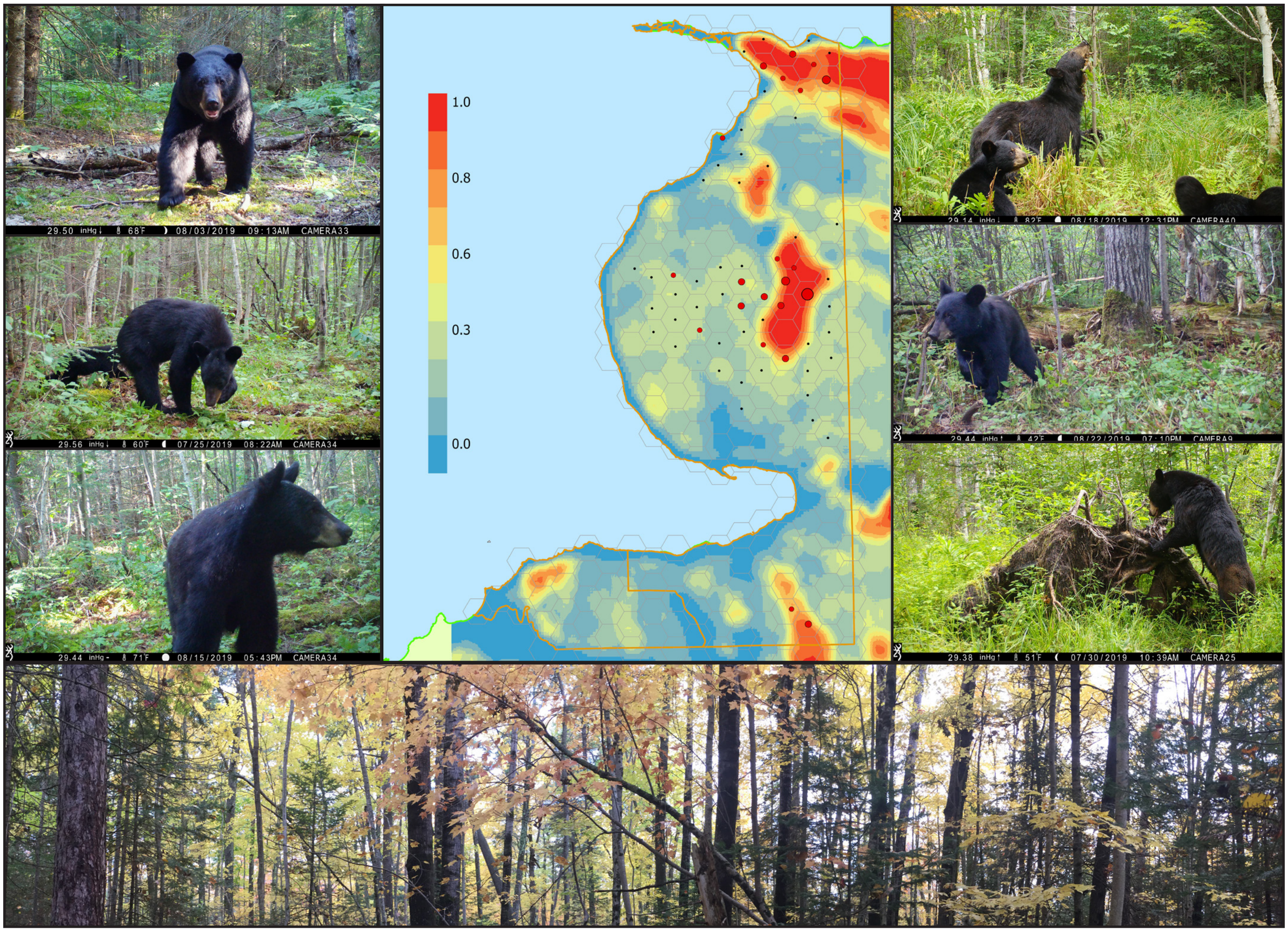
Makwa (American Black Bear) Distribution and Habitat Use within the 1855 Little Traverse Bay Bands Of Odawa Indians Reservation



Prepared by:
Clay M. Wilton
Michigan Natural Features Inventory
P.O. Box 13036
Lansing, MI 48901-3036

For:
Little Traverse Bay Bands of Odawa Indians
Natural Resources Department; C/O Bill Parsons
March 1, 2020

Report No. 2020-08

ODAWA NATURAL RESOURCES DEPARTMENT

MICHIGAN STATE UNIVERSITY | Extension

Michigan Natural Features Inventory

ACKNOWLEDGMENTS

We thank the Little Traverse Bay Bands of Odawa Indians (LTBB) for financial and logistical support during this survey. LTBB Odawa Natural Resources Department staff were instrumental in ensuring successful deployment and maintenance of camera traps, including Maxwell Field, Kevin Haynes, Archie Kiogima Jr., Spencer McCormack, and Bill Parsons. Thanks for making the hot, buggy days in the swamps enjoyable! We thank Burr Mitchell (Michigan DNR) for access assistance in Wilderness State Park and Jennifer Kleitch (Michigan DNR) for logistical support on State Forest lands. We are grateful to the landowners who were kind enough to allow us access to isolated sections of State Forest. Courtney Ross (MNFI - Huron Pines AmeriCorps) provided substantial assistance classifying thousands of camera trap images and Tyler Petroelje (SUNY ESF) provided insightful conversations and assistance with study design and occupancy modeling. We thank Josh Cohen, Brian Klatt, and Michael Monfils (MNFI) for continued scientific and logistical support throughout this project.

Numerous mammalian species were photographed during our camera trap survey, including American badger, American marten, North American porcupine, red fox, fisher, bobcat, American black bear, coyote, and white-tailed deer.

Suggested Citation:
Wilton, C.M. 2020. Makwa (American Black Bear) Distribution and Habitat Use within the 1855 Little Traverse Bay Bands Of Odawa Indians Reservation. Michigan Natural Features Inventory Report Number 2020-08, Lansing, MI. pp. 38

Cover Photo: American black bears (*Ursus americanus*) photographed on remote camera traps during this survey.

TABLE OF CONTENTS

Study area at Wilderness State Park illustrating various lowland (left) and upland (right) natural communities included within this study.

ABSTRACT

Estimates of species distribution, abundance, and habitat use are important guiding metrics for wildlife managers. However, obtaining estimates of abundance or density are often logistically prohibitive for many agencies tasked with managing wildlife populations. Advancements in both field survey technologies and statistical models are improving our ability to monitor rare and elusive animal populations without the need to estimate abundance or density. We used camera traps to estimate habitat use and predict the distribution of American black bears (*Ursus americanus*) in relation to land cover characteristics within the 1855 Little Traverse Bay Bands of Odawa Indians (LTBB) Reservation (877-km^2). We established a survey grid of 63, 4-km^2 hexagonal cells across the 1855 LTBB Reservation and selected cells providing access to public land (i.e., State Forest, State Parks). We placed 1 camera at the center of each grid cell or nearest public land location within a forested cover type. We programmed cameras to take 5 pictures per trigger with a 3-second delay between successive triggers. We used a predator trapping lure to encourage nearby animals to travel within a camera's detection zone and deployed cameras for 90 days during July to October 2019. Fifty-three percent of camera locations occurred in upland deciduous forest, 39% in lowland forest, and 8% in upland coniferous forest cover types. We collected 137,706 images, comprising 27,541 unique events (i.e., total number of animal detections and false triggers). We identified 22 unique mammal species, including 12 native members of the Order Carnivora. We detected black bears at 33% of survey sites; sites with black bear detections had proportionately more lowland forest than sites without detections. At sites having black bear detections, the number of daily detections averaged 1.03 (range = 1 – 16). Most black bear detections occurred on State Forest land in the east-central portion of the 1855 LTBB Reservation (e.g., Pleasantview Swamp) and within Wilderness State Park. Overall occupancy/use probability derived from the top supported model was 0.41 (95% CI = 0.24–0.61) and overall detection probability was 0.12 (95% CI = 0.08–0.21). Within the most supported model, lowland forest had a large and significant positive effect on probability of black bear occupancy/use (β = 1.94, SE = 0.67, p-value = 0.004) and mean Enhanced Vegetation Index (EVI) had a comparatively lower and non-significant effect (β = 0.83, SE = 0.56, p-value = 0.137). Understanding wildlife distribution and habitat use patterns that influence distribution is challenging for highly mobile species, but important for implementing successful landscape scale conservation strategies. Results of this study may serve as a foundation for wildlife managers to monitor the impacts of natural and anthropogenic land use changes on large-scale habitat use patterns by black bears. We demonstrate the utility of using camera traps to monitor rare and elusive carnivores in relation to various spatial and temporal drivers of distribution and habitat use. Specifically, these results emphasize the importance of protecting large tracts of lowland forest with connectivity to eastern lowland complexes, while maintaining upland forests surrounding these lowlands that provide seasonally diverse soft and hard mast forage.

A female black bear and her dependent young investigating a camera trap site in a small clearing within a dense lowland forest.

INTRODUCTION

Estimates of species distribution, abundance, and habitat use are important guiding metrics for wildlife management and conservation. Large carnivores throughout North America are of high management or conservation priority because they are often disproportionately vulnerable to extinction or extirpation (Ripple et al. 2014), are regulated by harvest (Etter and Mayhew 2008), have a high risk of human-wildlife conflict (Wilton et al. 2014a), are indicators of ecosystem integrity (Fecske et al. 2002), and may convey top-down regulation of ecosystem structure and function (Terbogh et al. 1999).

American black bears (*Ursus americanus*) are an omnivorous carnivore inhabiting much of the forested landscape throughout North America. Though bears utilize a variety of forested and non-forested cover types, throughout their range they demonstrate an overall affinity to forested landscapes and are considered a forest obligate species (Maehr 1997). In northeastern North America, black bears typically inhabit a range of habitat types, from forested hardwood-conifer swamps to beech-birch-coniferous forests, and prefer areas at least partially characterized by dense understory vegetation (Pelton et al. 1999). They are a generalist omnivore with plant matter (e.g., herbaceous plants, soft mast, hard mast) comprising most of their diet (Eagle and Pelton 1983). Bears have large home ranges (26–465 km^2; Carter et al. 2010) and are capable of extensive movements driven primarily by natal dispersal, breeding behavior, and seasonal variation in food abundance and distribution (Moore et al. 2014, Noyce and Garshelis 2011).

Black bears occur throughout most of Michigan, with the most recent statewide population survey estimating about 19,000 bears occupying about 90,650-km^2 of suitable bear habitat throughout the state (MI DNR 2008a), with an estimated 1500 (1180–1950) bears occurring in the northern Lower Peninsula (NLP) of Michigan in 2009 (MI DNR, unpublished data; as cited in Waples et al. 2018). Recent sightings extending into the southern Lower Peninsula suggest the state's bear population may be expanding its distribution and/or abundance. Several studies of bears in Michigan have focused on estimating habitat selection (Carter et al. 2010), population abundance (Dreher et al. 2007, Etter and Mayhew 2008), population genetics (Draheim et al. 2016, Moore et al. 2014, Waples et al. 2018), and distribution of bear incident reports (McFadden-Hiller et al. 2016). The Michigan DNR uses hunting as the primary tool for managing bear distribution and abundance within ecologically and socially acceptable carrying capacities (MI DNR 2008b).

However, obtaining estimates of abundance or density at the spatiotemporal scales necessary for effective conservation and discerning population responses to management actions often are logistically prohibitive for many agencies tasked with managing wildlife populations, especially for rare, elusive, and highly mobile species (Ballantyne 2008, Wilton et al. 2014b). Advancements in both field survey technologies and statistical models are improving our ability to monitor rare and elusive animal populations without the need to estimate abundance or density (e.g., Kery and Royle 2015, MacKenzie et al. 2018). Other sampling methods and population parameters based around collection of detection/non-detection data may be more appropriate and feasible for discerning population level information at finer spatial resolutions (Gould et al. 2019, Long et al. 2011). Numerous sampling methods exist for collecting detection/non-detection data without the need to physically capture or directly observe animals. Camera traps are an increasingly used method for non-invasively surveying highly mobile and elusive carnivores throughout the world (Steenweg et al. 2016a), and their application to monitoring the occurrence of species in an occupancy modeling framework (MacKenzie et al. 2002) may provide a lower cost and efficient tool for monitoring the status of carnivore populations (Steenweg et al. 2016b).

At their core, occupancy models estimate the probability of an animal (or any "thing") being present at a site (Ψ), while explicitly estimating detection probability (p) from repeated site visits (MacKenzie et al. 2002). Therefore, occupancy models assume that at least 1 animal falls within a spatial sampling unit such that the abundance of this animal in a spatial unit is greater than zero (Kery and Royle 2015). Site and/or observation level covariates can be incorporated into the model to improve inference and minimize bias (Kery and Royle 2015).

Recent extensions of the occupancy model framework have enabled explicit estimation of various ecological processes and population dynamics, including metapopulation dynamics, species richness, multiple-season occupancy, species co-occurrence, and site abundance (Kery and Royle 2015, MacKenzie et al. 2018, Royle and Nichols 2003). Although occurrence is only a generalization of abundance, it is often positively associated with abundance, where changes in abundance are generally detected by changes in spatial occurrence (He and Gaston 2000). Moreover, the methodological and logistical constraints of modeling abundance often make modeling occurrence the next best approach (MacKenzie et al. 2005). One of the primary benefits of occupancy modeling is that it accounts for false-negative measurement errors by explicitly modeling the detection process jointly with probability of occupancy (MacKenzie et al. 2002).

A current limitation of the application of occupancy models to the study of large carnivores is that they require the occurrence status of a site to remain occupied by the focal species for the duration of study (closure) and that the probability of occupancy at one site does not influence the probability of occupancy at another site (site independence; MacKenzie et al. 2018). Violation of these basic model assumptions occur when estimating site occupancy of highly mobile and wide-ranging species, such as large carnivores, which can introduce bias in occupancy estimates (Hayes and Monfils 2015, Sollmann 2018). When these violations occur, interpretation of site occupancy as the probability of static occurrence may shift to the probability that a sampling unit is "used" for at least some period during the study. This interpretation only holds if animals move randomly in and out of sample units (Gould et al. 2019, MacKenzie 2006).

Black bears are wide-ranging carnivores and have among the largest home ranges of any large mammal in the region (Carter et al. 2010). Therefore, we adopt the interpretation of "site use" to imply that the formal state of site occupancy of a sample unit is violated (Gould et al. 2019). This interpretation is often of greater ecological interest as it allows for inference of habitat use at a site as a function of modeled covariates (e.g., land cover).

Camera trap deployed in a lowland forest in Wilderness SP.

We define habitat as any area where the sum of the resources that are required for an animal's occupancy (survival and reproduction) are found, and habitat use as the way an animal uses these resources in its habitat (Garshelis 2000, Hall et al. 1997). For example, an animal's habitat use may vary seasonally with variation in habitat-specific forage availability. We also adopt the interpretation of habitat selection as the hierarchical process of choosing which resources to use within a habitat (Johnson 1980), where selection may be inferred if a habitat component is used disproportionately to its availability across the landscape.

Michigan Natural Features Inventory (MNFI) partnered with the Little Traverse Bay Bands of Odawa Indians (LTBB) to implement a population survey of black bear and other medium- to large-bodied mammals occurring within the 1855 LTBB Reservation (hereafter Reservation) lands. The purpose of this project is to provide LTBB biologists with current information on the distribution and habitat use of black bear and the ecological and anthropogenic drivers of current bear distribution. Specifically, our objective was to estimate black bear habitat use on public lands within the Reservation using a camera trap-based occupancy modeling framework to create a seamless map of predicted bear habitat use throughout the Reservation. We test various hypotheses about the influence of land cover and land use classifications as ecological and anthropogenic drivers of black bear habitat use.

METHODS

Study Area

The 1855 LTBB Reservation covers 877-km^2 in the northern Lower Peninsula (NLP) of Michigan in Emmet and Charlevoix counties, with the majority in Emmet County. For the present survey, our area of interest was about 845-km^2 of the Reservation located on the NLP mainland and is located within the Red Oak Bear Management Unit (BMU; MI DNR 2008b). Human population density was about 30 people/km^2

(U.S. Census Bureau, 2010) within Emmet County and is concentrated primarily in the cities of Charlevoix, Petoskey, and Harbor Springs, which make up much of the 2% developed land uses in the Reservation. Housing density decreases sharply away from these city centers, with much of the landscape dominated by upland forest, lowland forest, open wetland, and agricultural land use. Mackinac State Forest and State Park lands comprise about 25% of the Reservation's land area. About 70% of the Reservation is forested, with 41% upland deciduous forest, 12% lowland forest, 8% upland conifer forest, 5% mixed forest, and 7% agriculture. Elevation reaches a maximum of 398 meters and much of the forested landscape is characterized by rolling to steep hills. Extensive lowland forests and wetlands occur primarily in the east-central area surrounding Lark's Lake and Wycamp Lake (a.k.a. Spirit Lake), the northern end comprising Wilderness State Park, and the southern end surrounding the Bear River.

Sampling Design

We used ArcGIS 10.6.1 (Environmental Systems Research Institute, Inc., Redlands, California, USA) to establish a 4-km^2 hexagonal random grid over the Reservation to form the basis of our sampling design. This grid size was used to maximize detection of black bear, while simultaneously maximizing landscape coverage and detection of other medium- to large-bodied carnivores (e.g., American marten [*Martes americana*], fisher [*Pekania pennanti*], coyote [*Canis latrans*], bobcat [*Lynx rufus*]). Carter et al. (2010) found that male and female black bears in the NLP of Michigan selected for habitat characteristics at 9-km^2 and 4-km^2 spatial scales, respectively and Norton et al. (2018) found that female black bears in the Upper Peninsula of Michigan had mean core (i.e., 50%) home range isopleths of 4.45-km^2 (SE = 2.28-km^2). Therefore, we felt a 4-km^2 grid was appropriate for both modeling black bear habitat use parameters at a meaningful resolution while maintaining sufficient camera trap density and spatial coverage to satisfy logistical constraints and maximize flexibility of data applications. Due to land access restrictions, we limited survey areas to grid cells containing access to public lands (i.e., State Forest, State Park). This resulted in an array of 63 sampling cells totaling 252-km^2 (Figure 1). The center of each randomly derived grid cell or nearest public land location within a forested cover type served as a starting location for selecting camera trap placement.

Field Sampling

We programmed cameras to take 5 pictures per trigger with a 3-second delay between successive triggers. We used a predator trapping lure (Caven's Gusto, Minnesota Trapline Products Inc.) to encourage nearby animals to travel within a camera's detection zone by placing a small amount of the lure about 2 meters above ground on vegetation to act as a long-distance call lure and on vegetation or logs located at the center of a camera's detection zone. We deployed cameras for about 90 days during 22 July 2019 to 23 October 2019.

Within a 100-meter radius of the randomly located GPS point, we searched until a location having a suitable field of view to allow medium- to large-bodied mammals to be photographed was found.

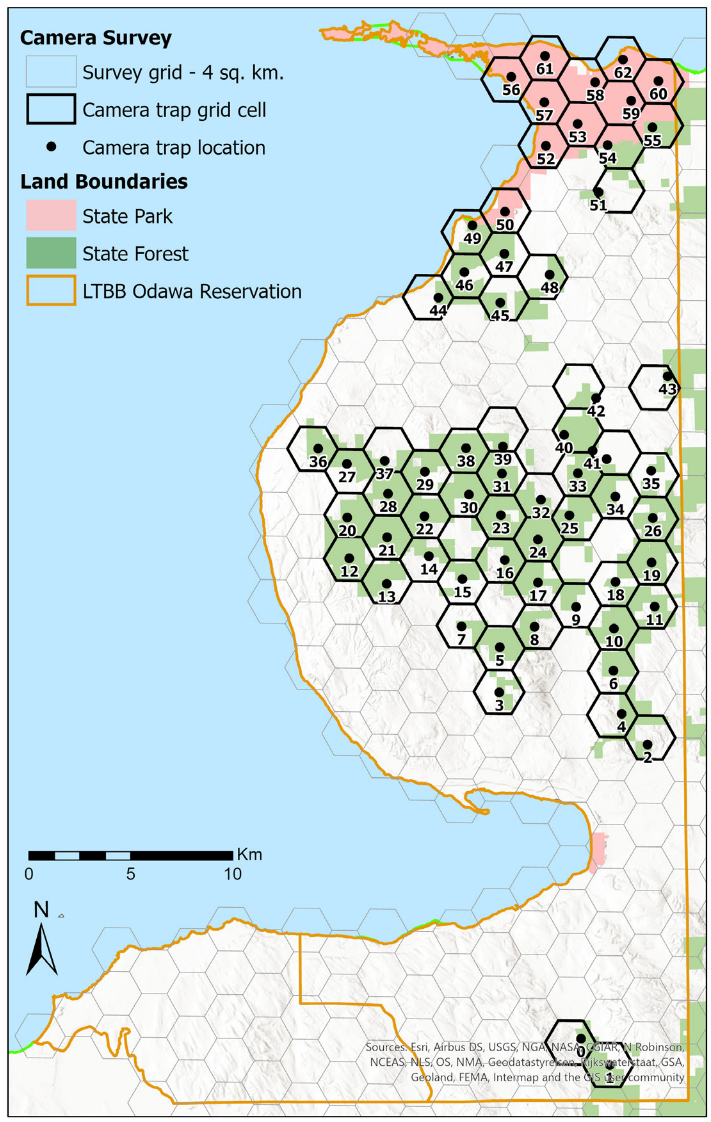


Figure 1. Locations of 63 camera traps deployed within a random 4-km^2 survey grid distributed over public lands.

A black bear investigating the scent lure placed in front of a camera's detection zone to encourage nearby animals to pass in front of the camera.

Camera site selection was further refined by aiming the camera's detection zone towards available fine-scale natural features that facilitate animal movement and detection of the target species, including game trails, streams, rivers, old logging roads, topographic features, and large coarse woody debris. We avoided placing cameras on human-use roads and trails to minimize theft/vandalism.

Cameras were mounted about 50 cm above ground to a tree and about 3–5 meters from the target detection zone (e.g., game trail, log). If a trail or log feature was used, we mounted the camera at about a 45-degree angle to the trail to maximize detection of traveling animals. We trimmed vegetation obstructing the camera's detection zone and vegetation that may falsely trigger the camera.

We recorded whether the camera was set facing a game trail, log, or other natural feature (Set Type) and measured the maximum distance a camera was able to detect a passing animal (Detection Distance). This metric serves as an index of horizontal vegetation density that may obstruct a camera's view and detection probability. We also noted any unique natural or anthropogenic features that may influence detection or site occupancy (e.g., timber harvest, prescribed fire, powerline cut, topographic characteristics, windthrow) that could not be extracted using available GIS data. We described basic dominant species composition of the canopy and sub-canopy, as well as general characteristics of the immediate habitat surrounding a camera site.

We triggered cameras upon arrival and before leaving each site by holding an informational whiteboard with date, time, camera ID, visit #, and observer initials. This provided a confirmation of a camera's operational status and a basic digital backup of a site's datasheet. We checked cameras every 3–4 weeks to collect memory cards, replace batteries as needed, maintain camera operation, and replenish scent lure. While walking to and from a camera trap site, we searched for evidence of carnivore occurrences (i.e., track, scat, foraging, actual sighting) and recorded the total distance and time walked using a handheld GPS-unit.

Image Processing

We downloaded images from memory cards after each camera check and organized images into folders distinguished by camera site (e.g., "Station0") and subfolders by camera visit number (e.g., "visit1"). This folder structure was designed to function with the R package "camtrapR" (Niedballa et al. 2016), which reads images according to this specified structure and renames each image file with its respective station ID, visit number, date taken, time taken, and image sequence number (e.g., station0__visit1__2019-07-25__16-16-32(1).JPG). This naming structure is formatted to enable camtrapR to extract species-specific detection histories by camera site, date, and time.

We used Adobe Lightroom Classic CC software (hereafter Lightroom; Adobe, San Jose, CA, USA) to classify species and manage image organization. Lightroom utilizes a hierarchical keyword structure (e.g., Species > [black bear, bobcat, coyote, etc.]) that writes species classifications back into an image's EXIF metadata. These keyword tags are accessed through camtrapR and form the foundation of converting a collection of images into a database for statistical analysis. This process is critical for efficient database management and quality control as each image classification is permanently associated with the physical image. To facilitate queries of the image database for users without access to Lightroom, the species' common name was appended to the end of each file name. For example, using a computer's File Explorer (Windows) search bar, typing 'black bear' will filter images accordingly. We can also provide subsets of the image database for any species or species group of interest upon request.

All images of mammalian and avian species detected at camera traps were classified. If species-level identification was not possible due to image quality, we used the next most detailed classification level (e.g., "unknown carnivore" > "unknown mammal" > "unknown"). We also grouped raccoon (*Procyon lotor*), Virginia opossum (*Didelphis virginiana*), striped skunk (*Mephitis mephitis*), and North American porcupine (*Erethizon dorsatum*) into "other mammal", and all squirrel, rabbit, and small rodent into "small mammal". We grouped all avian detections into the tag "other Aves", except for raptors, which were grouped into "raptor".

Modeling Habitat Use

We defined a positive bear detection at a camera site as at least 1 bear image collected per day. For each camera site, we developed a daily detection history, where a "1" indicates a positive bear detection and a "0" represents a non-detection event. For example, a detection history of "01011" illustrates a detection history where a bear was not detected on the first day, detected on the second day, not detected on the third day, and detected on the last 2 days.

We calculated a relative abundance index (RAI; Conroy 1996) using the equation RAI = (D/TN)*100, where D is the number of independent daily detections and TN is the total number of trap nights per camera trap (Allen et al. 2017).

Due to the sparse positive detections typical of carnivore surveys and associated limitations of zero-inflated datasets, we collapsed the raw 1-day detection history into 16, 6-day occasions. This period was the shortest occasion length that permitted convergence of the most basic (i.e., null) occupancy model.

We used single-species, single-season occupancy modeling (MacKenzie et al. 2002) in a likelihood-based model selection framework (Akaike Information Criterion (AIC); Arnold 2010) to test and rank the relative support among hypotheses about factors affecting black bear habitat use from our detection-nondetection data. We tested 4 covariates expected to influence black bear detection probability. Although not of particular ecological interest, overall model fit and accuracy depends on accounting for negative biases in the detection process. We hypothesized that detection may be influenced by who the camera was set by (Set By), what feature a camera was directed at (game trail, coarse woody debris, other; Set Type), the maximum distance a camera could be triggered by a person (Detection Distance), and by survey period (Time). The covariate Time was investigated by dividing the field season length into 4 equal length intervals to test for changes in bear detection over each quarter of the survey duration.

We developed an a priori set of models to investigate factors influencing black bear habitat use. For each covariate, we extracted values at a 4-km^2 spatial scale as this represents approximate habitat selection within an average bear home range (Norton et al. 2018). We hypothesized that habitat use may be influenced by: 1) the proportion of lowland forest (LF) comprising a camera's 4-km^2 grid cell, 2) the proportion of upland deciduous forest (UDF) comprising a camera's 4-km^2 grid cell, 3) the proportion of agricultural land (AGR) comprising a camera's 4-km^2 grid cell, 4) spatial variation in primary productivity (mean EVI), and 5) road density. We included lowland forest and upland deciduous forest because these are the most dominant natural land cover classes in the study area and are likely to be important drivers of bear resource selection (Carter et al. 2010). Agricultural lands may positively or negatively influence bear habitat use depending on the extent, type, and intensity of agricultural land use practices (Duquette et al. 2017). Spatial variation in primary productivity provides an index of the dispersion of food availability across the landscape and may affect animal distribution (Gould et al. 2019). Road density may increase human disturbance, perceived risk, and reduce survival (Duquette et al. 2017).

Specifically, we hypothesized that black bear habitat use would increase with increasing proportion of lowland forest cover and decrease with increasing proportion of upland deciduous forest cover. We used LANDFIRE's Existing Vegetation Type (EVT) classification layer (30-m^2 resolution) to extract all land cover covariates (Rollins 2009) and reclassified 25 focal EVT group names into 5 ecological classes, including 'upland deciduous forest', 'upland conifer forest', 'mixed forest', 'lowland forest', 'agriculture', and all other classes (Appendix I). We predicted that habitat use would increase with increasing mean primary productivity, using the enhanced vegetation index (EVI) as a correlate of food availability (Merkle et al. 2013; Nijland et al. 2016). The EVI can be used to quantify vegetation greenness and is generated every 16 days from 250-meter Moderate Resolution Imaging Spectrometer (MODIS) datasets (Huete et al. 2002). We downloaded each 16-day EVI dataset encompassing the camera trap survey period, averaged EVI cell values across each raster dataset, and then averaged these values within each camera grid cell. Finally, we predicted bear habitat use would decrease with increasing road density. We measured road density at each camera grid cell as the kilometers of road per 4-km^2 grid cell.

We used a two-step approach to first determine the most parsimonious model explaining detection probability, and then included these detection covariates in all combinations of our occupancy models (Erb et al. 2012). All covariates were first standardized by subtracting the mean and dividing by the standard deviation of each covariate. During the first step, we included all possible occupancy covariates as a constant while investigating each combination of detection covariates. In the second step, the resulting most supported detection model was held constant while all combinations of occupancy covariates were investigated. We then used the final most supported model describing detection probability and occupancy probability to predict and describe black bear habitat use throughout the study area.

We considered models to have competing support if they were within 2.00 ΔAIC of the most supported model and assessed proportional support for each model using AIC weights (w_i; Burnham and Anderson 1998). Because the selection of a "best" model using this approach does not equate to a "good" model per se, we assessed the most supported model from AIC using a goodness-of-fit (GOF) test (MacKenzie and Bailey 2004). We examined the significance of each covariate in the top model by determining if the 95% confidence interval (CI) of the beta coefficients overlapped zero (significance = non-overlapping CI). All analyses were performed in program RStudio (v. 1.2.5033; R Core Team 2019).

Predicting Species Distribution Across The Study Area

To predict the expected probability of bear habitat use across the entire Reservation study area, we evaluated each 30-m^2 raster pixel as a function of the covariate values of all the cells within a 4-km^2 circular buffer around each pixel location. We chose a 4-km^2 buffer to match the area of the camera grid cells used in building the occupancy model set. This process generates a hypothetical situation where a camera trap can be envisioned at each pixel in the study area and the probability of habitat use at each pixel depends on the values of all neighboring cells within the specified 4-km^2 buffer. The predicted probability of habitat use is then a function of the most supported occupancy model.

We extracted the mean covariate values across the study area for the most supported model using the Focal Statistics toolset in ArcGIS Pro (v. 2.5.0, Environmental Systems Research Institute, Inc., Redlands, California, USA). This algorithm evaluated each cell in the specified raster layer (e.g., land cover) and calculated the mean of all cells within each 4-km^2 neighborhood. To evaluate the proportion of lowland forest across the study area, we collapsed all lowland forest types to a value of '1' and all other land cover classifications to a value of '0'. This resulted in the mean neighborhood statistic of each cell being equivalent to the proportion of lowland forest within a 4-km^2 circle. We evaluated mean EVI using the same process, but since integer values were retained, the algorithm's output was the mean EVI value within a 4-km^2 circle. We then used the most supported occupancy model results to estimate the expected probability of bear habitat use at each pixel in the raster defining the proportion of lowland forest and mean EVI at a 4-km^2 spatial scale across the Reservation.

RESULTS

Field sampling

We deployed 64 camera traps during 22–26 July 2019 and retrieved all cameras during 21–23 October 2019, with 1 camera (station 33) being retrieved on 26 September 2019 due to landowner request (Figure 2). Because we set 2 cameras in grid cell 41, we dropped 1 camera with the fewest detections from statistical analyses to maintain consistency across sites. This survey period translates to a total survey effort of 5,594 trap nights. Average camera deployment period was 89 days (range = 65–91 days). All camera traps were operational during their respective deployment periods. We experienced no camera theft or vandalism of camera trap sites.

Image Processing

Camera traps collected 137,706 images, comprising 27,541 unique triggers (i.e., total number of animal detections and false triggers). We classified 88,667 images of animals to species or group level. False triggers and white-board photos comprised 47,655 images (35%). We identified 22 unique mammal species, including 12 native members of the Order Carnivora across 6 Families (Appendix II). See Appendix III for a list of carnivore species detections by station.

Black bears triggered cameras 566 times at 21 unique camera sites. We detected black bears at 33% (i.e., naïve occupancy) of survey sites; sites with black bear detections had proportionately more lowland forest at the grid cell scale (4-km^2) than sites without detections. Most detections, and the highest frequency of detections, were concentrated in and around the Pleasantview Swamp and Wilderness State Park (Figures 3–4). At sites having black bear detections, the number of daily detections averaged 1.03 (range = 1 – 16), with 65 total daily detections across sites (Figure 5). Detections were most frequent across cameras around 0600 hours and 1900 hours, with another peak around 0000 hours (Figure 6).

Black bear cubs were detected at 6 camera sites, with the maximum number of observed cubs per site ranging from 1 to 3 individuals. Five out of 6 sites with cub detections occurred at sites having ≥ 50% lowland forest cover (Table 2, Figure 7). There was no apparent trend in number of black bear detections over time (Figure 8).

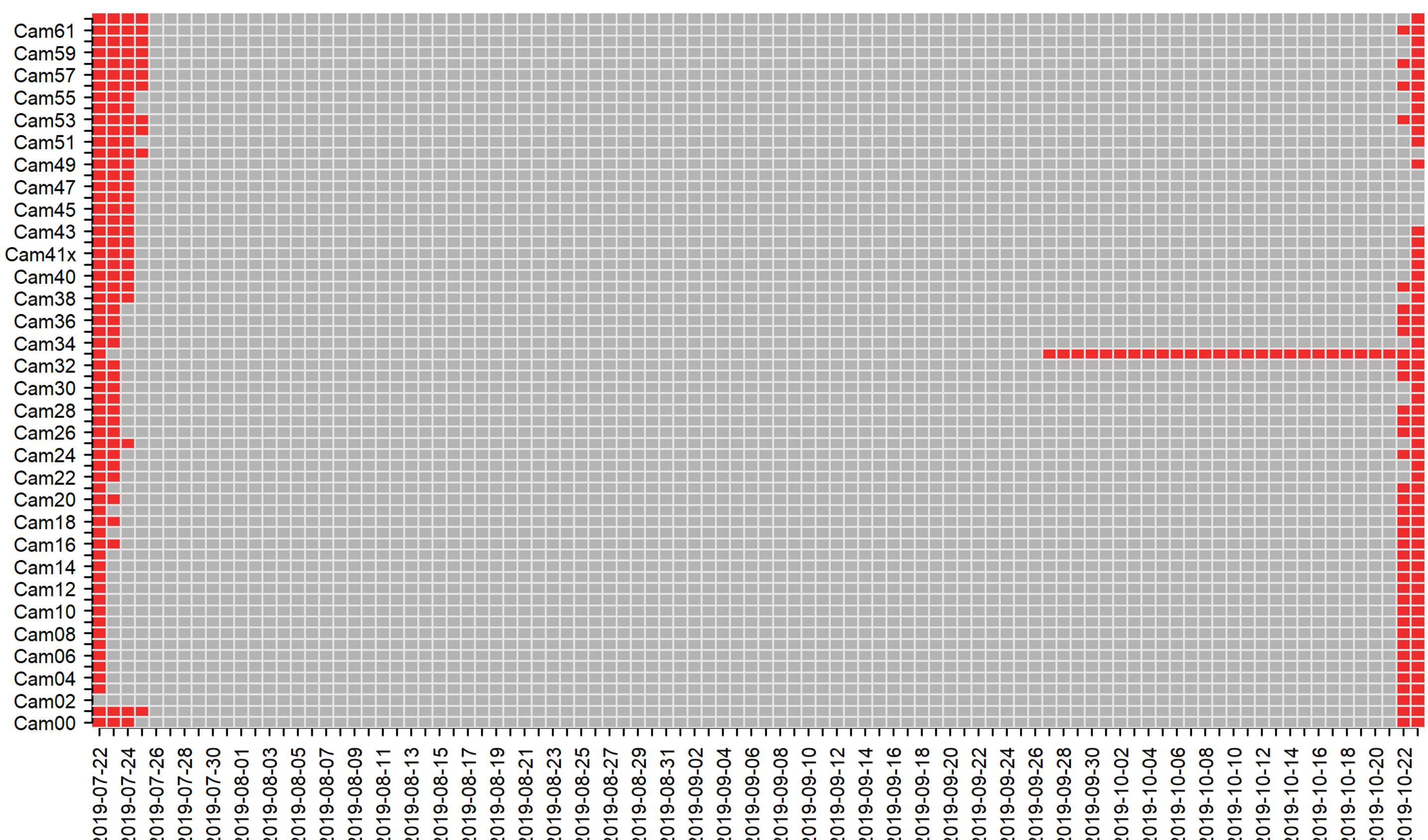


Figure 2. Matrix displaying the operative days (gray squares) and inoperative days (red squares) for each camera (y-axis) during the deployment period (21 July 2019 – 23 October 2019).

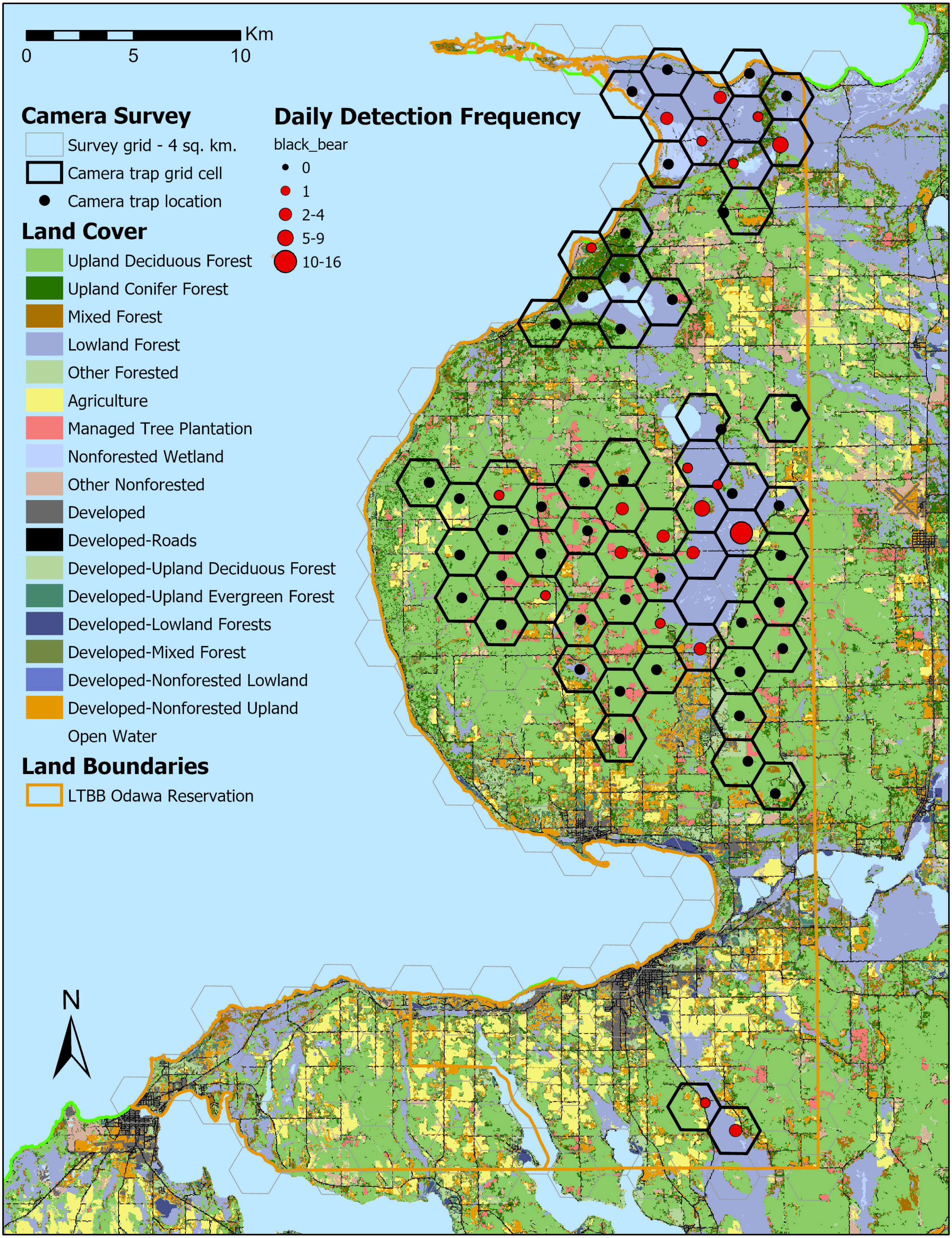


Figure 3. Location of camera traps and associated frequency of daily black bear detections in relation to reclassified LANDFIRE cover types.

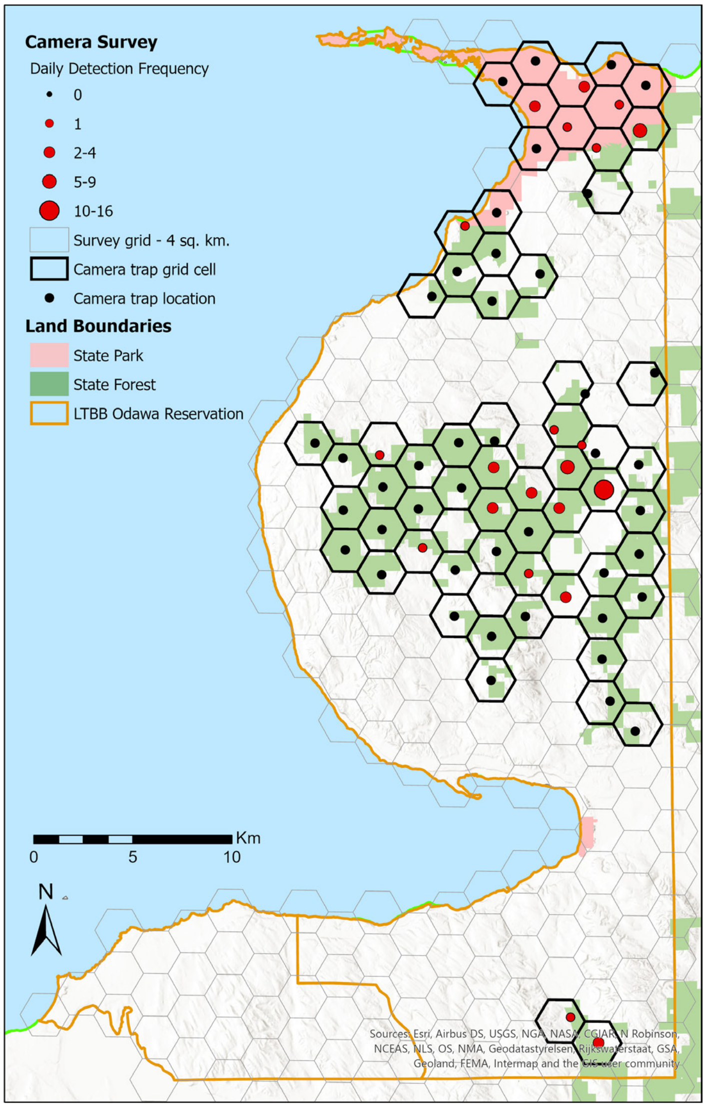


Figure 4. Location of camera traps and associated frequency of daily black bear detections in relation to State Forest and State Park lands.

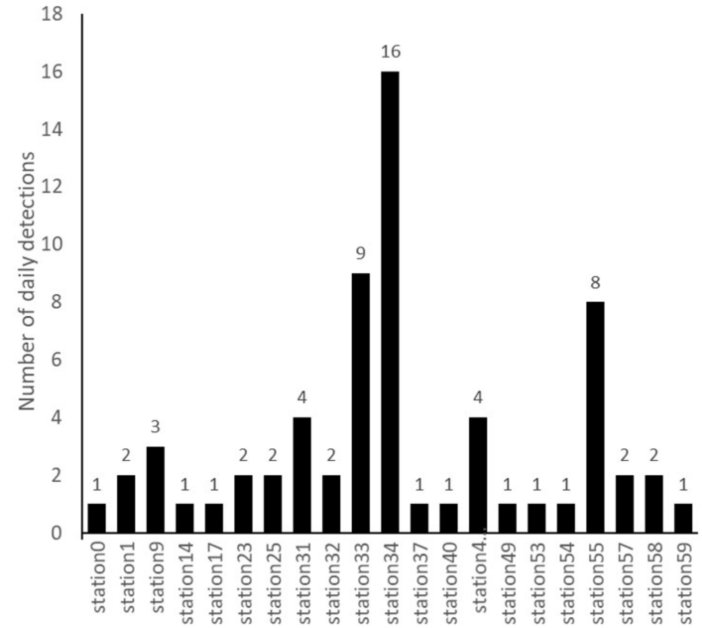


Figure 5. Distribution of daily black bear detections at each camera trap (station) where at least 1 bear was detected (*n* = 21 stations).

Modeling Habitat Use

Covariates used to evaluate probability of habitat use varied greatly among sites (Figures 3, 9, 10). At the specific location of a camera trap, 50% of camera locations were deployed in upland deciduous forest, 31% in lowland forest, and 11% in upland coniferous forest or mixed forest, and 8% in other cover type classifications. Similarly, most camera site cells were dominated (≥ 50% of cover class) by either upland deciduous forest (n = 33 sites) or lowland forest cover types (n = 15 sites). No other cover type classification comprised ≥ 50% of a surveyed cell. Overall, mean upland deciduous forest cover among sites was 47.1% (SD = 32.8%), mean lowland forest cover was 23.0% (SD = 29%), and mean agricultural cover was 1.4% (SD = 3.1; Table 3).

Cover types were similar between surveyed grid cells and the entire Reservation area, though the proportion of lowland forest made up about twice as much of the surveyed area relative to its composition across the Reservation. Moreover, of all the cells bears were detected in, upland deciduous forest comprised 31% of the land area and lowland forest comprised 44% of the land area, compared to 47% and 23% across the entire survey grid, respectively. Relative to the availability of lowland forest across the surveyed grid cells, black bears appeared to be using this cover type disproportionately to its availability (Figure 11).

As expected, the RAI generally tracked with increases in percent lowland forest at the grid cell level and the highest RAI's were concentrated in the Pleasantview Swamp and Wilderness State Park (Appendix IV). The overall mean RAI across sites was 1.16 detections/100 trap nights (SD = 2.87, range = 0.00 – 17.78).

Covariates used to model detection probability included 'Set Type' (factor with 3 levels: 'log', 'trail', 'other'), 'Set By' (factor with 5 levels: 'CW', 'KH', 'MF', 'MF.CW', 'SM'), 'Detection Distance' (numeric), and 'Time' (factor with 4 levels: 1, 2, 3, 4). Camera traps were set on a trail feature 25 times, a log feature 17 times, and other features 21 times. We note that more than 1 feature was occasionally utilized at a camera trap, but we attempted to select the dominant feature to model as a detection covariate. Detection distance, the maximum distance a camera trap could detect an animal, ranged from 10–60 feet ($\bar{x}$ = 26.1 ft).

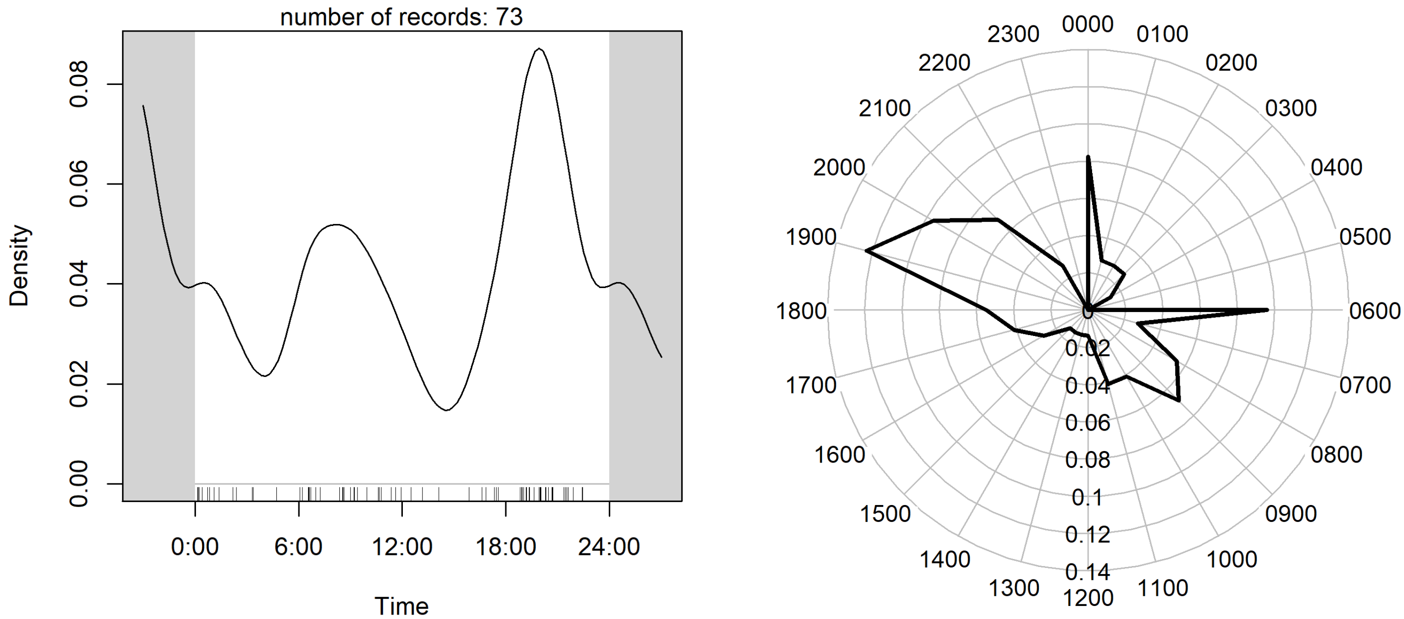


Figure 6. Diel activity plots of 73 black bear detections, illustrating the density (top) and proportion (bottom) of detections aggretated by hour.

Black bear cubs were detected frequently at station 34, a site dominated by lowland forest.

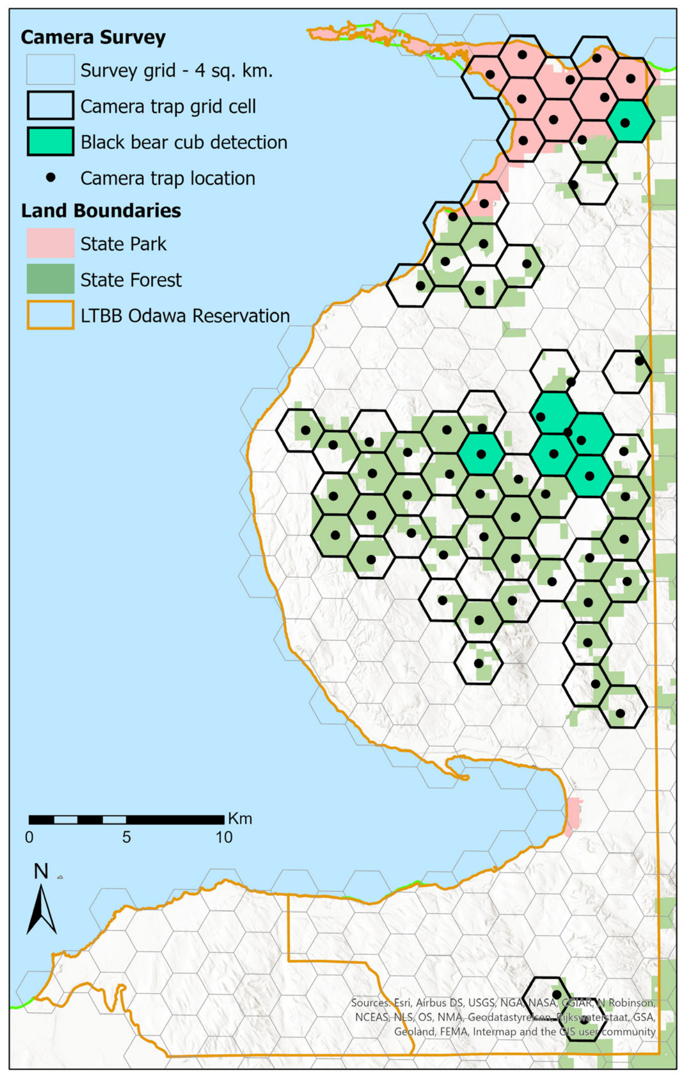


Figure 7. Site locations of dependent young detections. All but one were at sites dominated by lowland forest.

Table 2. Maximum number of dependent young detected at camera traps and the cover type and percent lowland forest associated with the grid cell of each station.

Station	Date	Max count	Cover type	% Lowland Forest
31	9/24	3	Upland Deciduous	0.02
33	8/5	1	Lowland Forest	56.51
34	8/15	3	Lowland Forest	75.08
40	8/18	2	Lowland Forest	88.50
41	8/15	3	Lowland Forest	71.76
55	9/11	2	Lowland Forest	63.31

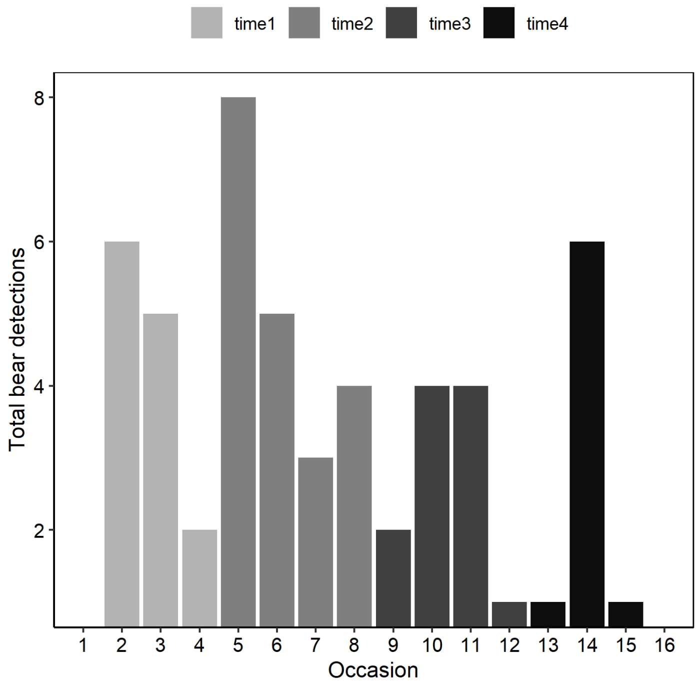


Figure 8. Total number of bear detections occuring at each of the 16, 4-day sampling occasions. Values are further descritized into 4 time periods used to test for an effect of survey duration on bear detection probability.

The most-supported model describing black bear detection probability included ‘Set Type’, ‘Set By’, and ‘Detection Distance’ and was supported 2.5 times as much ($w_i = 0.5$) as the second ranked model ($w_i = 0.2$). Although the second ranked model may be considered competing (i.e., $\Delta AIC \leq 2.00$), it only differed from the top model by 1 additional parameter (‘Time’), which was not significant at $\alpha = 0.05$. Therefore, it’s inclusion in the top model set was statistically driven, rather than ecologically important (Arnold 2010). This condition also applies to the inclusion of the third ranked competing model (Table 4). Therefore, we used the single most supported model to describe predictors of black bear detection probability.

Within the most supported model, detection probability increased with increasing camera detection distance ($\beta = 0.38$, SE = 0.19, p-value = 0.05). Black bear detection probability was greatest for cameras set on game trail features ($p = 0.23$, 95% CI = 0.17 – 0.31, p-value = 0.002), whereas detection probability for ‘other’ set types was 0.08 (95% CI = 0.03 – 0.20) and for ‘log’ features was 0.06 (95% CI = 0.02 – 0.14), but were not significant at $\alpha = 0.05$. Although we do not consider ‘Time’ to be an informative predictor of detection probability, we note

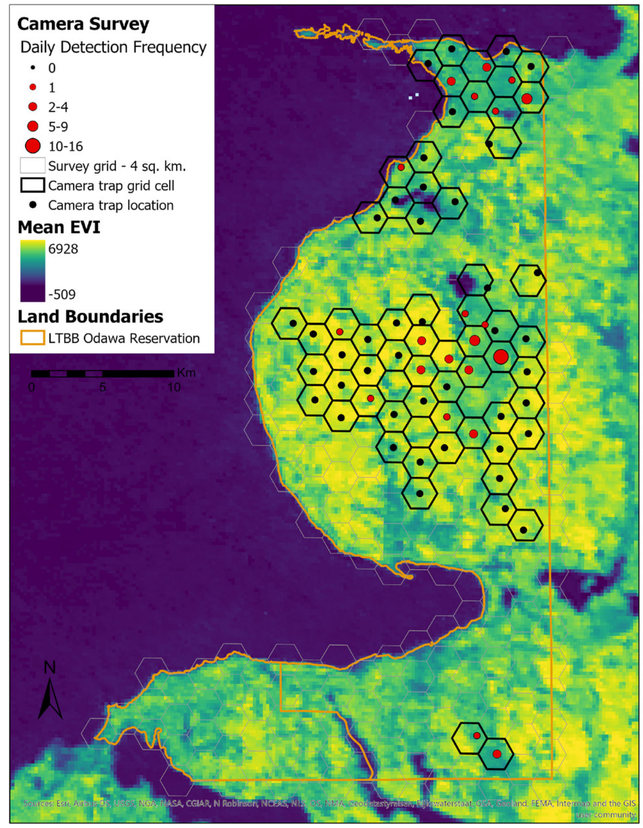


Figure 9. Mean Enhanced Vegetation Index (EVI) used to determine the effect of primary productivity on black bear distribution and habitat use.

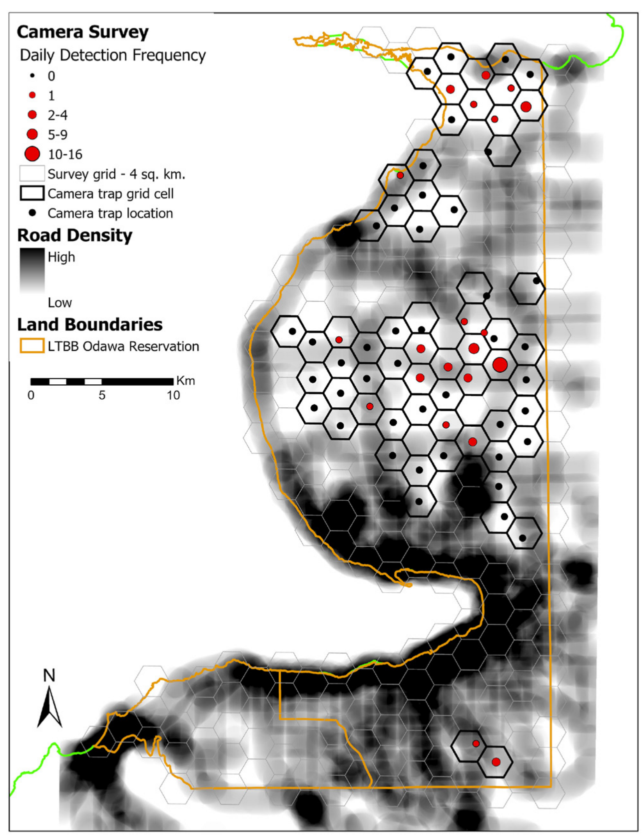


Figure 10. Road density estimated at a 4-km^2 resolution. Note that road density was measured as kilometers of road per 4-km^2 in our model.

that detection probability increased slightly from time period 1 to period 2 ($p = 0.23$, 95% CI = 0.15 – 0.33) and decreased about 45% from period 2 to 3, then remained constant at 0.13 (95% CI = 0.06 – 0.24) during period 4. It is also important to note that these time periods have no ecological relationship but were simply a convenient way to investigate change in detection probability over time.

Using the most supported detection model from above, we tested 20 model combinations developed to discern the most important ecological and/or anthropogenic drivers of black bear habitat use (Table 5). Six models were within 2.00 ΔAIC of the most supported model, which included combinations of all modeled covariates (lowland forest, upland deciduous forest, agriculture, mean EVI, and road density). The most supported model included lowland forest and mean EVI as covariates and was supported 1.6 times as much ($w_i = 0.23$) as the second ranked model ($w_i = 0.15$). Like the model selection results for detection probability, we conclude that the other covariates within the competing model set are uninformative parameters and do not explain bear habitat use better than the top-ranked model. Moreover, lowland forest was included in all but 1 of the 10 models that comprised 100% of the cumulative model weight and was not included in any lower ranked models (Table 5). Therefore, we feel the single most supported model best explains black bear occupancy and habitat use.

Lowland forest was the only consistently significant ($\alpha \leq 0.05$) covariate in all competing models, except when upland deciduous forest was included as an

Table 3. Mean values of environmental and anthropogenic site covariates derived from each surveyed 4-km^2 grid cell used to model probability of habitat use.

Site Covariate	Mean	SD	Min	Max
Lowland forest (%)	23.0	29.0	0.0	88.5
Upland deciduous forest (%)	47.1	32.8	0.0	93.7
Agriculture (%)	1.4	3.1	0.0	18.5
Mean EVI	4876.1	1001.3	1945.0	6140.0
Road Density (km/4km^2)	0.4	0.4	0.0	1.4

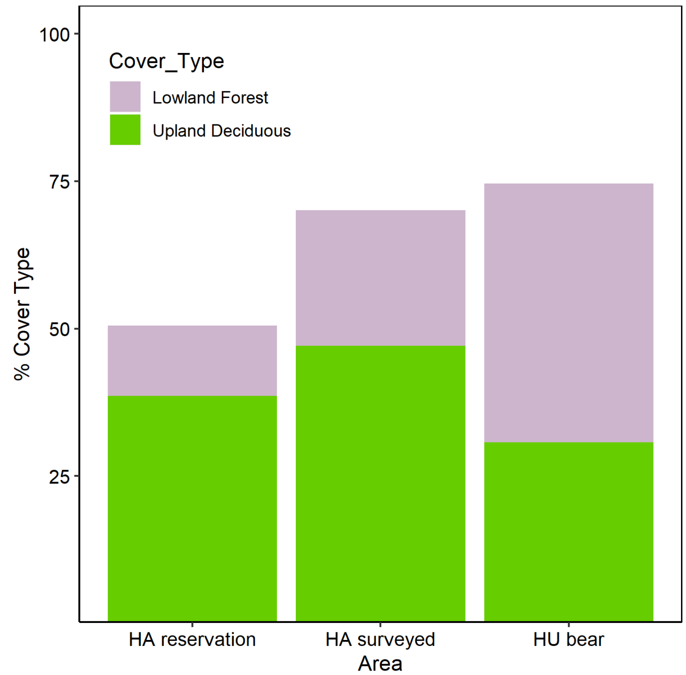


Figure 11. Black bear habitat availability (HA) within the Reservation and camera trap survey grid compared to habitat use (HU), as measured by the proportion of lowland forest and upland deciduous forest within grid cells that detected black bear.

Black bears were detected frequently at station 34, a site characterized by dense lowland forest with a thick shrub layer.

Black bear detected at station 34 during peak diel activity.

Table 4. Step one of a two-step model selection approach where the top ranked detection probability model (*p*) is assessed while holding the occupancy probability model (Ψ) constant using the full set of possible covariates. Number of model parameters (K), Akaike's Information Criterion (AIC), the difference in AIC between the top ranked model and the *i*th ranked model (ΔAIC), model weight (w_i), and model deviance (-2*log-likelihood) are presented for each candidate model. Only models with $w_i > 0.00$ are displayed (16 total candidate models).

Formula	K	AIC	ΔAIC	w_i	Deviance
p(Detection.Distance + Set.By + Set.Type) Ψ(global)	13	319.6	0.00	0.50	293.6
p(Detection.Distance + Set.By + Set.Type + Time) Ψ(global)	16	321.5	1.84	0.20	289.5
p(Set.By + Set.Type) Ψ(global)	12	321.5	1.86	0.20	297.5
p(Set.By + Set.Type + Time) Ψ(global)	15	323.0	3.41	0.09	293.0

Table 5. Step two of a two-step model selection approach where the top ranked detection probability model [p(Detection.Distance + Set.By + Set.Type)] identified in step one is used in the assessment of each candidate occupancy probability model (Ψ). Number of model parameters (K), Akaike's Information Criterion (AIC), the difference in AIC between the top ranked model and the *i*th ranked model (ΔAIC), model weight (w_i), and model deviance (-2*log-likelihood) are presented for each candidate model. Only models with $w_i > 0.00$ are displayed (20 total candidate models).

Formula	K	AIC	ΔAIC	w_i	Deviance
Ψ(LF + MeanEVI)	11	316.2	0.00	0.23	294.2
Ψ(LF)	10	317.2	0.94	0.15	297.2
Ψ(LF + UDF + MeanEVI)	12	317.3	1.05	0.14	293.3
Ψ(LF + MeanEVI + Road Density)	12	317.7	1.43	0.11	293.7
Ψ(UDF + MeanEVI)	11	318.2	1.96	0.09	296.2
Ψ(AGR + LF + MeanEVI)	12	318.2	1.99	0.09	294.2
Ψ(LF + Road Density)	11	318.8	2.60	0.06	296.8
Ψ(AGR + LF)	11	319.1	2.83	0.06	297.1
Ψ(MeanEVI + LF + AGR + Road Density)	13	319.6	3.39	0.04	293.6
Ψ(AGR + LF + Road Density)	12	320.8	4.57	0.02	296.8

additive effect with lowland forest (Figure 12). Although upland deciduous forest had a strong negative effect (β = -1.44, SE = 1.52) on bear habitat use when included in a model with lowland forest and mean EVI, its influence was not significant (p-value = 0.34). This suggests upland deciduous forest is a confounding covariate and does not improve model performance over that which only includes lowland forest and mean EVI. However, both upland deciduous forest and mean EVI were significant when included in a model together (Figure 12). Overall, the top supported model (Ψ ~ lowland forest + mean EVI) provides the best explanation of black bear habitat use and the goodness-of-fit test suggests the observed frequency of black bear detections supports what was expected under this model ($\hat{c}$ = 0.24, p-value = 0.864; MacKenzie and Bailey 2004).

Within the most supported model, lowland forest had a large and significant positive effect on probability of black bear habitat use (β = 1.94, SE = 0.67, p-value = 0.004) and mean EVI had a comparatively lower and non-significant effect (β = 0.83, SE = 0.56, p-value = 0.137; Figure 12). Interpreting these beta coefficient values indicates that the probability of a site being used by a black bear was 0.41 (SE = 0.10) for sites at the mean surveyed percentage of lowland forest (23%), compared to a 0.13 (SE = 0.07) probability of habitat use for sites at the minimum surveyed percentage of lowland forest (0%) and a 0.98 (SE = 0.03) probability of use for sites at the maximum surveyed percentage of lowland forest (89%, Figure 13). At the 4-km^2 camera site level, estimated probability of black bear habitat use increased markedly when the percentage of lowland

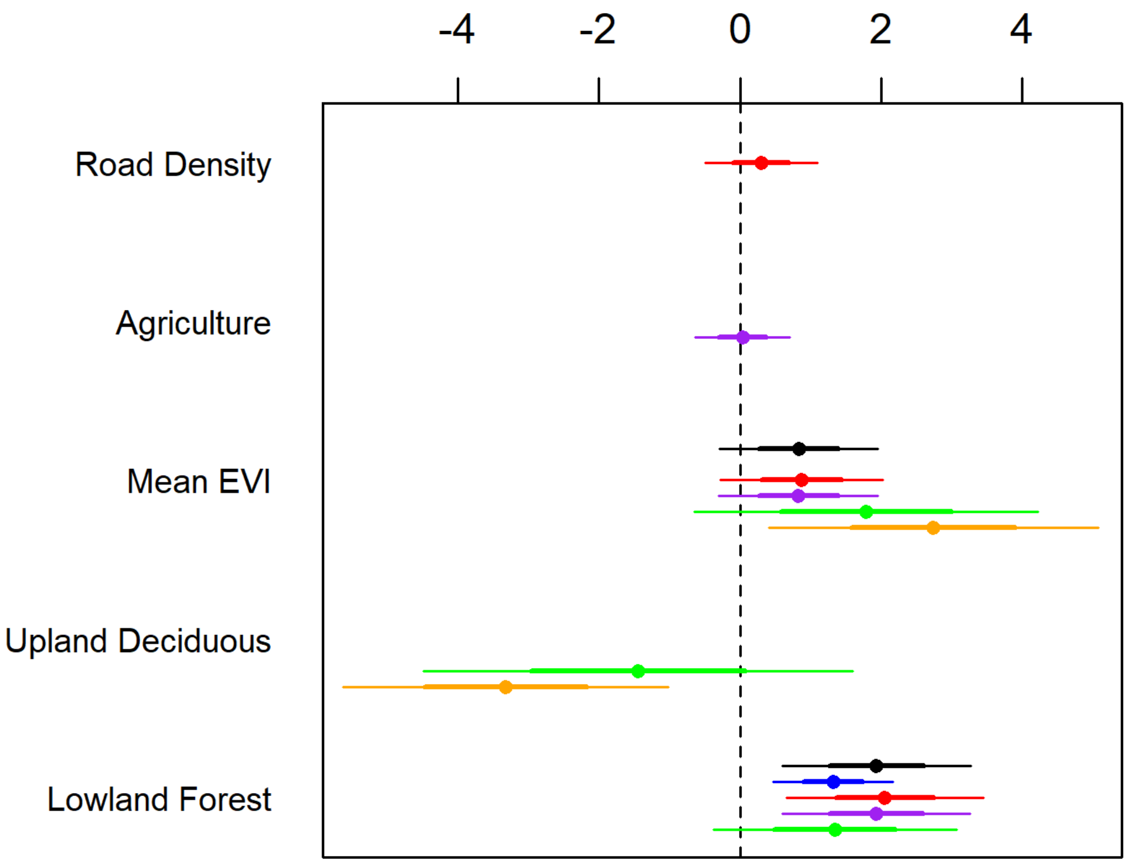


Figure 12. Scaled ($\bar{x}$ = 0, SD = 1) beta (β) coefficients from all competing models (ΔAIC ≤ 2.00; Table 5) and their 95% confidence intervals, where overlapping zero suggests non-significance (i.e., poor explanatory power; α = 0.05). Colors correspond to covariates appearing in the same model together (e.g., black points/lines display results from the top ranked model Ψ(LF + MeanEVI)). Model rank is displayed in order of top to bottom (i.e., black>blue>red>etc.). Increasing and decreasing coefficient values away from zero correspond to an increasing and decreasing relative magnitude of effect among covariates on probability of habitat use, respectively.

Occupancy modeling predicted that black bears have a significantly (α ≤ 0.05) greater probability of using lowland forests (left) than upland deciduous forests (right). The left photo shows a female black bear detected at station 41 along the northern end of the Pleasantview Swamp and the right photo shows another female bear detected at station 31 on State Forest land dominated by upland deciduous forest. Note that sex was determined by dependent young visible in other images.

forest exceeded about 21% (Figure 14). Likewise, the probability of a site being used by a black bear across the surveyed range of mean EVI values (1945 – 6140) was 0.06 (SE = 0.09) to 0.67 (SE = 0.18, Figure 13). Overall probability of bear habitat use derived from the top supported model was 0.41 (95% CI = 0.24–0.61) and overall detection probability was 0.12 (95% CI = 0.08–0.21).

Applying the top model across the observed values of site-specific covariates (i.e., lowland forest and mean EVI) and the observed bear detection histories at each site, we estimated the conditional occupancy state for each camera site (Figure 15a). This estimate represents our “best guess” of whether a surveyed site was used or not used by a black bear at least 1 time during the survey period (Kery and Royle 2015). Note that if a bear was detected at a site at least once, its probability of bear habitat use is exactly 1.0 with zero uncertainty, whereas sites that did not detect a black bear may have a probability of habitat use ≥ 0 but < 1.0. These sites are of particular interest because they demonstrate the expected occupancy probability based on a site’s percent lowland forest and mean EVI, the detection probability at a given site, and the number of times (i.e., days) a site was surveyed. Importantly, only camera sites that did not detect black bear but had a high proportion of lowland forest received a high conditional occupancy probability. Only 2 sites in Wilderness State Park (station 60 and 61) met this condition, receiving an occupancy probability of 0.76 and 0.87 (Figure 15a).

In contrast, the predicted occupancy (Figure 15b) represents the expected probability of habitat use for a site that is not conditioned on the observed data, but instead derived from the same statistical population of sites having the same given covariate values (lowland forest, mean EVI). Therefore, camera sites that had a positive black bear detection may have a predicted occupancy probability < 1.0, because its probability is now a function of the top supported model and a site’s given covariate values, rather than the observed site-level bear detection histories. This result demonstrates the important influence of lowland forest in predicting black bear habitat use, where only sites located in the largest blocks of lowland forest received a predicted probability of habitat use ≥ 0.80 (Figure 15b, red grid cells).

Predicting Species Distribution Across The Study Area

The predicted site-level occupancy provides the process by which we predicted bear habitat use throughout the Reservation (Figure 16). This map demonstrates the dominant positive influence of lowland forest on predicted black bear distribution and habitat use. Note that black bear distribution is represented in terms of the estimated probability of at least 1 black bear using each 900-m^2 raster cell based on the calculated percent lowland forest and mean EVI within a 4-km^2 buffer around each raster cell (MacKenzie et al. 2018). That is, the predicted probability of habitat use if a camera trap was placed at the center of every 900-m^2 raster cell within the Reservation. This map improves upon the site-level predicted bear habitat use map (Figure 15b) by visualizing predicted habitat use based on physical landscape features and boundaries, rather than arbitrary grid cells. Inspection of regions dominated by upland deciduous forest and other landcover types illustrates the positive relationship between bear habitat use and mean EVI, where relatively greater predicted habitat use values are associated with greater mean EVI (i.e., upland deciduous forest; Figures 9 and 16).

We also present a map of the standard error and 95% confidence intervals of estimated black bear distribution (Figure 16), indicating where in the Reservation the model has greater or lower uncertainty about the predicted distribution of black bear with respect to the top supported model. This map illustrates the importance of lowland forest patch size to predicted bear habitat use. Smaller patches, for example in the southwest region, have slightly lower predicted habitat use and are associated with higher standard errors compared to the larger lowland forest patches of the Pleasantview Swamp and Wilderness State Park.

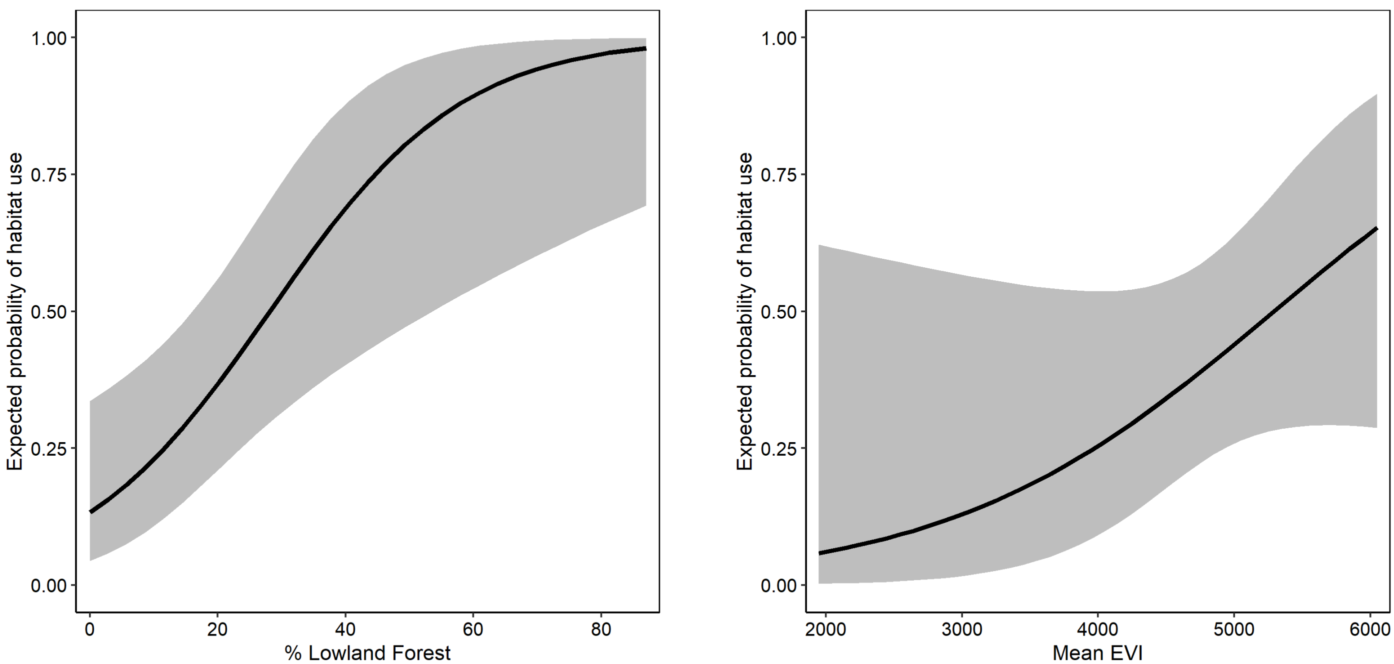


Figure 13. Change in expected probability of black bear habitat use as a function of top-ranked site covariates, including the percent of lowland forest within each surveyed 4-km^2 grid cell (left) and the mean Enhanced Vegetation Index within each grid cell (right). Gray bands represent 95% confidence intervals.

DISCUSSION

Modeling Habitat Use and Distribution

The observed detection data and predicted black bear habitat use from our top ranked model strongly support the hypothesis that black bear distribution and habitat use is driven primarily by the proportion of lowland forest at a 4-km^2 scale, with increasing use also associated with increasing primary productivity (mean EVI). We only tested the influence of landscape-level predictors at the 4-km^2 scale, but resource selection by black bears may occur at several scales (Johnson 1980) within and among bear age, sex, or reproductive status (Carter et al. 2010, Duquette et al. 2017, Long et al. 2011). The spatial scale we used to test habitat use and distribution metrics has been shown to be an important scale of habitat selection for core home ranges of female bears in this region (Carter et al. 2010, Norton 2019) and emphasizes the importance of our findings for female bears, a priority for conservation and management goals.

Lowland forests, including both hardwood and conifer swamp forests, are ecologically important landscapes for black bear forage, cover, reproduction, and denning requirements. These habitats support high forb and graminoid plant richness during the period coinciding with our survey (July–October) and may represent important summer forage for black bears

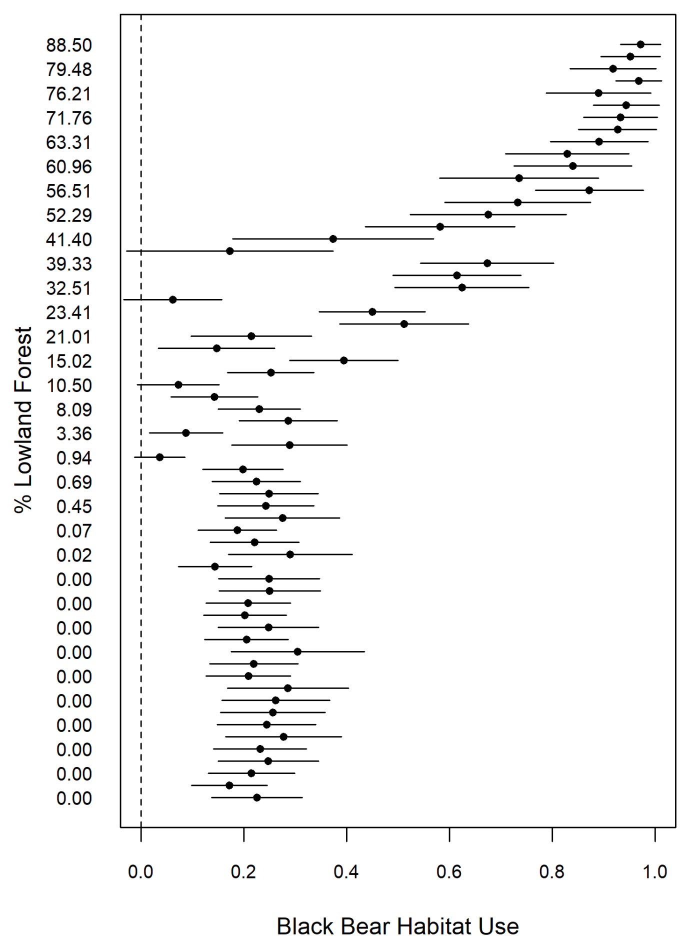


Figure 14. Expected site-specific probability of black bear habitat use (Ψ) in relation to the percent lowland forest cover within each grid cell. Derived from the top ranked model Ψ(LF + MeanEVI).

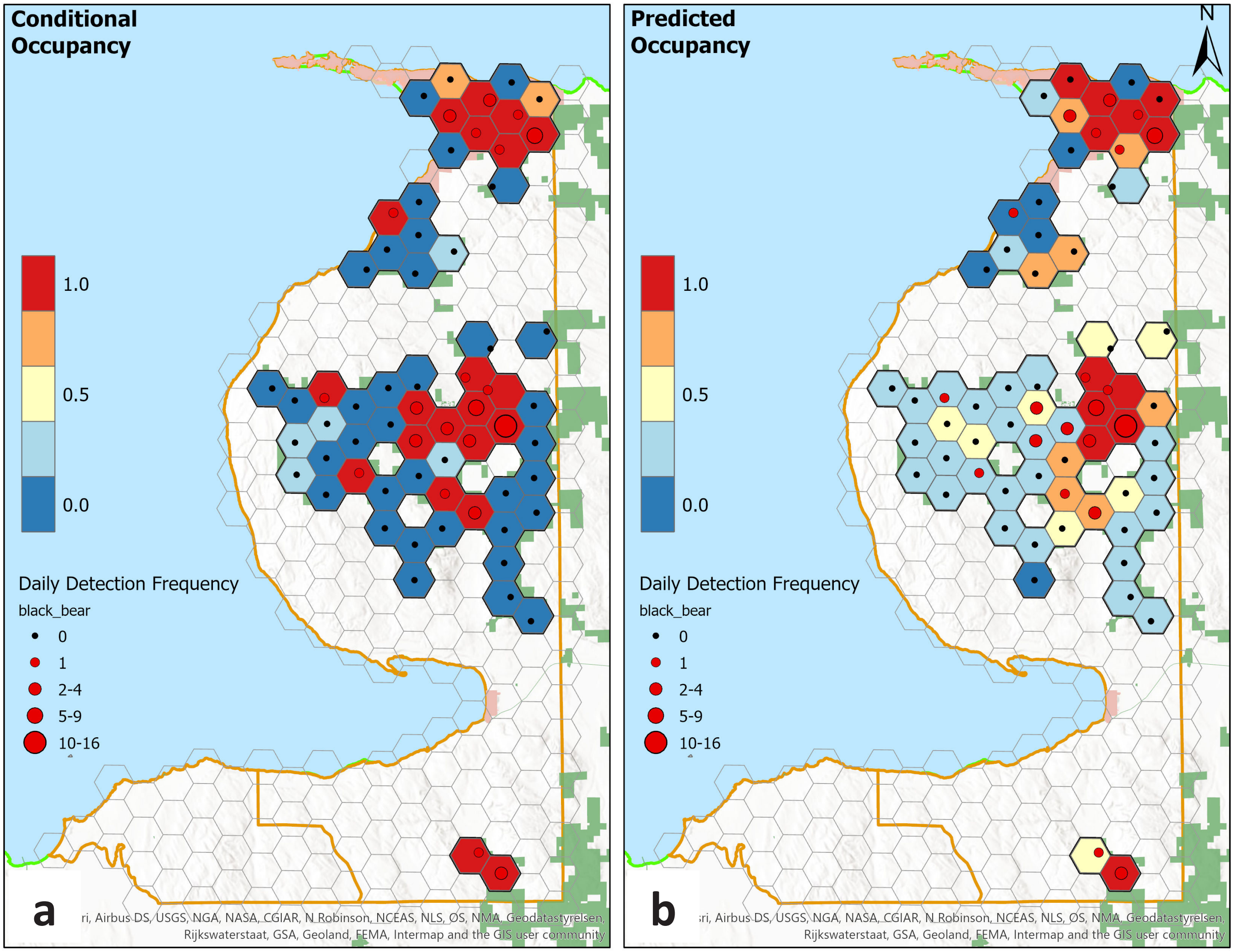


Figure 15. Map 'a' (left) represents our "best guess" of whether a surveyed site was used or not used by a black bear at least 1 time during the survey period based on the top model applied across observed values of covariates. Map 'b' (right) represents the expected probability of habitat use for a site that is not conditioned on the observed data.

(Noyce and Coy 1990). Vegetation productivity has been shown to be especially important for female black bear resource selection at multiple spatial scales (Duquette et al. 2017).

Lowland forests in northern Michigan are often associated with a high tree density and thick shrub layer and provide important thermal cover and refuge from anthropogenic disturbance in the surrounding upland landscape, particularly for female black bears with cubs (Fecske et al. 2002). Lowland forests represent some of the least modified and largest contiguous landscapes remaining in northern Michigan (Comer et al. 1995), and their persistence on the landscape may provide important generational denning habitat for female bears (Costello et al. 2008), provided suitable dry den sites are available within lowland forest complexes (Hellgren and Vaughan 1989, Kolensky and Strathearn 1987). Varying forest management practices of upland northern hardwood and mixed conifer stands occurring on State Forests, combined with greater human population density and activity, may affect bear resource selection (Norton 2019) and further increase the importance of secluded lowland forests to female bear habitat use. The apparent affinity of bear cub detections to the largest contiguous areas of lowland forest supports the hypothesis that this habitat has a high capacity to maximize food acquisition and minimize disturbance to reproducing female black bears in a landscape increasingly threatened by human population expansion and habitat fragmentation.

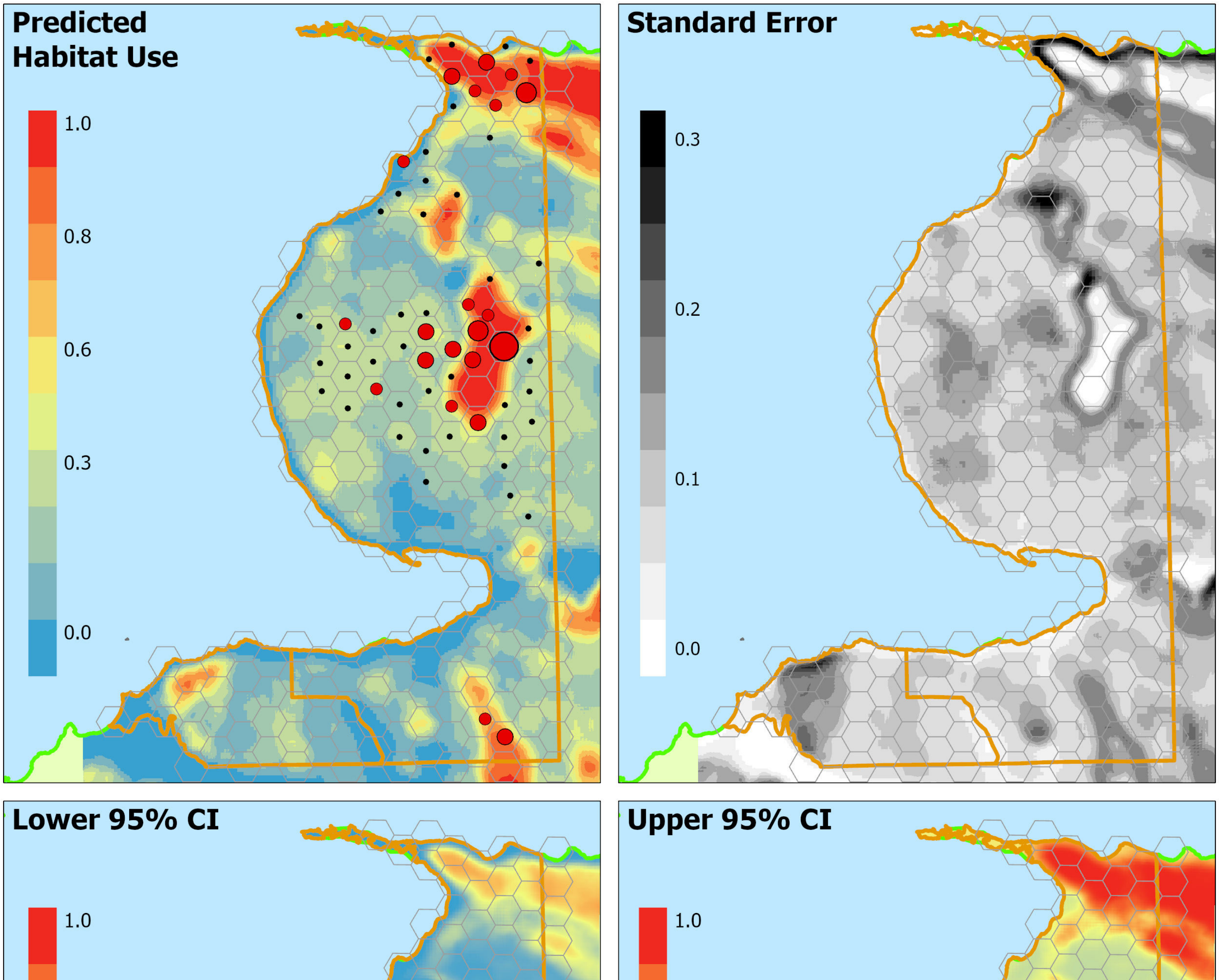


Figure 16. Predicted black bear distribution across the study area as a function of lowland forest and mean EVI at a 4-km^2 scale with daily detection frequencies overlaid (top left). Orange to red colors demonstrate the dominant positive influence of lowland forest on predicted black bear distribution and habitat use.

It is important to note that these results may be strongly seasonally dependent and may change markedly with seasonal shifts in bear resource selection (Lyons et al. 2003, Noyce and Garshelis 2011). Numerous studies have demonstrated the importance of landscape-scale habitat diversity and its relationship to spatiotemporal variation in food abundance to seasonal shifts in black bear habitat selection (Costello and Sage 1994, Samson and Huot 2002, Noyce and Garshelis 2011). Conducting the same survey during the fall season (September – December) may yield disparate estimates of habitat use as black bears migrate into upland deciduous forests when hard mast becomes increasingly available and important during a time of hyperphagia prior to winter denning (Norton 2019, Rogers 1993, Sadeghpour and Ginnett 2011). Although anecdotal, few bear detections occurred in the upland deciduous forests west of the Pleasantview Swamp, and the most westward detections occurred in mid-August to mid-October. These sites also collected few repeated detections ($\overline{x} = 2.0$, range = 1–4), suggesting this area may have contained mostly transient individuals searching for abundant fall mast crops during the latter half of our survey period.

Model selection results supported lowland forest over upland deciduous forest as an explanatory driver of bear habitat use. Although upland deciduous forest was included in 2 competing models, its influence on bear use was only significant when not combined with lowland forest. Therefore, inclusion of upland deciduous forest cover was confounded with lowland forest cover and was therefore uninformative for prediction of bear habitat use. That is, lowland forest better accounted for the observed spatial variance in bear detections. As already noted, this outcome is likely mediated by the interacting effects of seasonal food availability and habitat refuges associated with lowland forest during our survey period. Several studies have found the hard mast resource associated with upland deciduous forests to be important components of black bear resource selection (Lyons et al. 2003, MacFarland 2009, Rogers 1993), and we stress that the results of this survey do not imply that upland deciduous forests are not important black bear habitat components in our study area, just that our survey did not encompass the range of seasonally dependent drivers of spatial resource selection.

Although our measure of primary productivity (mean EVI) had a non-significant positive effect on predicted bear habitat use, its inclusion in the top ranked model demonstrates the overall importance of areas rich in plant matter to bear ecology (Costello et al. 2001). Its inclusion, but lack of significance, may provide further support for the importance of lowland forests. Areas of greatest mean EVI corresponded primarily to upland deciduous forests in the western portion of the surveyed State Forest land and represent areas of early successional to maturing managed forests that likely provide an important source of soft mast during mid to late summer. Though the lowland forests had relatively low mean EVI and may provide lower fruit production (Noyce and Coy 1990), the increase in realized or perceived safety of the secluded and dense lowland forests and accessible forage may outweigh the food resources associated with areas of greater primary productivity. Alternatively, these areas of higher mean EVI may represent high primary productivity that is inaccessible to black bear. Many of the upland deciduous stands in the study area were characterized by high maple (*Acer* spp.) canopy cover (high EVI), but low herbaceous ground cover and richness (Noyce and Coy 1990). Therefore, these areas may be used less until hard mast becomes available in the fall.

Forest pests and diseases may have substantial current and future impacts on black bear ecology in the NLP. Northern Michigan's upland deciduous forests are extensively impacted by beech bark disease (*Cryptococcus fagi*) and oak wilt (*Ceratocystis fagacearum*), diseases that are decimating American beech (*Fagus grandifolia*) and oak (*Quercus* spp.) populations in the Midwest (Houston 1994, Menges et al. 1984). In forests where these tree species are dominant components of the canopy, these diseases have the potential to greatly impact hard mast availability and forest composition for black bear and other wildlife species that depend on this resource (MI DNR 2017). Although beech bark disease has already greatly impacted forests throughout our study area, having a baseline estimate of bear habitat use for the region may provide an effective means for assessing landscape level impacts of current or future forest pests and diseases.

The percentage of agricultural land around camera sites was not supported as a predictor of bear habitat use in our study area. Black bears are known to use agricultural lands that provide seasonal forage but were selected less than available forested habitats

(Fecske et al. 2002). Given the low availability of agricultural cover types within our surveyed area, it's not surprising that this resource was not supported at the resolution of our model's predictive power.

Black bears used lowland forest cover disproportionately to its availability across the surveyed landscape. Although we did not formally assess habitat selection or preference during this study, it is important to recognize how a population appears to be distributed over the landscape relative to the proportions of available potential habitat in the study area. The strong relationship between cub detections and lowland forest also suggests lowland forest has high importance to bear reproductive success (Garshelis 2000). That is, lowland forest may contribute more to the sustenance of the bear population relative to other available and more extensive habitats. However, our spatiotemporal study design may have affected inference of bear habitat selection. For example, the timing and duration of our study may have precluded observations of bear using upland deciduous forest to the same or greater extent as lowland forest. Therefore, we can conclude that bear display at least partial selection for lowland forest during July to October, but do not necessarily avoid upland deciduous forest throughout the non-denning period (Garshelis 2000).

This population's apparent fidelity to lowland forests may in part be a function of bear density within the study area. The ideal free distribution hypothesis predicts that animals will use habitat such that it maximizes access to resources while minimizing risk, but at high population density individuals may be forced to use less suitable habitat (Fretwell and Lucas 1969). Likewise, at low densities animals may show strong selection for better habitat. If lowland forests provide the greatest access to resources that benefit their fitness (e.g., forage quality) while minimizing risk (e.g., dense cover), then this area's black bear habitat may be unsaturated (i.e., low density). If this hypothesis is supported, the predicted pattern of habitat use from our occupancy model suggests that during summer and early fall this black bear population selects for lowland forests because resource competition is minimal (Sollmann et al. 2016). If this population occurred at high density, we might expect to see more evenly distributed detections across available bear habitat. This hypothesis makes the strong conclusion that surveyed habitats predicted to be used less frequently than lowland forest are considered low quality. However, when bear density is low, in the context of the ideal free distribution hypothesis, we contend that bear habitat selection may vary by season and density, permitting habitat types to be considered "low quality" in one season, but not necessarily in another. Although no estimate of density is currently available at the resolution of the Reservation, the density of hunter harvest records can serve as a proxy for bear density (Draheim et al. 2016). The distribution of hunter harvested bears during 2002–2010 (see Waples et al. 2018 Figure 1) appears to correspond closely with the distribution of lowland forests within the Reservation and generally supports our conclusion of density dependent habitat selection. We note, however, that only a coarse assessment of harvested bear locations was available via Waples et al. (2018) and that its relationship to our results is purely anecdotal.

Although road density was not an important predictor of bear habitat use in our study area, this metric has been found to influence bear resource use throughout their range (Brody and Pelton 1989, Carter et al. 2010, Duquette et al. 2017). There are several reasons why road density lacked predictive support in our models. The range of surveyed road densities did not represent the high end of the range of road densities found throughout the Reservation, confounding our ability to infer the effect of high road density on bear habitat use. Additionally, our analysis did not segregate predictors of habitat use by sex-age class. Carter et al. (2010) found that bear use of roads differed between adult and sub-adult bears. The complex relationship between bear sex-age class and reproductive status with road density and road type, along with the interaction of spatiotemporal scale-dependent habitat selection, make discerning positive or negative effects of roads challenging without detailed, and possibly long-term, research (Duquette et al. 2017). Although it is possible to segregate camera trap data by coarse age class (e.g., adult vs. subadult) and reproductive status (e.g., with or without dependent young), the small sample size and short duration of this single-season survey would preclude meaningful inference.

Although not within the scope of this study, our results highlight the potential importance of contiguous expanses of lowland forest to serve as dispersal corridors across the NLP (Figure 17). These areas span eastward across the NLP from the Pleasantview

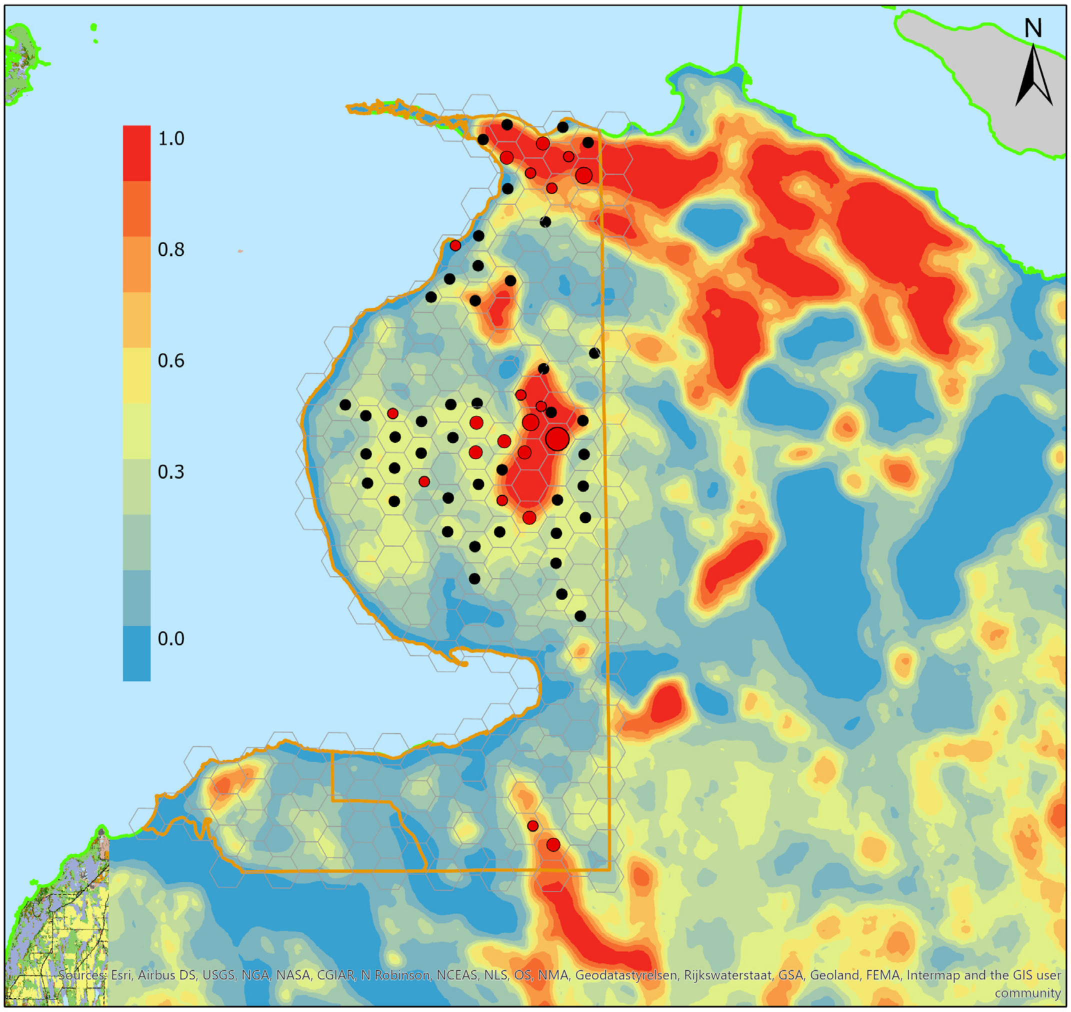


Figure 17. Predicted black bear distribution as a function of lowland forest and mean EVI extended throughout a larger area of the NLP to highlight potentially important dispersal corridors. Note that inference from this map should be used with caution due to extrapolation issues beyond the study area.

Swamp and Wilderness State Park, reaching large tracts of State Forest embedded in a matrix of roads and developed lands. Travel corridors are important landscape features for large carnivores because they mediate potentially risky travel through increasingly fragmented landscapes (Shepherd and Whittington 2006). These extensive lowland forests and wetland complexes may represent critical habitat connectivity across the Red Oak BMU and we emphasize the utility of camera traps and occupancy models to detect and make large scale predictions about habitat use and connectivity. However, we caution that this inference extends beyond the intended boundary of our study area and that the reliability of this extrapolation declines with increasing distance from our study area. For example, changing proportions and types of land cover may result in differential habitat use, which may also be used differently across changing bear density.

Interestingly and importantly, our results are consistent with recent findings of bear source-sink dynamics as inferred from individual-based genetic net flux graphs (Draheim et al. 2016). This research correlated genetic source-sink dynamics with habitat suitability throughout the NLP, identifying landscape-level regions of low to high genetic flow (i.e., landscape connectivity). Their models identified the Pleasantview Swamp, Wilderness State Park, and the Bear River complex as having moderate to high genetic connectivity (see Draheim et al. 2016 Figure 2a), precisely the same regions important to bear habitat use identified through our camera trap-based occupancy model. The combined inference from our study and Draheim et al. (2016) substantiates our predicted importance of lowland forest complexes in the NLP for maintaining bear landscape and genetic connectivity. Taken together, these studies contribute to a growing body of research important to understanding black bear ecology in the NLP and provide resource managers invaluable information on monitoring and managing bear habitat and population demographics.

We calculated a relative abundance index for each site as a reference to traditional methods of analyzing presence/absence data in relation to sampling effort (O'Brien et al. 2003). However, we stress that these relative abundances are strictly indices based on photographic rates and their influence by movement patterns, camera trap setup, habitat location, and various other factors confound the relationship between RAI and true abundance. We do not recommend comparing these values across study areas or species or using these values to inform management objectives (Sollmann 2018). Rather, we recommend basing inferences on black bear habitat use and population status (i.e., predicted distribution) from our occupancy models that explicitly account for imperfect detection and sampling biases (Kery and Royle 2015). Although abundance and occupancy should correlate empirically (i.e., if occupancy is > 0, abundance is ≥ 1), changes in abundance are not necessarily detected within an occupancy framework, especially for wide ranging species (e.g., large carnivores) that violate occupancy model assumptions of closure and site independence (MacKenzie et al. 2018, Sollmann 2018). We note that advanced model extensions to the occupancy framework and other statistical methods for detection/non-detection data are evolving rapidly and may soon be capable of estimating abundance and/or density from wide-ranging animals with high precision and accuracy (Evans and Rittenhouse 2018, Kery and Royle 2015, Joseph et al. 2009, Royle and Nichols 2003).

A young black bear detected at station 9 along the southern end of the Pleasantview Swamp.

Nearly all detections of dependent young occurred within dense lowland forests that provide important cover and forage during a time when mortality risk is greatest.

Conclusions and Management Recommendations

Understanding wildlife distribution and habitat use patterns that influence distribution is challenging for highly mobile species, but important for implementing successful landscape scale conservation strategies. Occupancy models provide a robust foundation for estimating these population parameters while accounting for imperfect detection. Using occupancy models and camera traps, our study revealed landscape level habitat features important for black bear habitat use and distribution. Specifically, these results emphasize the importance of protecting large tracts of lowland forest with connectivity to eastern complexes, while maintaining upland forests surrounding lowlands that provide seasonally diverse soft and hard mast forage.

Management targeted towards maintaining or increasing female bear population density and cub survival should focus on protecting large, contiguous forested wetlands and enhancing understory cover and forage within surrounding upland forested cover types that together provide seasonally important and diverse bear forage (Lariviere 2001, Fecske et al. 2002). By focusing management efforts on altering food diversity, abundance, and spatiotemporal distribution, in addition to harvest regulations, land and wildlife managers can affect black bear population dynamics (Noyce and Coy 1990).

The spatial distribution of predicted bear habitat use suggests this region of the NLP may harbor a low-density population persisting below habitat saturation levels. Although we do not present abundance estimates of black bear, we suggest bear harvest in this area should be conservative if management objectives are to maintain or increase abundance within the Reservation. Facilitating bear population growth or maintenance may best be achieved by maintaining contiguous corridors of lowland forest occurring throughout the study area. Specifically, the potential corridor along the southern study area encompassing the Bear River, along the West Branch Maple River connecting the Pleasantview Swamp with the lowland forest complexes to the east, and between Wilderness State Park and the large lowland forests to the east in Cheboygan county should be maintained or protected.

Understanding where bears occur and are most likely to occur based on various landscape-scale factors is important for implementing proactive management strategies and knowing where to focus limited resources towards effective bear management and conservation. Strategies may include where to direct land conservation and restoration efforts (Long et al. 2011) and where to implement targeted and effective nuisance bear control (McFadden-Hiller et al. 2016, Wilton et al. 2014a).

By combining camera trap-based occupancy surveys randomly distributed across our study area, we were able to produce robust estimates of black bear habitat use and distribution at a meaningful scale. Moreover, our study design and modeling framework permitted the prediction of bear habitat use across every pixel of a landscape of interest, producing a seamless species distribution map that is a function of important ecological drivers of black bear distribution. This survey and statistical methodology can be applied to the estimation of habitat use and distribution of species that are highly mobile, elusive, or logistically prohibitive to monitor with more intensive methods.

Although our results appear robust and support the literature on black bear ecology, we recommend testing several additional covariates that may further explain and refine black bear habitat use, including forest patch size, fragmentation index, distance to core lowland forest patch, size of core lowland forest patch, distance to road, and available forest management treatments. In addition, it may be important to test the effect of habitat covariates on bear habitat use at multiple spatial scales.

Future work involving camera traps for any species detected by this method can leverage the existing sampling design and methodology presented in this project. In this regard, camera traps have the distinct advantage of simultaneously sampling numerous terrestrial mammalian and avian species over large spatial scales. By shifting survey efforts away from a single species target to a broad surveillance monitoring framework, researchers and managers can compare predictors of population trends across many species using the same methodology (Steenweg et al. 2016). This is particularly beneficial for monitoring entire animal communities, whose distributions are increasingly affected by fragmentation, climate change, disease, and invasive species, processes of which occupancy models and their extensions are well equipped to describe (Kery and Royle 2015, Long et al. 2011). To help mitigate the impact of these risks to population viability, further efforts to apply this methodology may best be directed at identifying functional landscape connectivity, or lack thereof, for species of interest at regional (e.g., NLP) or population-level scales.

A mature male black bear, often accompanied by a female, detected at station 33 in the Pleasantview Swamp.

LTBB Odawa and MNFI staff deploying camera traps in Wilderness State Park and State Forest land within the Reservation.

REFERENCES

Allen ML, Morales MJ, Wheeler M, Clare JDJ, Mueller MA, Olson LO, Pemble K, Olson ER, Van Stappen J, Van Deelen TR (2017) Survey techniques and community dynamics of the carnivore guild in the Apostle Islands National Lakeshore (2014-2017). Final Report to the National Park Service 64 pp.

Arnold TW (2010) Uninformative parameters and model selection using Akaike's Information Criterion. Journal of Wildlife Management 74, 1175–1178. https://doi.org/10.2193/2009-367.

Ballantyne C (2008) McCain's beef with bears? pork. Scientific American. Nature America Inc. (http://www.scientificamerican.com/article/mccains-beef-with-bears/).

Brody AJ, Pelton MR (1989) Effects of roads on black bear movements in western North Carolina. Wildlife Society Bulletin 17: 5–10.

Burnham KP, Anderson DR (1998) Model selection and inference: a practical information-theoretic approach. New York: Springer; 1998.

Carter NH, Brown DG, Etter DR, Visser LG (2010) American black bear habitat selection in northern Lower Peninsula, Michigan, USA, using discrete choice modeling. Ursus 21: 57–71.

Comer PJ, Albert DA, Wells HA, Hart BL, Raab JB, Price DL, Kashian DM, Corner RA, Schuen DW (1995) Michigan's presettlement vegetation, as interpreted from the General Land Office surveys 1816-1856. Michigan Natural Features Inventory, Lansing, MI. 76 pp.

Conroy MJ (1996) Abundance indices. In Measuring and monitoring biological diversity: standard methods for mammals: 179–192. Wilson D. E., Cole, F. R., Nichols, J. D., Rudran R. & Foster, M. S. (Eds). Washington DC: Smithsonian Institution Press.

Costello CM, Creel SR, Kalinowski ST, Vu NV, Quigley HB (2008) Sex-biased natal dispersal and inbreeding avoidance in American black bears as revealed by spatial genetic analyses. Molecular Ecology 17:4713–4723.

Costello CM, Jones DE, Green Hammond KA, Inman RM, Inman KH, Thompson BC, Deitner RA, Quigley HB (2001) A Study of Black Bear Ecology in New Mexico With Models for Population Dynamics and Habitat Suitabiltiy (Final Report No. W-131-R), Federal Aid in Wildlife Restoration Project. New Mexico Department of Game and Fish, Santa Fe, New Mexico, USA.

Costello CM, Sage RW Jr (1994) Predicting black bear habitat selection from food abundance under 3 forest management systems. Bears: Their Biology and Management 9, 375–387.

Draheim HM, Moore JA, Etter D, Winterstein SR Scribner KT (2016) Detecting black bear source–sink dynamics using individual-based genetic graphs. Proc R Soc London B. 283:20161002.

Dreher BP, Winterstein SR, Scribner KT, Lukacs PM, Etter DR, Rosa GJ, Lopez VA, Libants S, Filcek KB (2007) Noninvasive estimation of black bear abundance incorporating genotyping errors and harvested bear. The Journal of Wildlife Management 71: 2684–2693.

Eagle TC, Pelton MR (1983) Seasonal nutrition of black bears in the Great Smoky Mountains National Park. International Conference on Bear Research and Management 5: 94–101.

Erb PL, McShea WJ, Guralnick RP (2012) Anthropogenic influences on macro-level mammal occupancy in the Appalachian Trail corridor. PLoS ONE 7(8): e42574. doi:10.1371/journal.pone.0042574.

Etter DR, Mayhew SL (2008) 2005 Northern Lower Peninsula bear genetic capture-recapture survey. Wildlife Division Report No. 3490. Michigan Department of Natural Resources.

Evans M, Rittenhouse TAG (2018). Evaluating spatially explicit density estimates of unmarked wildlife detected by remote cameras. J Appl Ecol. 2018: 1–10.

Fecske DM, Barry RE, Precht FL, Quigley HB, Bittner SL, Webster T (2002) Habitat use by female black bears in western Maryland. Southeastern Naturalist 1:77–92.

Fretwell SD, Lucas HLJ (1969) On territorial behaviour and other factors influencing habitat distribution in birds. Acta Biotheoretica 19:16–36.

Garshelis DL (2000) Delusions in habitat evaluation: measuring use, selection, and importance. In: Boitani, L., Fuller, T.K. (Eds.), Research Techniques in Animal Ecology: Controversies and Consequences. Columbia University Press, New York, pp. 111–164.

Gould MJ, Gould WR, Cain JW III, Roemer GW (2019) Validating the performance of occupancy models for estimating habitat use and predicting the distribution of highly-mobile species: A case study using the American black bear. Biological Conservation 234 (2019) 28–36.

Hall LS, Krausman PR, Morrison ML (1997) The habitat concept and a plea for standard terminology. Wildlife Society Bulletin 25: 173–182.

Hayes DB, Monfils MJ (2015) Occupancy modeling of bird point counts: implications of mobile animals. The Journal of Wildlife Management. DOI: 10.1002/jwmg.943.

He F, Gaston KJ (2000) Estimating species abundance from occurrence. The American Naturalist 156, 553–559.

Hellgren EC, Vaughan MR (1989). Denning Ecology of Black Bears in a Southeastern Wetland. The Journal of Wildlife Management 53(2):347–353.

Houston DR (1994) Major new tree disease epidemics: beech bark disease. Annual Review of Phytopathology 32(1):75–87.

Huete A, Didan K, Miura T, Rodriguez EP, Gao X, Ferreira LG (2002) Overview of the radiometric and biophysical performance of the MODIS vegetation indices. Remote Sensing of Environment 83, 195–213.

Johnson DH (1980) The comparison of usage and availability measurements for evaluating resource preference. Ecology 61: 65–71.

Joseph LN, Elkin C, Martin TG, Possingham HP (2009) Modeling abundance using N-mixture models: the importance of considering ecological mechanisms. Ecological Applications 19(3):631–42.

Kery M, Royle JA (2016) Applied hierarchical modeling in ecology: analysis of distribution, abundance and species richness in R and BUGS; volume 1 – prelude and static models. Academic Press.

Kolenosky GB, Strathearn SM (1987) Winter denning of black bears in east-central Ontario. Int. Conf. Bear Res.& Manage. 7:305-16.

Larivière S (2001) Ursus americanus. Mammalian Species 647: 1–11.

Long RA, Donovan TM, MacKay P, Zielinski WJ, Buzas JS (2011) Predicting carnivore occurrence with noninvasive surveys and occupancy modeling. Landscape Ecology 26:327–340.

Lyons AL, Gaines WL, Servheen C (2003) Black bear resource selection in the northeast Cascades, Washington. Biological Conservation 113: 55-62.

Macfarland DM (2009) Population estimation, habitat associations and range expansion of black bears in the upper Midwest. Dissertation, University of Wisconsin, Madison, Wisconsin, USA.

MacKenzie DI (2006) Modeling the probability of resource use: the effect of, and dealing with, detecting a species imperfectly. The Journal of Wildlife Management 70, 367–374.

MacKenzie DI, Bailey LL (2004) Assessing the fit of site-occupancy models. J. Agric. Biol. Environ. Stat. 9, 300e318.

MacKenzie DI, Nichols JD, Lachman GB, Droege S, Royle JA, Langtimm CA (2002) Estimating site occupancy rates when detection probabilities are less than one. Ecology 83:2248–2255.

MacKenzie DI, Nichols JD, Royle JA, Pollock KH, Bailey LL, Hines JE (2018) Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence Second Edition. Academic Press.

MacKenzie DI, Nichols JD, Sutton N, Kawanishi K, Bailey LL (2005) Improving inferences in population studies of rare species that are detected imperfectly. Ecology 86, 1101e1113.

Maehr DS (1997) The comparative ecology of bobcat, black bear, and Florida panther in south Florida. Bulletin of the Florida Museum of Natural History 40, 1–176.

McFadden-Hiller JE, Beyer DE, Jr., Belant JL (2016) Spatial distribution of black bear incident reports in Michigan. PLoS ONE 11(4): e0154474. doi:10.1371/journal.pone.0154474.

Menges ES, Loucks OL (1984) Modeling a disease-caused patch disturbance: Oak wilt in the midwestern United States. Ecology 65(2):487-98.

Merkle JA, Robinson HS, Krausman PR, Alaback P (2013) Food availability and foraging near human developments by black bears. Journal of Mammalogy 94, 378–385.

Michigan Department of Natural Resources (2008a) A review of bear management in Michigan. White Paper 33 pp.

Michigan Department of Natural Resources (2008b) Michigan black bear management plan. Wildlife Division Report No. 3497. Michigan Department of Natural Resources.

Michigan Department of Natural Resources (2017) Michigan white-tailed deer stand specific habitat management guidelines.

Moore JA, Draheim HM, Etter D, Winterstein S, Scribner KT (2014) Application of large-scale parentage analysis for investigating natal dispersal in highly vagile vertebrates: a case study of American black bears (Ursus americanus). PLoS ONE 9, e91168. (doi:10.1371/journal.pone.0091168).

Niedballa J, Sollmann R, Courtiol A, Wilting A (2016) camtrapR: an R package for efficient camera trap data management Methods in Ecology and Evolution 2016, 7, 1457–1462.

Nijland, W, Bolton DK, Coops NC, Stenhouse G (2016) Imaging phenology: scaling from camera plots to landscapes. Remote Sensing of Environment 177, 13–20.

Norton DC (2019) Effects of infanticide risk and timber harvest on American black bear space use. MS Thesis, Northern Michigan University, Michigan, USA.

Norton DC, Belant JL, Bruggink JG, Beyer DE, Jr., Svoboda NJ, Petroelje TR (2018) Female American black bears do not alter space use or movements to reduce infanticide risk. PLoS ONE 13(9): e0203651.

Noyce KV, Coy PL (1990) Abundance and productivity of bear food species in different forest types of northcentral Minnesota. Int Conf Bear Res Manage 8:169–181 .

Noyce KV, Garshelis DL (2011) Seasonal migrations of black bears (Ursus americanus): causes and consequences. Behav Ecol Sociobiol 65: 823–835.

O'Brien TG, Kinnaird MF, Wibisono HT (2003) Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. Animal Conservation 6(2): 131–139.

Pelton MR, Coley AB, Eason TH, Martinez DD, Pederson JA, van Manen FT, Weaver KM (1999) American black bear conservation action plan. Pages 144–156 in Servheen C, Herrero S, and Peyton B, compilers. Bears. Status survey and conservation action plan. International Union for Conservation of Nature / Species Survival Commission bear and polar bear specialist groups. International Union for Conservation of Nature, Gland, Switzerland; and Cambridge, England, UK.

Rogers LL (1993) The role of habitat quality in the natural regulation of black bear populations. Proc. 4th Western Black Bear Workshop: 95–102. Yosemite National Park, California. Technical Report NPS/NRWR/NRTR-93/12.

Rollins MG (2009) LANDFIRE: a nationally consistent vegetation, wildland fire, and fuel assessment. Int. J. Wildland Fire 18, 235–249. https://doi.org/10.1071/WF08088.

Royle JA, Nichols JD (2003) Estimating abundance from repeated presence–absence data or point counts. Ecology 84: 777–790.

Ripple WJ, Estes JA, Beschta RL, Wilmers CC, Ritchie EG, Hebblewhite M, Berger J, Elmhagen B, Letnic M, Nelson MP, Schmitz OJ, Smith DW, Wallach AD, Wirsing AJ (2014) Status and ecological effects of the world's largest carnivores. Science 343(6167): 1241484. DOI: 10.1126/science.1241484.

Sadeghpour MH, Ginnett TF (2011) Habitat selection by female American black bears in northern Wisconsin. Ursus 22(2):159–166.

Samson C, Huot J (2001) Spatial and temporal interactions between female American black bears in mixed forests of eastern Canada. Can. J. Zool. 79: 633–641.

Shepherd B, Whittington J (2006) Response of wolves to corridor restoration and human use management. Ecol. Soc. 11: 1. doi:10.5751/ES-01813-110201.

Sollmann R (2018) A gentle introduction to camera-trap data analysis. African Journal of Ecology 56:740–749, 10.1111/aje.12557.

Sollmann R, Gardner B, Belant JL, Wilton CM, Beringer J (2016) Habitat associations in a recolonizing, low-density black bear population. Ecosphere 7(8):e01406. 10.1002/ecs2.1406

Steenweg R, Hebblewhite M, Kays R, Ahumada J, Fisher JT, Burton C, Townsend SE, Carbone C, Rowcliffe JM, Whittington J, Brodie J, Royle JA, Switalski A, Clevenger AP, Heim N, Rich LN (2016) Scaling up camera traps: monitoring the planet's biodiversity with networks of remote sensors. Front. Ecol. Environ. 15: 26–34.

Steenweg R, Whittington J, Hebblewhite M, Forshner A, Johnston B, Pertersen, D, Shephard B, Lukacs P. 2016. Camera-based occupancy monitoring at large scales: power to detect trends in grizzly bears across the Canadian Rockies. Biol Conserv 201: 192–200.

Terborgh J, Estes JA, Paquet P, Ralls K, Boyd-Heger D, Miller BJ, Noss RF (1999) The role of top carnivores in regulating terrestrial ecosystems. In: Soule´ ME, Terborgh J (eds) Continental conservation: scientific foundations of regional reserve networks. Island Press, Washington, pp 39–64.

U.S. Census Bureau (2010). County population data. https://data.census.gov/cedsci/. Accessed 01 March 2020.

Waples RS, Scribner KT, Moore JA, Draheim HM, Etter D, Boersen M (2018) Accounting for age structure and spatial structure in eco-evolutionary analyses of a large, mobile vertebrate. Journal of Heredity 2018: 1–15, doi:10.1093/jhered/esy018.

Wilton CM, Belant JL, Beringer J (2014a) Distribution of American black bear occurrences and human-bear incidents in Missouri. Ursus 25: 53–60.

Wilton CM, Puckett EE, Beringer J, Gardner B, Eggert LS, et al. (2014b) Trap array configuration influences estimates and precision of black bear density and abundance. PLoS ONE 9(10): e111257. doi:10.1371/journal.pone.0111257

Appendix I. Reclassification of LANDFIRE's existing vegetation classification used to estimate the percentage of each cover type class per 4-km^2 grid cell.

Group Name - Reclassified	Group Name - Original	Physiognomy
Agriculture	Agricultual-Aquaculture	Agricultural
Agriculture	Agricultural-Bush fruit and berries	Agricultural
Agriculture	Agricultural-Close Grown Crop	Agricultural
Agriculture	Agricultural-Fallow/Idle Cropland	Agricultural
Agriculture	Agricultural-Orchard	Agricultural
Agriculture	Agricultural-Pasture and Hayland	Agricultural
Agriculture	Agricultural-Row Crop	Agricultural
Agriculture	Agricultural-Row Crop-Close Grown Crop	Agricultural
Agriculture	Agricultural-Vineyard	Agricultural
Agriculture	Agricultural-Wheat	Agricultural
Developed	Developed-High Intensity	Developed-High Intensity
Developed	Developed-Low Intensity	Developed-Low Intensity
Developed	Developed-Medium Intensity	Developed-Medium Intensity
Developed	Quarries-Strip Mines-Gravel Pits-etc.	Quarries…
Developed-Lowland Forests	Developed-Wetland Mixed Forest	Developed
Developed-Mixed Forest	Developed-Upland Mixed Forest	Developed
Developed-Nonforested Lowland	Developed-Wetland Herbaceous	Developed
Developed-Nonforested Lowland	Developed-Wetland Shrubland	Developed
Developed-Nonforested Upland	Developed-Upland Herbaceous	Developed
Developed-Nonforested Upland	Developed-Upland Shrubland	Developed
Developed-Roads	Developed-Roads	Developed-Roads
Developed-Upland Deciduous Forest	Developed-Upland Deciduous Forest	Developed
Developed-Upland Evergreen Forest	Developed-Upland Evergreen Forest	Developed
Lowland Forest	Atlantic Swamp Forests	Riparian
Lowland Forest	Eastern Floodplain Forests	Riparian
Lowland Forest	Eastern Small Stream Riparian Forests	Riparian
Lowland Forest	Peatland Forests	Riparian
Managed Tree Plantation	Managed Tree Plantation	Conifer
Mixed Forest	Pine-Hemlock-Hardwood Forest	Conifer
Mixed Forest	Pine-Hemlock-Hardwood Forest	Conifer-Hardwood

Appendix I. continued...

Group Name - Reclassified	Group Name - Original	Physiognomy
Mixed Forest	Pine-Hemlock-Hardwood Forest	Hardwood
Mixed Forest	Spruce-Fir-Hardwood Forest	Conifer
Mixed Forest	Transitional Forest Vegetation	Conifer
Nonforested Wetland	Inland Marshes and Prairies	Riparian
Nonforested Wetland	Introduced Herbaceous Wetland Vegetation	Riparian
Nonforested Wetland	Wet Meadow	Riparian
Open Water	Open Water	Open Water
Other Forested	Hardwood Flatwoods	Hardwood
Other Forested	Ruderal Forest	Conifer-Hardwood
Other Nonforested	Atlantic Dunes and Grasslands	Grassland
Other Nonforested	Great Lakes Alvar	Shrubland
Other Nonforested	Introduced Perennial Grassland and Forbland	Exotic Herbaceous
Other Nonforested	Introduced Upland Vegetation-Shrub	Exotic Tree-Shrub
Other Nonforested	Sparse Vegetation	Sparsely Vegetated
Other Nonforested	Tallgrass Prairie	Grassland
Other Nonforested	Transitional Herbacous Vegetation	Grassland
Other Nonforested	Transitional Shrub Vegetation	Shrubland
Upland Conifer Forest	Jack Pine Forest	Conifer
Upland Conifer Forest	Jack Pine Forest	Conifer-Hardwood
Upland Conifer Forest	Jack Pine Forest	Hardwood
Upland Conifer Forest	Red Pine-White Pine Forest and Woodland	Conifer
Upland Conifer Forest	Red Pine-White Pine Forest and Woodland	Conifer-Hardwood
Upland Conifer Forest	Red Pine-White Pine Forest and Woodland	Hardwood
Upland Deciduous Forest	Aspen-Birch Forest	Hardwood
Upland Deciduous Forest	Beech-Maple-Basswood Forest	Hardwood
Upland Deciduous Forest	Black Oak Woodland and Savanna	Hardwood
Upland Deciduous Forest	Bur Oak Woodland and Savanna	Hardwood
Upland Deciduous Forest	White Oak-Red Oak-Hickory Forest	Hardwood
Upland Deciduous Forest	Yellow Birch-Sugar Maple Forest	Hardwood

Appendix II. A subset of focal animal species identified in camera trap images. Unique Events refers to the number of images taken of a given species that occurred at least 30 minutes apart (note that occupancy detections were based on daily detections and may differ from values here). Number of Stations refers to the number of unique camera sites where a species was detected.

Common Name	Order	Family	Species Name	Unique Events	Number of Stations
White-tailed Deer (buck)	Artiodactyla	Cervidae	*Odocoileus virginianus*	170	41
White-tailed Deer (all)	Artiodactyla	Cervidae	*Odocoileus virginianus*	1364	64
American Badger	Carnivora	Mustelidae	*Taxidea taxus*	20	14
American Black Bear	Carnivora	Ursidae	*Ursus americanus*	73	22[a]
American Marten	Carnivora	Mustelidae	*Martes americana*	3	3
American Mink	Carnivora	Mustelidae	*Neovison vison*	1	1
Bobcat	Carnivora	Felidae	*Lynx rufus*	32	13
Coyote	Carnivora	Canidae	*Canis latrans*	342	57
Fisher	Carnivora	Mustelidae	*Pekania pennanti*	2	1
Long-tailed Weasel & Short-tailed Weasel	Carnivora	Mustelidae	*Mustela frenata & Mustela erminea*	56	23
Red Fox	Carnivora	Canidae	*Vulpes vulpes*	53	17
Northern Flying Squirrel	Rodentia	Sciuridae	*Glaucomys sabrinus*	223	20
Other mammal[b]	NA	NA	*NA*	873	58
Small mammal[c]	NA	NA	*NA*	1886	54

[a] Includes detections at both cameras deployed in grid cell 41; number of unique sites for occupancy analysis is 21.

[b] Other mammal = raccoon, Virginia opossum, striped skunk, and North American porcupine.

[c] Small mammal = squirrel (except flying squirrel), rabbit, and small rodent (e.g., *Peromyscus* spp.)

Appendix III. Species-level classifications for focal carnivore species and their associated frequency of detections aggregated at 30-minute intervals at each camera trap station.

Station	Common Name	Order	Family	Species Name	Unique Events
station10	American Badger	Carnivora	Mustelidae	*Taxidea taxus*	2
station11	American Badger	Carnivora	Mustelidae	*Taxidea taxus*	3
station14	American Badger	Carnivora	Mustelidae	*Taxidea taxus*	2
station2	American Badger	Carnivora	Mustelidae	*Taxidea taxus*	1
station23	American Badger	Carnivora	Mustelidae	*Taxidea taxus*	1
station24	American Badger	Carnivora	Mustelidae	*Taxidea taxus*	2
station29	American Badger	Carnivora	Mustelidae	*Taxidea taxus*	1
station30	American Badger	Carnivora	Mustelidae	*Taxidea taxus*	1
station32	American Badger	Carnivora	Mustelidae	*Taxidea taxus*	1
station33	American Badger	Carnivora	Mustelidae	*Taxidea taxus*	1
station36	American Badger	Carnivora	Mustelidae	*Taxidea taxus*	1
station37	American Badger	Carnivora	Mustelidae	*Taxidea taxus*	1
station51	American Badger	Carnivora	Mustelidae	*Taxidea taxus*	1
station6	American Badger	Carnivora	Mustelidae	*Taxidea taxus*	2
station0	American Black Bear	Carnivora	Ursidae	*Ursus americanus*	1
station1	American Black Bear	Carnivora	Ursidae	*Ursus americanus*	2
station14	American Black Bear	Carnivora	Ursidae	*Ursus americanus*	1
station17	American Black Bear	Carnivora	Ursidae	*Ursus americanus*	1
station23	American Black Bear	Carnivora	Ursidae	*Ursus americanus*	2
station25	American Black Bear	Carnivora	Ursidae	*Ursus americanus*	2
station31	American Black Bear	Carnivora	Ursidae	*Ursus americanus*	7
station32	American Black Bear	Carnivora	Ursidae	*Ursus americanus*	2
station33	American Black Bear	Carnivora	Ursidae	*Ursus americanus*	11
station34	American Black Bear	Carnivora	Ursidae	*Ursus americanus*	17
station37	American Black Bear	Carnivora	Ursidae	*Ursus americanus*	1
station40	American Black Bear	Carnivora	Ursidae	*Ursus americanus*	1
station41	American Black Bear	Carnivora	Ursidae	*Ursus americanus*	1
station41x	American Black Bear	Carnivora	Ursidae	*Ursus americanus*	4
station49	American Black Bear	Carnivora	Ursidae	*Ursus americanus*	1
station53	American Black Bear	Carnivora	Ursidae	*Ursus americanus*	2
station54	American Black Bear	Carnivora	Ursidae	*Ursus americanus*	1
station55	American Black Bear	Carnivora	Ursidae	*Ursus americanus*	8
station57	American Black Bear	Carnivora	Ursidae	*Ursus americanus*	2
station58	American Black Bear	Carnivora	Ursidae	*Ursus americanus*	2
station59	American Black Bear	Carnivora	Ursidae	*Ursus americanus*	1
station9	American Black Bear	Carnivora	Ursidae	*Ursus americanus*	3
station11	American Marten	Carnivora	Mustelidae	*Martes americana*	1
station30	American Marten	Carnivora	Mustelidae	*Martes americana*	1
station31	American Marten	Carnivora	Mustelidae	*Martes americana*	1

Appendix III. continued...

Station	Common Name	Order	Family	Species Name	Unique Events
station9	American Mink	Carnivora	Mustelidae	*Neovison vison*	1
station1	Bobcat	Carnivora	Felidae	*Lynx rufus*	3
station18	Bobcat	Carnivora	Felidae	*Lynx rufus*	1
station32	Bobcat	Carnivora	Felidae	*Lynx rufus*	1
station45	Bobcat	Carnivora	Felidae	*Lynx rufus*	1
station46	Bobcat	Carnivora	Felidae	*Lynx rufus*	7
station47	Bobcat	Carnivora	Felidae	*Lynx rufus*	8
station49	Bobcat	Carnivora	Felidae	*Lynx rufus*	1
station52	Bobcat	Carnivora	Felidae	*Lynx rufus*	2
station59	Bobcat	Carnivora	Felidae	*Lynx rufus*	1
station6	Bobcat	Carnivora	Felidae	*Lynx rufus*	1
station60	Bobcat	Carnivora	Felidae	*Lynx rufus*	2
station62	Bobcat	Carnivora	Felidae	*Lynx rufus*	3
station9	Bobcat	Carnivora	Felidae	*Lynx rufus*	1
station0	Coyote	Carnivora	Canidae	*Canis latrans*	3
station1	Coyote	Carnivora	Canidae	*Canis latrans*	4
station11	Coyote	Carnivora	Canidae	*Canis latrans*	1
station12	Coyote	Carnivora	Canidae	*Canis latrans*	1
station13	Coyote	Carnivora	Canidae	*Canis latrans*	3
station14	Coyote	Carnivora	Canidae	*Canis latrans*	8
station16	Coyote	Carnivora	Canidae	*Canis latrans*	1
station17	Coyote	Carnivora	Canidae	*Canis latrans*	1
station18	Coyote	Carnivora	Canidae	*Canis latrans*	5
station2	Coyote	Carnivora	Canidae	*Canis latrans*	1
station20	Coyote	Carnivora	Canidae	*Canis latrans*	10
station21	Coyote	Carnivora	Canidae	*Canis latrans*	3
station22	Coyote	Carnivora	Canidae	*Canis latrans*	2
station23	Coyote	Carnivora	Canidae	*Canis latrans*	1
station24	Coyote	Carnivora	Canidae	*Canis latrans*	3
station25	Coyote	Carnivora	Canidae	*Canis latrans*	1
station26	Coyote	Carnivora	Canidae	*Canis latrans*	29
station27	Coyote	Carnivora	Canidae	*Canis latrans*	1
station28	Coyote	Carnivora	Canidae	*Canis latrans*	1
station29	Coyote	Carnivora	Canidae	*Canis latrans*	9
station3	Coyote	Carnivora	Canidae	*Canis latrans*	2
station30	Coyote	Carnivora	Canidae	*Canis latrans*	7
station31	Coyote	Carnivora	Canidae	*Canis latrans*	1
station32	Coyote	Carnivora	Canidae	*Canis latrans*	2
station33	Coyote	Carnivora	Canidae	*Canis latrans*	4
station34	Coyote	Carnivora	Canidae	*Canis latrans*	36

Appendix III. continued...

Station	Common Name	Order	Family	Species Name	Unique Events
station35	Coyote	Carnivora	Canidae	*Canis latrans*	32
station36	Coyote	Carnivora	Canidae	*Canis latrans*	4
station37	Coyote	Carnivora	Canidae	*Canis latrans*	12
station38	Coyote	Carnivora	Canidae	*Canis latrans*	3
station39	Coyote	Carnivora	Canidae	*Canis latrans*	1
station4	Coyote	Carnivora	Canidae	*Canis latrans*	2
station40	Coyote	Carnivora	Canidae	*Canis latrans*	2
station41	Coyote	Carnivora	Canidae	*Canis latrans*	6
station41x	Coyote	Carnivora	Canidae	*Canis latrans*	64
station42	Coyote	Carnivora	Canidae	*Canis latrans*	5
station43	Coyote	Carnivora	Canidae	*Canis latrans*	7
station45	Coyote	Carnivora	Canidae	*Canis latrans*	6
station46	Coyote	Carnivora	Canidae	*Canis latrans*	1
station47	Coyote	Carnivora	Canidae	*Canis latrans*	4
station48	Coyote	Carnivora	Canidae	*Canis latrans*	1
station5	Coyote	Carnivora	Canidae	*Canis latrans*	1
station50	Coyote	Carnivora	Canidae	*Canis latrans*	1
station51	Coyote	Carnivora	Canidae	*Canis latrans*	1
station52	Coyote	Carnivora	Canidae	*Canis latrans*	3
station53	Coyote	Carnivora	Canidae	*Canis latrans*	5
station54	Coyote	Carnivora	Canidae	*Canis latrans*	1
station55	Coyote	Carnivora	Canidae	*Canis latrans*	6
station56	Coyote	Carnivora	Canidae	*Canis latrans*	1
station57	Coyote	Carnivora	Canidae	*Canis latrans*	9
station58	Coyote	Carnivora	Canidae	*Canis latrans*	1
station59	Coyote	Carnivora	Canidae	*Canis latrans*	1
station6	Coyote	Carnivora	Canidae	*Canis latrans*	1
station60	Coyote	Carnivora	Canidae	*Canis latrans*	2
station61	Coyote	Carnivora	Canidae	*Canis latrans*	7
station62	Coyote	Carnivora	Canidae	*Canis latrans*	10
station7	Coyote	Carnivora	Canidae	*Canis latrans*	2
station5	Fisher	Carnivora	Mustelidae	*Pekania pennanti*	2
station11	Red Fox	Carnivora	Canidae	*Vulpes vulpes*	1
station18	Red Fox	Carnivora	Canidae	*Vulpes vulpes*	4
station2	Red Fox	Carnivora	Canidae	*Vulpes vulpes*	2
station20	Red Fox	Carnivora	Canidae	*Vulpes vulpes*	4
station21	Red Fox	Carnivora	Canidae	*Vulpes vulpes*	2
station22	Red Fox	Carnivora	Canidae	*Vulpes vulpes*	13
station24	Red Fox	Carnivora	Canidae	*Vulpes vulpes*	1
station29	Red Fox	Carnivora	Canidae	*Vulpes vulpes*	2

Appendix III. continued...

Station	Common Name	Order	Family	Species Name	Unique Events
station32	Red Fox	Carnivora	Canidae	*Vulpes vulpes*	1
station35	Red Fox	Carnivora	Canidae	*Vulpes vulpes*	1
station4	Red Fox	Carnivora	Canidae	*Vulpes vulpes*	7
station43	Red Fox	Carnivora	Canidae	*Vulpes vulpes*	2
station49	Red Fox	Carnivora	Canidae	*Vulpes vulpes*	3
station50	Red Fox	Carnivora	Canidae	*Vulpes vulpes*	5
station51	Red Fox	Carnivora	Canidae	*Vulpes vulpes*	2
station6	Red Fox	Carnivora	Canidae	*Vulpes vulpes*	2
station62	Red Fox	Carnivora	Canidae	*Vulpes vulpes*	1
station11	Weasel spp.	Carnivora	Mustelidae	*Mustela* spp.	2
station20	Weasel spp.	Carnivora	Mustelidae	*Mustela* spp.	2
station21	Weasel spp.	Carnivora	Mustelidae	*Mustela* spp.	3
station23	Weasel spp.	Carnivora	Mustelidae	*Mustela* spp.	7
station25	Weasel spp.	Carnivora	Mustelidae	*Mustela* spp.	3
station26	Weasel spp.	Carnivora	Mustelidae	*Mustela* spp.	4
station27	Weasel spp.	Carnivora	Mustelidae	*Mustela* spp.	1
station30	Weasel spp.	Carnivora	Mustelidae	*Mustela* spp.	3
station32	Weasel spp.	Carnivora	Mustelidae	*Mustela* spp.	1
station33	Weasel spp.	Carnivora	Mustelidae	*Mustela* spp.	1
station34	Weasel spp.	Carnivora	Mustelidae	*Mustela* spp.	1
station36	Weasel spp.	Carnivora	Mustelidae	*Mustela* spp.	1
station38	Weasel spp.	Carnivora	Mustelidae	*Mustela* spp.	1
station40	Weasel spp.	Carnivora	Mustelidae	*Mustela* spp.	3
station41	Weasel spp.	Carnivora	Mustelidae	*Mustela* spp.	3
station43	Weasel spp.	Carnivora	Mustelidae	*Mustela* spp.	2
station45	Weasel spp.	Carnivora	Mustelidae	*Mustela* spp.	1
station47	Weasel spp.	Carnivora	Mustelidae	*Mustela* spp.	8
station48	Weasel spp.	Carnivora	Mustelidae	*Mustela* spp.	2
station49	Weasel spp.	Carnivora	Mustelidae	*Mustela* spp.	3
station5	Weasel spp.	Carnivora	Mustelidae	*Mustela* spp.	1
station53	Weasel spp.	Carnivora	Mustelidae	*Mustela* spp.	1
station54	Weasel spp.	Carnivora	Mustelidae	*Mustela* spp.	1
station61	Weasel spp.	Carnivora	Mustelidae	*Mustela* spp.	4
station9	Weasel spp.	Carnivora	Mustelidae	*Mustela* spp.	3

Appendix IV. Black bear Relative Abundance Index (RAI) for each camera trap station, calculated as the number of independent (daily) detections per 100 trap nights. Results are sorted by decreasing number of daily detections.

Station	No. daily detections	Trap nights	RAI	% LF
station34	16	90	17.8	75.1
station33	9	65	10.2	56.5
station55	8	89	9.1	63.3
station31	4	89	4.5	0.0
station41x	4	89	4.4	71.8
station9	3	90	3.3	39.3
station58	2	87	2.3	79.5
station1	2	87	2.3	62.6
station57	2	88	2.3	59.6
station25	2	89	2.2	79.2
station32	2	89	2.2	0.0
station23	2	90	2.2	0.1
station54	1	89	1.1	52.3
station49	1	89	1.1	0.9
station59	1	88	1.1	84.8
station53	1	87	1.1	61.0
station0	1	88	1.1	23.4
station17	1	90	1.1	22.2
station37	1	89	1.1	0.0
station40	1	89	1.1	88.5
station14	1	90	1.1	0.5
station61	0	87	0.0	76.2
station60	0	88	0.0	69.3
station48	0	90	0.0	55.1
station45	0	90	0.0	44.2
station42	0	89	0.0	41.4
station56	0	87	0.0	40.2
station35	0	89	0.0	35.9
station24	0	89	0.0	32.5
station62	0	88	0.0	23.8
station46	0	90	0.0	21.0
station47	0	90	0.0	18.7
station18	0	89	0.0	15.0
station7	0	90	0.0	12.5
station52	0	88	0.0	10.5

Appendix IV. continued...

Station	No. daily detections	Trap nights	RAI	% LF
station50	0	89	0.0	8.5
station51	0	89	0.0	8.1
station43	0	89	0.0	5.7
station44	0	90	0.0	3.4
station8	0	90	0.0	1.6
station15	0	90	0.0	0.8
station16	0	89	0.0	0.7
station30	0	90	0.0	0.5
station11	0	90	0.0	0.1
station5	0	90	0.0	0.1
station3	0	90	0.0	0.0
station10	0	90	0.0	0.0
station12	0	90	0.0	0.0
station13	0	90	0.0	0.0
station19	0	90	0.0	0.0
station2	0	91	0.0	0.0
station20	0	89	0.0	0.0
station21	0	90	0.0	0.0
station22	0	90	0.0	0.0
station26	0	89	0.0	0.0
station27	0	89	0.0	0.0
station28	0	89	0.0	0.0
station29	0	90	0.0	0.0
station36	0	89	0.0	0.0
station38	0	89	0.0	0.0
station39	0	88	0.0	0.0
station4	0	90	0.0	0.0
station6	0	90	0.0	0.0