travelling more, either expanding their home ranges or going on excursions outside their home ranges more frequently or for longer durations. Several studies have reported that home range size in black bears, especially adult females, is inversely related to natural food abundance and quality – abundant food and high quality habitat often results in reduced home range size (Lindzey and Meslow 1977, Lindzey et al. 1986, Powell et al. 1997, Koehler and Pierce 2003). Home ranges of adult females should be large enough to encompass sufficient resources across many seasons and years, and also accommodate their female offspring, which ultimately will inherit some of it. Males, by contrast, establish home ranges that include multiple breeding females, so the position and size of female home ranges, as well as female density, would, besides food conditions, also affect male home range size.

We used location data obtained from radiocollared bears to test the hypotheses that home ranges in the 2010s for females increased in size since the 1980s due to reduced food, and that male home ranges increased from the combination of reduced foods, larger female home ranges, and reduced female density. We further hypothesized that seasonal migrations of both sexes outside their home ranges were more frequent in the 2010s.

OBJECTIVES

1. Determine whether home range size has changed since the 1980s.
2. Determine whether seasonal migrations have changed since the 1980s.

STUDY AREA

Located in northcentral Minnesota, the Chippewa National Forest (CNF) study area falls in the transition zone between the boreal forests to the northeast and the temperate forests in the central part of the state. Our 620-km^2 study area was dominated (42% of area) by the eastern extent of the CNF; the remainder included part of the George Washington State Forest and other state-owned land (11%), county land (6%), private land (18%), commercial timber industry (8%) and open water (15%). The eastern two-thirds of the study area were upland forests dominated by various combinations of aspen (*Populus tremuloides, P. grandidentata*), maple (*Acer spp.*), red pine (*Pinus resinosa*), paper birch (*Betula papyfiera*), and balsam fir (*Abies balsamea*). The western third was largely lowlands dominated by speckled alder (*Alnus incana*), black spruce (*Picea marina),* tamarack (*Larix laricina*), black ash (*Fraxinus nigra*), northern white-cedar (*Thuja occidentalis*), quaking aspen and balsam poplar (*P. balsamifera*). Many lakes, forest roads, and recreational trails occur throughout the public land. This area was heavily hunted for bears due to the large extent of easily accessible public land. Larger oak stands and agricultural landscapes do not exist on the study area, but can be found to the south and west.

METHODS

Location data were collected during 2 sampling periods: 1981–1989 and 2015–2019 (henceforth, 1980s and 2010s respectively). We captured bears using either barrel traps or Aldrich foot snares. While bears were anesthetized with a mixture of ketamine–xylazine, we fit them with VHF radiocollars (Telonics Inc., Mesa, AZ; n=220 bear-years) during the 1980s, and Iridium GPS radiocollars (Telonics Inc., Mesa, AZ; n=67 bear-years) or store-on-board GPS pods (Telemetry Solutions, Concord, CA; n=3 bear-years) during the 2010s. We defined a bear-year as 1 year of data from an individual bear between post-den emergence and pre-den entrance (i.e., approx. mid-April to late-September). We collected location data on VHF radio-collared bears during weekly telemetry flights during the 1980s. With the GPS radiocollared bears, we programmed the collars to record data every 2-hours. We downloaded data from store-on-board GPS pods during winter den visits.

For the home range analysis, we subsampled the 2010s GPS data to match the frequency of the 1980s data. We selected unique bear-years from the 1980s that had a minimum of 15 locations (during approx. 3.5 months). We calculated the median time between locations within these datasets (4–10 days) to guide subsampling the 2010s data. We randomly subsampled the 2010s data at these intervals (n=100 iterations/bear-year), restricted to the hours sampled in the 1980s (0600–2100 hours), which yielded ~15 – 30 locations per bear-year.

In addition to subsampling the data, we also had to account for large seasonal migrations, which occur commonly in this population (Garshelis and Noyce 2011). We removed these from the calculation of home range area, and quantified them in a separate analysis. We identified migrations in a 3-step process (Figure 1). First, we assessed whether a step length between consecutive locations exceeded the median step length for that given bear-year. Second, we calculated the distance from this location to all previous locations: if it was >5 km for males or >2 km for females from any previous location, we considered it a possible migration and moved to step 3. Finally, if this location and the next 2 consecutive locations exceeded the median net squared displacement (NSD; Singh et al. 2016) for that given bear-year, we then categorized this progression of movements as a migration. The migration ended when the NSD of a bear location dropped below the median NSD, suggesting that it returned to its typical home range. After partitioning out migrations, we omitted bear-years with <15 relocations.

We recognize that with such few relocations per year, we may not be capturing the true area that a bear used; however, our goal was to determine whether the dispersion of locations had changed over time by using home range estimates, with approximately equal sampling, as an index of change (Signer et al. 2015). We used 2 different home range estimators: Minimum Convex Polygons (MCP; Mohr 1947) and ad-Hoc scaled Kernel Density Estimators (KDE; Kie 2013). The MCP approach generated the smallest convex polygon enclosing all locations; whereas, the ad-Hoc scaled KDE decreased the reference smoothing factor by increments of 0.01 until the smallest contiguous polygon was achieved. The purpose behind using 2 estimators was to test how sensitive our results were when analyzed in different ways.

To test for changes in home range size between the 2 sampling periods, we used linear mixed-effects models with a log-transformed response variable. We used the area of each estimated home range at the 95% and 50%-level as the response variable. For the 2010s rarified data, we averaged across the 100 subset iterations for a given bear-year to produce a home range estimate. Covariates included the sampling period (1980s or 2010s), demographic group (females with cubs, females without cubs, and males) and age (continuous variable). Furthermore, we added an interaction term between sampling period and demographic group to determine if home range size had changed differently among demographic groups. We included

a random intercept of bear ID to account for repeated measurements on the same bears over multiple years.

We created a binary variable for whether each bear-year contained a migration (1=yes; 0=no). In some instances with the rarified data, different subset iterations resulted in the same bear-year with and without migrations. We examined the proportion of subset iterations within each bear-year that identified the occurrence of a migration, and coded it as a migrating year if it was identified as such by >50% of the iterations. Additionally, we visually examined the full 2010s data to confirm that migrations occurred for bear-years that were questionable. We categorized migrations as occurring in either spring (i.e., April–June) or fall (July–October), and also measured the duration and maximum distance of the movement (measured from the first location of the bear-year after den emergence).

We used a generalized linear mixed-effects model (GLMM) with a binomial distribution and a linear mixed-effect model with a log-transformed response to test whether the probability of bears making a migration had changed, as well as patterns in duration and distance, since the 1980s. We used sampling period and demographic group as covariates and included an interaction term. We also controlled for the age of the bear in the model. A random intercept for bear ID was included to account for repeated measurements on the same bears over multiple years.

RESULTS

We calculated the home range size for 130 bear-years (n=52 male-years and 78 female-years) for 65 different individuals (n=33 M, 32 F) in the 1980s and 63 bear-years (37 male-years and 26 female-years) for 32 different individuals (n=20 M, 12 F) in the 2010s. While the KDE yielded larger home range estimates than the MCP, the magnitude of difference between the sampling periods was generally consistent. With both the KDE and MCP approach, average male home range size during the 2010s was approximately twice that in the 1980s, after accounting for age (Table 1, 2; Figure 2, 3; $P=0.015$, $P=0.011$, KDE and MCP, respectively). Female home range sizes in the 2010s also were generally larger than those in the 1980s (Table 1, 2; Figures 2, 3), after controlling for age. Home ranges of females with cubs in the 2010s were 2–3 times larger ($P=0.012$, $P=0.086$, KDE and MCP, respectively) and their core areas (50% KDE) were almost 4 times larger ($P=0.010$) than in the 1980s. Females without cubs in the 2010s had home ranges that were approximately twice the size of 1980s, using either KDE ($P=0.051$) or MCP ($P=0.053$). Core area size was not significantly different ($P=0.058$, $P=0.117$, KDE and MCP, respectively). Home ranges of bears increased with age. Within the first 10 years of a bear's life, 95% MCP home ranges doubled in size, on average; whereas, the core home range size increased by approximately 50% ($P=0.001$). KDE ranges increased less than MCP in the first 10 years (20% for 95% KDE, 30% for 50%KDE), but still significantly ($P=0.001$). There was no difference between the 2 sampling periods regarding home range expansion as they aged.

We detected 137 migrations (62% of bear-years) during the 1980s and 52 (74% of bear-years) during the 2010s. The propensity to migrate was not different from the 1980s to 2010s for males (65% vs. 75%, $P=0.095$), females with cubs (61% vs 86%, $P=0.248$), and females without cubs (62% vs. 71%, $P=0.447$). The probability of migrating increased by 10% every 5 years of a bear's life, until about 15 years old (then remained stable, $P=0.026$). The average duration of spring migrations was about 1 week shorter for males ($P=0.008$), females with cubs ($P=0.296$) and females without cubs ($P=0.047$) in the 2010s than the 1980s (Table 3). In fall, males ($P=0.255$), females with cubs ($P=0.219$), and females without cubs ($P=0.573$) were away from their home ranges for about 1 month in both the 1980s and 2010s (Table 4). The maximum spring migratory distance for each bear-year averaged 19 km for males, 5 km for females with cubs, and 6 km for females without cubs during the 1980s; in the 2010s, distances were similar

for males (mean = 17 km, *P*=0.713), females with cubs (mean=5 km, P=0.260), and females without cubs (Table 3; mean = 9 km, *P*=0.162). In fall, migrations were farther than in spring for all demographic groups, but not different between the 2 time periods (Table 4). Males in the 1980s traveled an average distance of 38 km compared to 41 km in the 2010s (*P*=0.863). The average fall migration distance for females with cubs was almost twice as large in the 2010s (27 km) than the 1980s (14 km) (although not significantly different, *P*=0.217); whereas, females without cubs traveled an average of 16 km in the 1980s and 14 km in the 2010s (*P*=0.783)

DISCUSSION

We found evidence to support our first hypothesis that home range size had increased since the 1980s. The home range size doubled for males and tripled for females. However, variability among individuals was high and our limited sample size of relocations may have hampered our statistical power, especially for 50% KDE and MCP. While some of our results were not statistically significant due to this variability, the consistent trend over time for both MCP and KDE estimators and both sexes suggest that home range size likely increased over the 3 decades in response to reduced food.

Bear density on the study area was significantly reduced from the 1980s to 2010s, but given the extensive overlap among ranges of bears, it seems unlikely that they expanded their home ranges just because there were fewer bears. Also, it is unlikely that competition for food is a major factor in bears, except possibly at very high densities, so a reduction in bear density did not provide more food per bear. Hence, in order to maintain body mass and reproduction, reduced foods prompted them to expand their home ranges. Male ranges also may have expanded to incorporate the larger and less densely-packed ranges of breeding females. It appeared that females with and without cubs had similar home range sizes, which suggests that mobility of cubs was not a limiting factor in home range size over the course of the active season.

Reduced food abundance did not cause bears to migrate more frequently, farther, or for longer despite the greater difficulty in locating far-flung bears by airplane in the 1980s versus GPS locations in the 2010s. We did observe a slight reduction in the duration of spring migrations for males and females with cubs in the 2010s and an apparent doubling in the fall migration distance for females with cubs in the 2010s. We believe these results may be related to the small sample size and high variability among individuals, particularly for the increase in fall migration distance for females. Two females made fall movements greater than 65 km with cubs; whereas, the remaining 5 female bear-years with cubs made movements more similar to the 1980s (i.e., 7-10 km). Garshelis and Noyce (2011) found that bears were less likely to migrate during years of poor natural foods to potentially avoid the risk of only finding poor foods elsewhere. Additionally, fall migrations may be influenced by human-related food sources: notably corn fields and hunters' baits. Preliminary results from our stable isotope analysis (a method for reconstructing annual assimilated diet) suggest that most bears in our study area had spent some time feeding on corn or corn-derived foods (such as high fructose corn syrup) in the fall. While there are no corn fields within the study area, we know that at least 30 study bears (either collared or ear-tagged) have used hunters' baits in some capacity (based on either direct reports by hunters or bears harvested at baits during 2015-2019).

Our results demonstrated the resilience of black bears to a substantial decline in natural foods, which they accomplished, in part, by altering their movements. However, other potential consequences of these movements should be noted. In Minnesota, harvest vulnerability varies by sex and age and is mediated by food availability, particularly key fall foods (Noyce and Garshelis 1997). While individuals maintained body conditions and reproduction similar to the 1980s despite the diminished foods, these bears are now traveling farther for food and

potentially supplementing their diet more with human-related foods, which may increase their exposure to bait piles and influence their harvest vulnerability. Understanding the variation among individuals and the repercussions it could have on current population models is vital for making informed management decisions.

ACKNOWLEDGMENTS

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Table 1. Average 95% Kernel Density Estimate and Minimum Convex Polygon home range estimates (km^2) with 95% CI for American black bears in the 1980s (1981-1989) and 2010s (2015-2019) in northcentral Minnesota. Estimates are from a linear mixed-effects model that accounts for age of the bear.

Demographic group	Minimum convex polygon		Kernel density estimate	
	1980s	2010s	1980s	2010s
Male	47 (34 – 64)*	89 (61 – 128)*	180 (126 – 256)*	359 (238 – 541)*
Female with cubs	9 (6 – 14)	19 (9 – 37)	24 (14 – 42)*	86 (37 – 199)*
Female without cubs	12 (9 – 16)	22 (13 – 35)	35 (25 – 49)	68 (39 – 119)

* Significant difference between time periods ($P < 0.05$).

Table 2. Average 50% Kernel Density Estimate and Minimum Convex Polygon home range estimates (km^2) with 95% CI for American black bears in the 1980s (1981-1989) and 2010s (2015-2019) in northcentral Minnesota. Estimates are from a linear mixed-effects model that accounts for age of the bear.

Demographic group	Minimum convex polygon		Kernel density estimate	
	1980s	2010s	1980s	2010s
Male	7 (5 – 10)*	17 (12 – 24)*	40 (28 – 55)*	79 (54 – 117)*
Female with cubs	2 (1 – 4)	4 (2 – 8)	6 (3 – 9)*	19 (9 – 42)*
Female without cubs	3 (2 – 3)	4 (3 – 7)	9 (6 – 12)	16 (9 – 27)

* Significant difference between time periods ($P < 0.05$).

Table 3. Spring (April – June) migration summary table for American black bears in the 1980s (1981-1989) and 2010s (2015-2019) in northcentral Minnesota. Numbers in parentheses indicate 1 SE.

Demographic group	1980s				2010s			
	Mean duration (days)	Max (days)	Mean Distance (km)	Max (km)	Mean duration (days)	Max (days)	Mean distance (km)	Max (km)
Males	41 (3)*	44	19 (3)	75	23 (1)*	40	17 (2)	66
Females with cubs	25 (5)*	32	5 (1)	6	18 (2)*	24	6 (1)	9
Females without cubs	28 (4)	58	6 (1)	13	23 (1)	34	9 (2)	27

* Significant difference between time periods ($P < 0.05$).

Table 4. Fall (July-September) migration summary table for American black bears in the 1980s (1981-1989) and 2010s (2015-2019) in northcentral Minnesota. Numbers in parentheses indicate 1 SE.

Demographic group	1980s				2010s			
	Mean Duration (Days)	Max (Days)	Mean Distance (km)	Max (km)	Mean Duration (Days)	Max (Days)	Mean Distance (km)	Max (km)
Males	30 (3)	62	38 (5)	209	33 (2)	68	41 (6)	139
Females with cubs	35 (5)	71	14 (2)	47	42 (4)	57	27 (11)	67
Females without cubs	35 (3)	79	16 (3)	101	33 (3)	63	14 (4)	80

* Significant difference between time periods ($P < 0.05$).
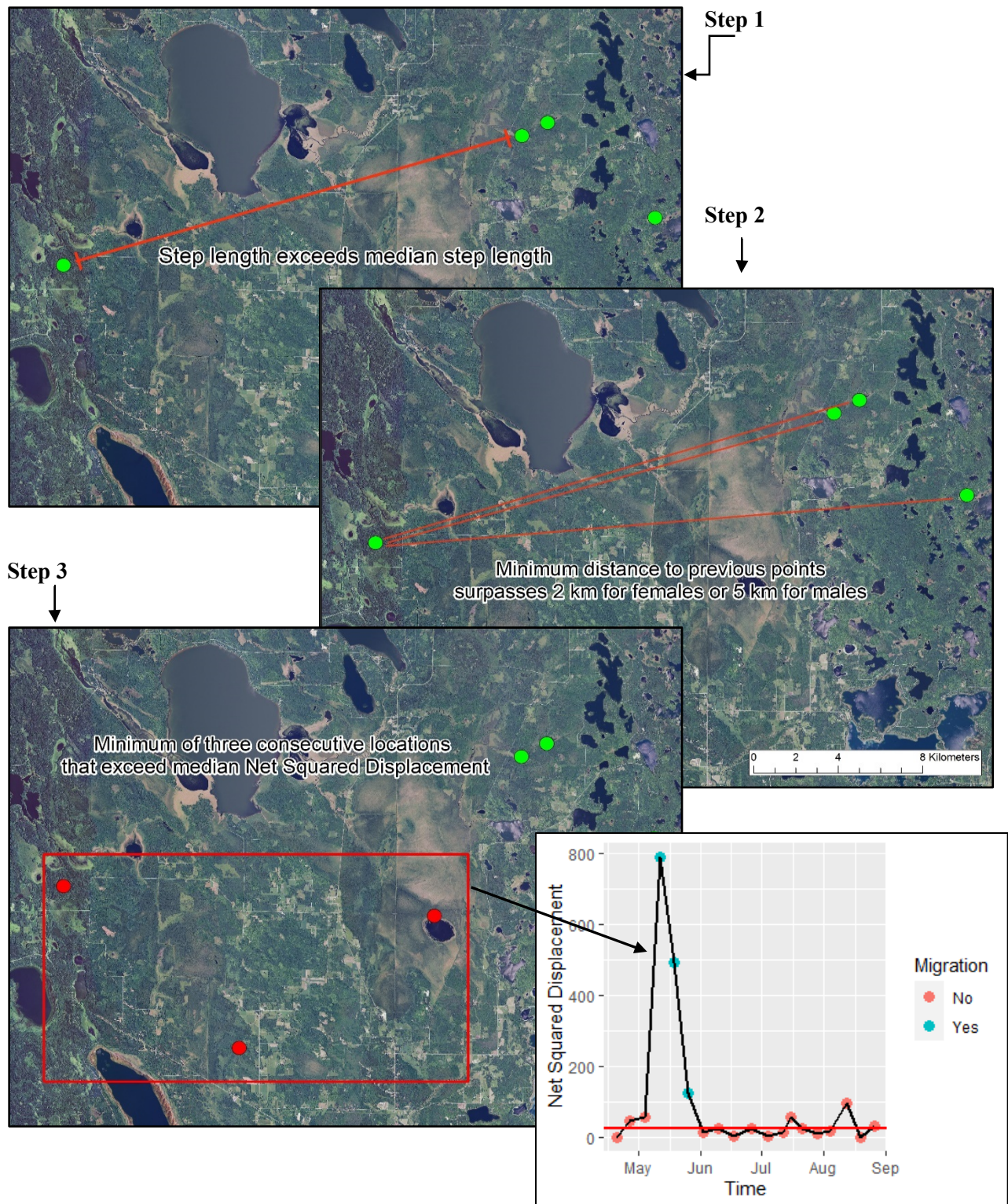
Figure 1. Flow chart depicting the 3-step process of identifying large seasonal migrations of American black bears. Migrations must contain a large abrupt movement, be far away from previous points, and must remain far away for a minimum of 3 consecutive locations.
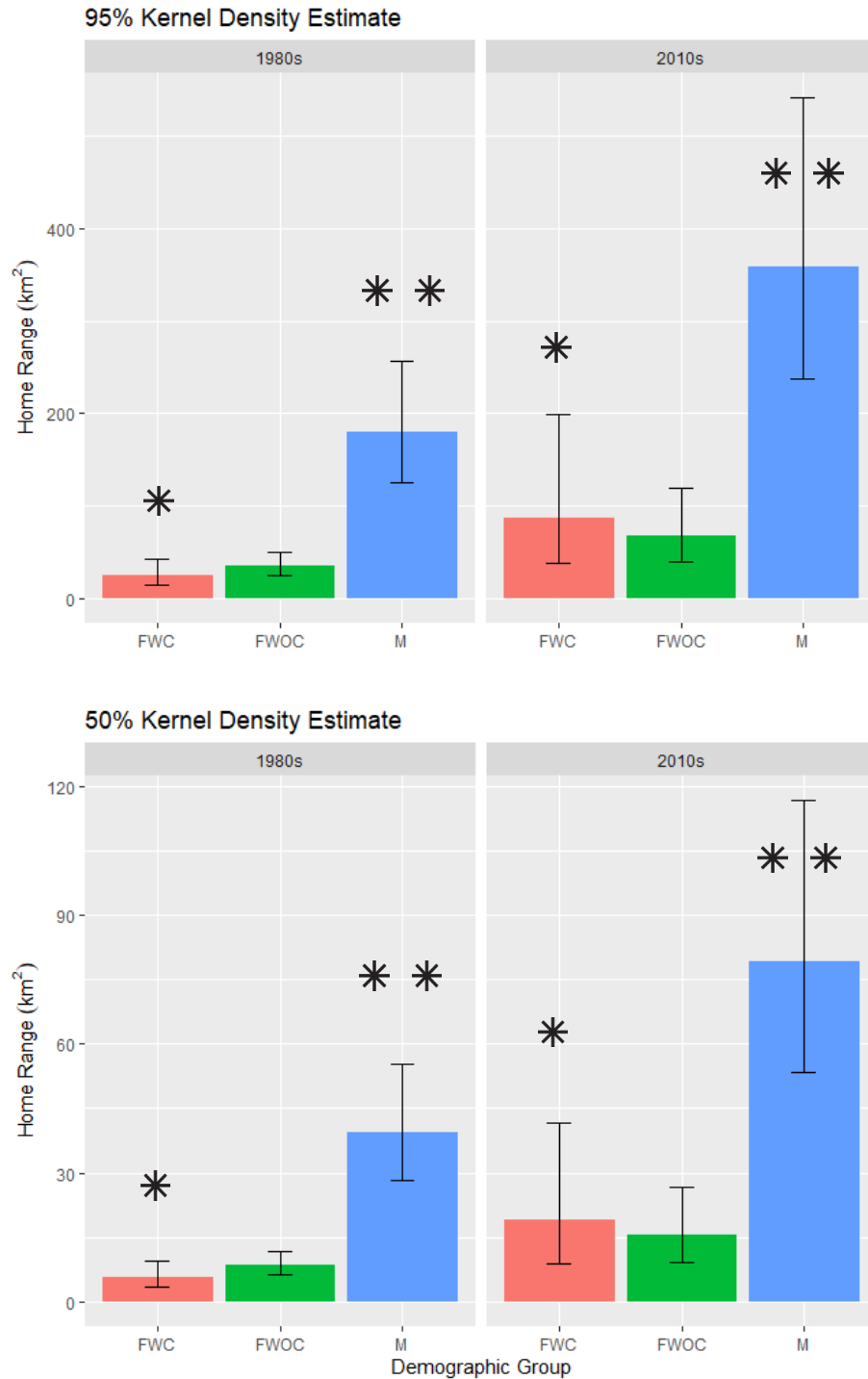
Figure 2. Bar graph of 95% and 50% ad-Hoc scaled Kernel Density Estimate home ranges for American black bear females with cubs (FWC), females without cubs (FWOC), and male (M) bears from the 1980s (1981 – 1989) and 2010s (2015 – 2019) in northcentral Minnesota. Error bars depict 95% confidence intervals. Matching asterisks indicate significant differences ($P < 0.05$).
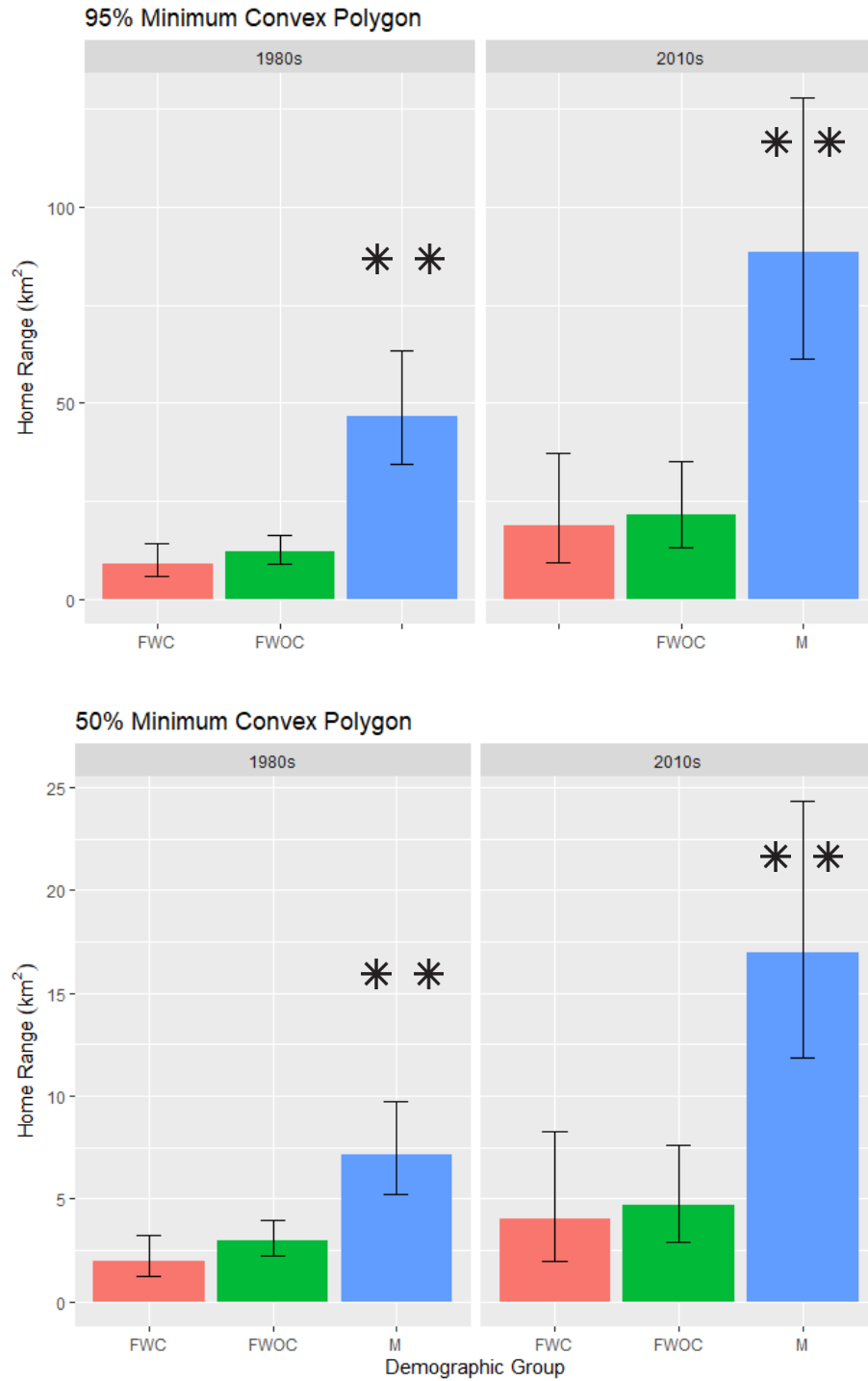
Figure 3. Bar graph of 95% and 50% Minimum Convex Polygon home ranges for American black bear females with cubs (FWC), females without cubs (FWOC), and male (M) bears from the 1980s (1981 – 1989) and 2010s (2015 – 2019) in northcentral Minnesota. Error bars depict 95% confidence intervals. Matching asterisks indicate significant differences ($P < 0.05$).