Journal of Mammalogy, 103(2):361–372, 2022
https://doi.org/10.1093/jmammal/gyab148

Bed site selection by female North American black bears (*Ursus americanus*)

Susan A. Mansfield,[1] Lynn L Rogers,[1] Sean Robison,[1] and Roger A. Powell[2,*]

[1] *Wildlife Research Institute, Ely, MN 55731, USA*
[2] *Department of Applied Ecology, North Carolina State University, Raleigh, NC 27695-7617, USA*

**To whom correspondence should be addressed: rpowell@ncsu.edu*

Sleep is important for memory consolidation and maintaining metabolic homeostasis, but sleep can expose animals to inclement weather and predators. Consequently, selection of sleeping sites is important. We tested three sets of hypotheses related to selection of bed sites by female American black bears (*Ursus americanus*) at two study sites. During 2009–2013, we outfitted 14 female black bears west of Ely, Minnesota, with Global Positioning System collars that reported bear locations every 10 min. We visited 101 bed sites, each identified from clusters of estimated locations where a bear was on site for ≥4 h on two or more occasions, and recorded bed characteristics, forest composition, canopy closure, and ground cover. We matched each bed site with a control site where we collected the same data. During 1987–1991, we outfitted three female black bears south of Ely with very high-frequency transmitter collars and walked with the bears to collect detailed behavioral data. We used the written data records to identify 62 bed sites where bears slept ≥2 h and where bed characteristics were documented. We matched each bed site with a control site approximately 6 h different when the bear was active. Of the bed sites, 132 were used during night and 31 during day. The two study areas differed in the amount of lowland habitats. At both sites, female bears chose bed sites disproportionately in lowland sites with high canopy cover and next to a tree, especially a white pine. Female bears with cubs selected upland bed sites more often than did females without cubs and also more often selected sites adjacent to a tree with coarse bark, which cubs could climb easily. Distances to roads and houses did not affect selection of bed sites by females either with or without cubs.

Key words: bear, bed site, predator avoidance, resource selection, rest site, *Ursus americanus*

All vertebrates require sleep and even visually oriented invertebrates rest during night (Dissel et al. 2015; Rößler et al. 2021; Pennisi 2021). In vertebrates, sleep is necessary for memory consolidation (Gais and Born 2004; Walker and Stickgold 2004; Vyazovskiy et al. 2008) and to maintain metabolic homeostasis by promoting removal of potentially neurotoxic waste products that accumulate in the central nervous system during wakefulness (Xie et al. 2013). Nonetheless, sleeping animals open themselves to risks, such as exposure to cold or predators (Lima et al. 2005; Cirelli and Tononi 2008; Amo et al. 2011; Rößler et al. 2021). Consequently, the choice of sleeping sites is important. Sleeping in burrows, tree cavities, or other dens provides protection from predators and from inclement weather (Powell and Brander 1977; Holler 1999; Baker and Hill 2003). Sleeping in groups in trees or in other areas with good visibility minimizes predation risk and enables selfish herds via shared vigilance (Hamilton 1971; Altmann 1980; Baldellou and Henzi 1992; Creel et al. 2005).

Across much of their range, adult American black bears (*Ursus americanus*) are not subject to predation except by humans (Pelton 2003). Although black bears forage near human residences, especially when distant natural foods are scarce (Merkle et al. 2013; Baruch-Mordo et al. 2014; Johnson et al. 2015; Gould 2020), they appear to have learned generally to avoid people (Rogers 2011; Stringham and Rogers 2017) and roads (Reynolds-Hogland and Mitchell 2007; Ditmer et al. 2018) when possible. Where black bear populations overlap with those of grizzly bears (*U. arctos*), wolves (*Canis lupus*), and pumas (*Puma concolor*), all black bears are vulnerable to predation while sleeping (Rogers 1987; Rogers and Mech 1981) and cubs are always susceptible to infanticide by males (Powell et al. 1997; Pelton 2003; Garrison et al. 2007). In addition, black bears throughout their range are vulnerable to the effects of hot, cold, and wet weather.

Consequently, black bears, especially mothers with cubs, should select bed sites wisely. Black bears often become inactive 1.5–2 h after sunset, resume activity 0.5–1 h before sunrise, and nap once or twice during the day for a total of 6–8 h of rest per day (Rogers 1987). Bears may become nocturnal to avoid humans (Beckmann et al. 2003), but the need for sleep remains.

Bears' choices of winter dens have been studied extensively (Jonkel and Cowan 1971; Pelton 2003; Powell 2005; Reynolds-Hogland et al. 2007; Gray et al. 2016; Chirichella et al. 2019). The limited literature on resting or sleeping sites (which we call "bed sites") during their active seasons emphasizes habitat and other landscape features (Bard and Cain 2020; Karelus et al. 2019) and provides little insight into how black bears choose specific bed sites. Bears probably have more options for bed sites than they have for den sites because den sites must provide more protection from extreme weather and potential predators. Bears occasionally rest during their active season in their own winter dens and in those of other bears (Mansfield, Powell, Rogers unpublished data).

Rogers and Lindquist (1992) observed that female black bears with cubs (hereafter "bear families") in northern Minnesota selected bed sites beneath large white pines (*Pinus strobus*) in spring, even though white pines of all sizes made up <0.4% of the trees in the forest. The coarse bark may enable cubs to climb white pines particularly easily (Rogers 1995), making beds near white pines safe when bear families are confronted with danger. In late summer and autumn, bear families did not favor beds under white pines so strongly (Rogers and Lindquist 1992). In contrast, female black bears without cubs (hereafter "lone females") appeared not to bed near white pines preferentially at any time (Rogers and Lindquist 1992).

We tested the generality of Rogers and Lindquist's observations and developed several additional hypotheses. Given the lack of literature on black bear bed sites, we tested first the basic premise that female black bears do not choose bed sites randomly with respect to environmental characteristics. In particular (Table 1), we hypothesized that all bears choose bed sites preferentially (i) far from roads and human residences where they are not fed; (ii) in wet or moist lowland areas (areas humans avoid and wolves avoid in summer; DelGuidice 2000; Nelson 2000); (iii) with overhead cover (protection from weather); (iv) with some ground cover (not bare rock and not water); (v) within a foraging area (having coarse woody debris for insect larvae, ground cover for green vegetation and fruits, and shrubs for fruits and nuts); (vi) each close to a tree a bear could climb (a "refuge tree"), preferentially with coarse bark or, specifically, a white pine; (vii) each with a strong horizontal branch, where cubs and their mothers might rest without having to cling to a vertical trunk. We also hypothesized that, compared to lone females, bear families choose beds more strongly according to characteristics i—vii above. Finally, we hypothesized that bear families choose sites more like those of lone females as their active season progresses, because cubs grow, gain skills and, therefore, need less protection from predators. By using data from two study sites with different bears and separated by decades in time, we gained support for the generality of our results, at least for the southern boreal region of North America.

Materials and Methods

Eagles Nest study area.—Our 300 km^2 main study area was in southern boreal forest in northeastern Minnesota centered in Eagles Nest Township (47° 51′ N, 92° 6′ W; hereafter "Eagles Nest"; Mansfield 2007), approximately 15 km southwest of Ely, Minnesota (Fig. 1). Some human residents of Eagles Nest had fed local black bears for over 50 years before our study. During our research, 17 households fed bears purposefully during at least a portion of the bears' active seasons. We established an additional feeding site and habituated local bears to human activities at that site. To "capture" bears, we offered high-quality nuts and acclimated some bears to our touch. During 1999 into 2014, we placed VHF transmitter collars (Telonics, Mesa, Arizona) on a total of 44 bears without the use of traps or immobilizing drugs. By using these methods, we avoided the short- and long-term problems caused by traps and drugs (Powell 2005; Cattet et al. 2008; Gilbert 2019). Most study bears were initially collared as yearlings with known kinship prior to family breakup. These habituated bears fell into three categories: (i) bears comfortable with us around community feeding stations but who did not allow us to approach them in the woods; (ii) bears who allowed us to approach them in the woods but left us if we tried to walk with them; and (iii) bears who allowed us to walk with them in the woods. Although these bears were habituated to the houses where they were intentionally fed and to our research team, this habituation did not automatically transfer to all locations and all humans. The bears generally avoided people other than our research team and become hyper-alert to humans and human sounds in unexpected places (Mansfield 2007).

During 2009–2014, we attached modified SPOT Personal Tracker GPS (global positioning system) units (Spot Image Corporation, Chantilly, Virginia) to the VHF collars of 14 female bears who allowed us to approach them in the woods. These study bears, ranging from 2 to 13 years old, belonged to one clan descended from a matriarch born in 1987. We monitored five of these 14 females for 5 years, two for 4 years, two for 3 years, two for 2 years, and three for 1 year, yielding 16 bear-years (data for 1 bear for 1 year) for bear families and 28 bear-years for lone females.

We disabled 911 alerts on the SPOT units and programmed them to collect location fixes every 10 min until batteries died (8–10 days). The SPOT units transmitted locations to a website, enabling us to observe movements of study bears on our computers in nearly real-time and allowing us to intercept bears in accessible locations to change batteries. To locate each bear, a member of our research team homed on the bear using VHF telemetry, calling to the bear while approaching. Some bears continued their activities, some waited for the team member, while others approached the team member. The team member offered

Table 1.—Hypotheses tested for choices of bed sites by adult female black bears. The Kawishiwi study site lacked data for testing all hypotheses and, therefore, some hypotheses were tested using data from both the Kawishiwi site and the Eagles Nest site while some hypotheses were tested using data only from the Eagles Nest site. Hypotheses in bold can not be rejected.

Site		Hypothesis	Comments	
1		**Female bears choose bed site preferentially**		
1a	Both sites	**In lowland area with high canopy cover and a refuge tree**		$F = 25.15$, d.f. = 7, $P < 0.05$
	Both sites	**In lowland area with high canopy cover and a refuge tree with coarse bark**		$F = 29.17$, d.f. = 7, $P < 0.05$
	Both sites	**In lowland area with high canopy cover and a white pine refuge tree**		$F = 31.04$, d.f. = 7, $P < 0.05$
1b	Eagles Nest	**In lowland area with high canopy cover, extensive ground cover, nearby food, and a refuge tree**	Ground cover and Food do not contribute to significance	$F = 14.60$, d.f. = 3, $P < 0.05$
	Eagles Nest	**In lowland area with high canopy cover, extensive ground cover, nearby food, and a refuge tree with coarse bark**	Ground cover and Food do not contribute to significance	$F = 26.52$, d.f. = 3, $P < 0.05$
	Eagles Nest	**In lowland area with high canopy cover, extensive ground cover, nearby food, and a white pine refuge tree**	Ground cover and Food do not contribute to significance	$F = 30.30$, d.f. = 3, $P < 0.05$
1c	Eagles Nest	**In lowland area With high canopy cover, extensive ground cover, nearby food, and a refuge tree with a sturdy, horizontal limb**	Food does not contribute to significance	$F = 56.51$, d.f. = 4, $P < 0.05$
	Eagles Nest	**In lowland area with high canopy cover, extensive ground cover, nearby food, and a refuge tree with coarse bark and a sturdy, horizontal limb**	Food does not contribute to significance	$F = 56.27$, d.f. = 5, $P < 0.05$
	Eagles Nest	**In lowland area with high canopy cover, extensive ground cover, nearby food, and a refuge white pine tree with a sturdy, horizontal limb**	Food does not contribute to significance	$F = 49.19$, d.f. = 5, $P < 0.05$
1d	Eagles Nest	Distant from roads		$F = 1.39$, d.f. = 1, $P > 0.05$
		But not so much when wild foods are scarce		$F = 0.61$, d.f. = 1, $P > 0.05$
1e	Eagles Nest	Distant from houses where they are not fed		$F = 0.08$, d.f. = 1, $P > 0.05$
		But not so much when wild foods are scarce		$F = 0.28$, d.f. = 1, $P > 0.05$
2		**Compared with lone females, females with cubs choose bed site preferentially**		
2a	Both sites	**In lowland area with high canopy cover and a refuge tree**	Canopy does not contribute to significance and families more likely to bed upland	$F = 7.70$, d.f. = 5, $P < 0.05$
	Both sites	**In lowland area with high canopy cover and a refuge tree with coarse bark**	Canopy does not contribute to significance and families more likely to bed upland	$F = 8.42$, d.f. = 5, $P < 0.05$
	Both sites	**In lowland area with high canopy cover and a white pine refuge tree**	Canopy does not contribute to significance and families more likely to bed upland	$F = 8.77$, d.f. = 5, $P < 0.05$
2b	Eagles Nest	**In lowland area with high canopy cover, extensive ground cover, nearby food, and a refuge tree**	Only refuge tree and nearby food contribute to significance	$F = 16.03$ d.f. = 2, $P < 0.05$
	Eagles Nest	**In lowland area with high canopy cover, extensive ground cover, nearby food, and a refuge tree with coarse bark**	Only nearby food contributes to significance	$F = 15.03$ d.f. = 1, $P < 0.05$
	Eagles Nest	**In lowland area with high canopy cover, extensive ground cover, nearby food, and a white pine refuge tree**	Only white pine tree and food contribute to significance	$F = 12.15$ d.f. = 2, $P < 0.05$
2c	Eagles Nest	In lowland area with high canopy cover, extensive ground cover, nearby food, and a refuge tree with a sturdy, horizontal limb	Presence of a refuge tree with a sturdy, horizontal limb does not contribute to significance	$F = 0.57$ d.f. = 1, $P > 0.05$
	Eagles Nest	In lowland area with high canopy cover, extensive ground cover, nearby food, and a refuge tree with coarse bark and a sturdy, horizontal limb	Not tested because presence of a refuge tree with coarse bark does not contribute to significance	
	Eagles Nest	In lowland area with high canopy cover, extensive ground cover, nearby food, and a refuge white pine tree with a sturdy, horizontal limb	Presence of a white pine tree with a sturdy, horizontal limb does not contribute to significance	$F = 0.72$ d.f. = 1, $P > 0.05$
2d	Eagles Nest	Distant from roads		$F = 0.07$, d.f. = 1, $P > 0.05$
2e	Eagles Nest	Distant from houses where they are not fed		$F = 2.20$, d.f. = 1, $P > 0.05$
3		Females with cubs chose bed sites whose characteristics converge towards those of sites chosen by lone females at the season of activity progresses for choosing		
3a	Eagles Nest	Upland vs. lowland bed sites	No convergence	$F = 0.51$, d.f. = 1, $P > 0.05$
3b	Eagles Nest	Bed sites with a refuge tree with coarse bark	No convergence	$F = 0.68$, d.f. = 1, $P > 0.05$
3	Eagles Nest	Bed sites with a white pine	No convergence	$F = 0.49$, d.f. = 1, $P > 0.05$
3d	Eagles Nest	Bed sites with food nearby	No convergence	$F = 0.51$, d.f. = 5, $P > 0.05$

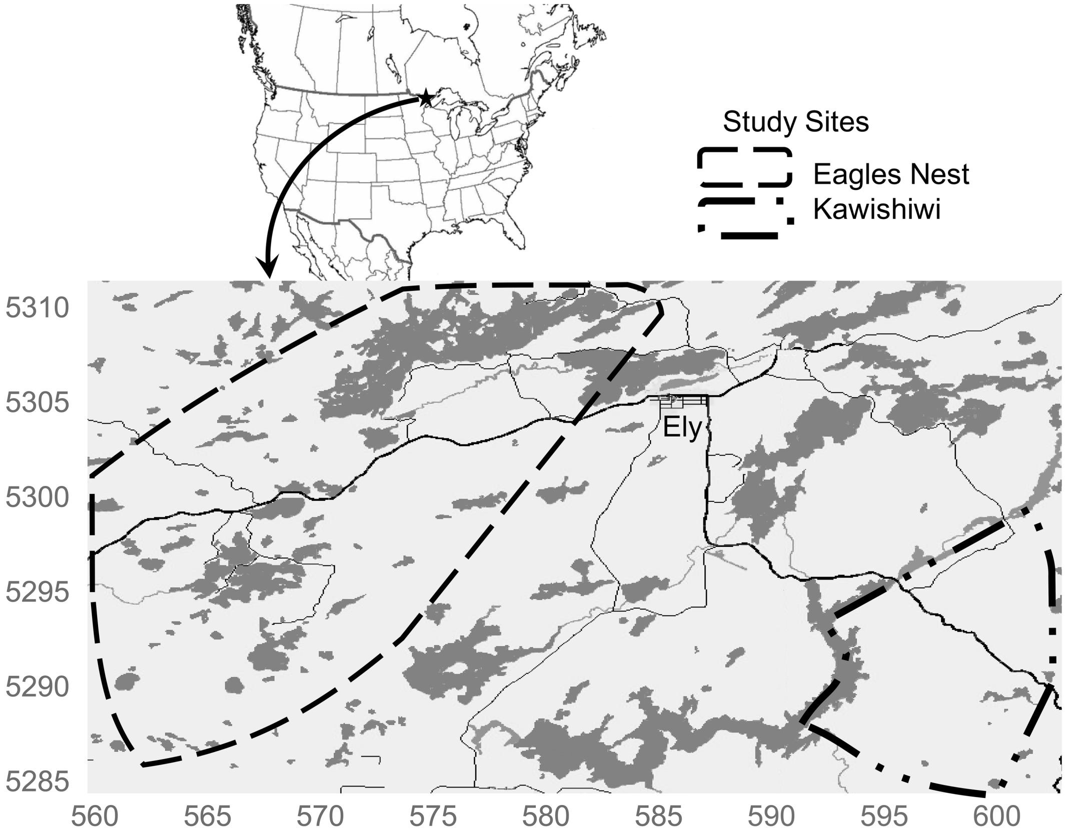

Fig. 1.—Study sites in northeastern Minnesota, United States. The Eagles Nest study site is to the west and the Kawishiwi study site to the east.

the bear a handful of nuts in exchange for access to replace the batteries. Feeding of bears was limited to the minimum needed to change batteries. After a battery change, bears were seldom followed and then only for limited periods.

To test the accuracy and precision of the SPOT Personal Trackers, we placed units in four forested test locations and located those sites on GoogleEarth. At two test areas, we used multiple units placed in different locations within 35 m of each other and left the units in place for 1 day to 2 weeks with a mean of 3 ± 3 days for a total of 75 trials. We placed one unit at each of the other two test locations and left them for four months. We wrapped test collars around logs of bear neck size and bear height above ground. We calculated the mean location for each collar reported by the SPOT units and compared that mean to the known location.

Bed site data.—To identify bed sites, we examined our GPS data for consecutive locations clustered within a 25-m radius for ≥4 h. To increase the likelihood that these were bed sites, we selected sites used at least twice by the same or different bears.

We identified 375 possible bed sites but eliminated 3 to which we did not have access. Of the remaining 372, we identified 111 bed sites within 500 m of known feeding stations, which were clustered because the households that fed bears were clustered. These bed sites were predominantly in lowland habitat, allowing the bears to avoid humans. Bears used these bed sites near feeding stations mainly in August and September after wild foods waned (Noyce and Coy 1990; Noyce and Garshelis 1997) but before bears denned. To make our results representative of bears in northern Minnesota, the vast majority of which are not fed, we selected 10 of the 111 sites randomly to include in our sample, all of which were in lowland habitat. No estimate exists for the number of bears in northern Minnesota that are fed and, therefore, we cannot know whether 10 sites was the best number to choose. From the remaining 261 sites, we selected 91 randomly, resulting in 101 sites to ground truth; a number which matched our time and resource constraints.

During summer 2016, we walked to the mean GPS location of each of the 101 bed sites and looked for the nearest obvious bear bed. We paired each bed site with a control site 100 m away in a random direction, representing a local place where a bear could have bedded instead of where she actually chose to bed. Although our choice of control sites did not preclude the sites from being bed sites by chance, that never happened. We collected the same data at control sites as at bed sites except for data on actual beds.

We identified a bear bed as a shallow depression approximately 30–50 cm across (Fig. 2). Occasionally, we found multiple bear beds within meters of each other at a site, or sites with no obvious beds despite other bear sign. We often found bear hair in beds or caught in the bark of nearby trees. Sometimes we found bites or claw marks on the bark of nearby trees. We recorded the location of each bed using a Garmin hand-held GPS unit (various models, Garmin International, Inc., Olathe, Kansas) and measured its length, width, and depth. We recorded species and diameter at breast height (dbh) of all trees with ≥15 cm dbh (large enough for cubs to climb) within a 5-m

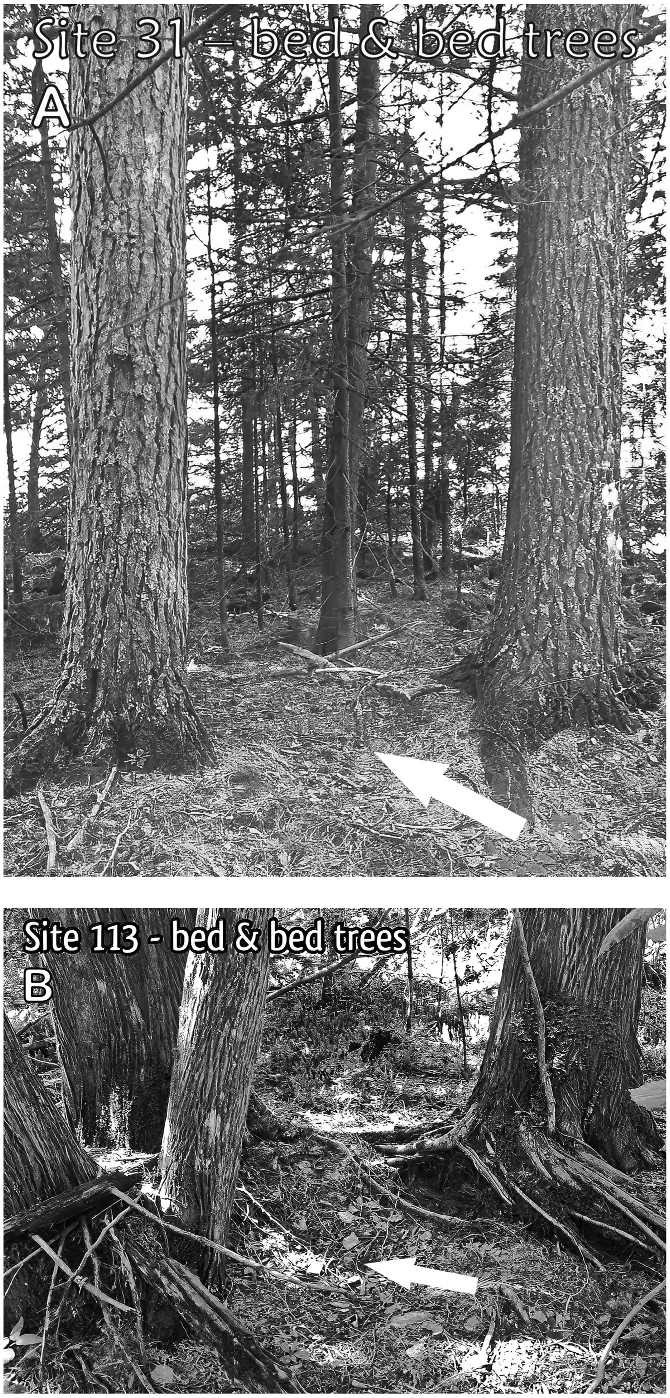

Fig. 2.—Examples of bed sites used by adult female black bears in northeastern Minnesota. Beds are indicated by white arrows. (A) Bed located between a large red pine (left) and a large white pine (right). (B) Bed located among large white cedars.

radius of the bed. If the edge of the bed was ≤1 m from a tree, we called the tree a "refuge tree" because an adult female bear could climb it immediately if disturbed. We documented the species of refuge trees, dbh, and bark texture. We considered refuge trees with coarse bark to include green and black ashes (*Fraxinus* spp.), white cedars, and aspens (*Populus* spp.) and white pines ≥25 cm dbh. Bark texture of these trees was similar to that reported by Rogers and Lindquist (1992) to be easy for cubs to climb. Refuge trees without coarse bark included red and jack pines, tamaracks, spruces, white birches, and aspens and white pines < 25 cm dbh. We estimated height of the lowest sturdy branch that could support an adult female bear, counted whether the tree had a single or multiple tops, and estimated the general health of the tree (Maser et al. 1979). For sites with no obvious bed, we used the mean GPS location as the bed. For control sites, we designated the tree closest to and #1 m from the site point (the "bed") as a "refuge" tree.

At each site, we photographed the overstory at the bed and at 5- and 10-m from the bed in the four cardinal directions, or from the refuge tree, if present. We derived percent canopy cover at each bed site from the overstory photos. First, we created a training sample in Erdas Imagine 2015 (Leica Geosystems, Atlanta, Georgia, United States) to teach the software to differentiate between spectral signatures associated with blue sky, white clouds, grey clouds, green foliage, and brown bark. We then performed a supervised classification of canopy images, which classified each pixel into one of the five classes. Lastly, we categorized each pixel as sky or tree to calculate percent canopy cover. We averaged percent canopy cover at the bed site with the canopy cover at 5 and 10 m distant.

We recorded ground cover of the bed itself and the percent ground cover within a 5-m radius using the following categories: rock, bare ground, vegetation, leaf litter, water, and woody debris. If no bed was obvious because the bear moved around the site, we collected data around the GPS mean. We recorded bear sign, including scats, bite marks, claw marks, hair, and evidence of foraging, and, using professional judgment, noted whether sign was from the current year. We categorized land cover into nine categories: upland—open, spruce-fir (*Picea* spp., *Abies balsamia*), shrub (*Corylus* spp., *Salix* spp.), upland hardwood (*Populus* spp., *Betula papyrifera*), mixed conifer-hardwood, and pine (*Pinus* spp.), and lowland—lowland conifer (*Thuja occicentalis, Larix laricina*), ash, and alder (*Alnus* spp.). We developed a variable for ground cover at each bed site using the proportion of ground covered by vegetation and leaf litter (excluding open water, if any). We developed a variable for nearby food using all data with the 5-m radius including vegetation, leaf litter, woody debris, and shrub land cover.

We measured the shortest distance from each bed to the nearest road and to the nearest house at which bears were not fed (hereafter "house(s) of non-feeder(s)"). We measured distances as the travel distances around large lakes lacking narrow areas bears could easy swim. Although bears alert to human sounds, their avoidance behavior depends on travel distance (Mansfield 2007). We estimated each bear's 95% utilization distribution for each year using a fixed kernel estimator with h = 100 and using Silverman's (1986) K_2. Then we measured the distances to the nearest road and nearest non-feeder house from every point within each bear's utilization distribution weighted by intensity of use. We ranked distances as near or far from roads and non-feeder houses using the threshold of 130 m, which was the approximate midpoint distance from roads at which bears in northwestern Minnesota began to elevate heart rate, indicating stress (Ditmer et al. 2018).

Kawishiwi study area.—We used additional behavioral data from a secondary, 30 km^2 study area along the Kawishiwi River 30 km to the east of Eagles Nest (47° 49′ N, 91° 45′ W; hereafter "Kawishiwi"; Rogers and Wilker 1992; Fig. 1).

In the mid-1980s, we live-trapped bears at this site using barrel traps, tranquilized them and outfitted them with VHF transmitter collars (Telonics, Mesa, Arizona). We handled bears in dens to adjust collars, to take measurements, and to obtain weights. Subsequently, we attracted bears to a baited scale, located within the study area at the Kawishiwi Field Laboratory of the North Central Forest Experiment Station of the US Department of Agriculture Forest Service. We then began the habituation process (Rogers and Wilker 1992) later used at Eagles Nest.

During 1987–1991, we followed three adult female Kawishiwi bears for 37, 432, and 758 h, collecting behavioral data on a small field computer (Rogers and Wilker 1992). These "follows" yielded two bear-years for bear families and three bear-years for lone females. We noted habitat characteristics while walking, including major land cover type, canopy closure, foods available, and trees near bed sites, and we drew rough maps of the bears' travels on USGS topographic maps. The habitat and bed data from these "follows" matched major data categories collected for bed sites in Eagles Nest. We used a shorter time period (≥2 h) for selecting bed sites at the Kawishiwi study site because we knew from direct observations that we chose bed sites. This resulted in 63 bed sites.

To obtain "control" sites for comparison with bed sites, we added 6 h from the time a bear established a bed site during a given follow and found that new time in the record. Were the bear active at that time, we used the habitat data for the bear's location as the control site. Were the bear resting, or were the new time beyond the time of the follow, we subtracted 6 h and used habitat data for that time were the bear active. We iterated this process at 2-h intervals until we found a time when the bear was active.

We note that habituating and following study animals in the field has a history dating back nearly a century (Carpenter 1934) is accepted as a standard method for the study of primate behavior (Carpenter 1934; DeVore 1963; Goodall 1963; Altmann and Altmann 1970; Altmann 1980, 1998; Sapolsky 2001; Merrick 2014 and many more), and has been used for long-term research on carnivores (Mech 1988; Mech and Cluff 2011). Our methods are consistent with this history. In addition, black bears are among the smartest of carnivorans, outstanding at problem solving (Benson-Amram et al. 2016), and able to identify individual people who are not a danger to them nor are a source of food (Mansfield 2007).

Statistical methods.—We used regression analyses (proc glm in SAS) to test most hypotheses. Because we first performed broad tests with several dependent variables and then removed variables that did not contribute to significance, we could set $\alpha = 0.05$. Before testing hypotheses, we tested for differences in upland vs. lowland habitats, canopy cover, and presence of a "refuge" tree between the control sites from our two study areas to learn whether we needed to block further tests by study area. We used a Bonferonni-z test to identify the land cover categories that contributed to the significant difference in upland vs. lowland at the two study areas. We also tested for differences in these environmental characteristics by distances that bed sites were from roads and from houses of non-feeders (SAS proc glm). We did this to learn whether we would have to control for this distance in other tests.

We started with three model statements for testing whether bed sites (both bear families and lone females) differed from control sites using data from both study areas. The model statements included variables for upland vs. lowland, canopy cover, and one of three variables for refuge trees (existence of a refuge tree, of a refuge tree with coarse bark, and of a white pine). If our regression results showed that any variables did not contribute to model significance, we used Type III sum of squares to remove the variable with the least support. We ran regressions again, repeating until each model included only variables that contributed to significance. If upland vs. lowland were retained, we used a Bonferonni-z test to identify the land cover categories that contributed to this variable being significant. If the refuge tree were retained, we used Bonferonni-z to identify the important tree species.

We did not use an Information Criterion (e.g., AIC) approach because we were not interested in finding the model that best described our data (Sober 2008) but, instead, needed to identify all variables that affected female bears' choices of bed sites.

Next, using data from Eagles Nest only (because data from Kawishiwi were not georeferenced), we tested whether the proportion of bears' beds near and far from roads and from houses of nonfeeders was greater than expected from the bears' annual 95% utilization distributions for that year. Our tests of distances to houses of nonfeeders were compromised because some of those houses were close to houses where bears were fed. To gain a better understanding of whether bears were forced to be near some houses where they were not fed, we tested whether annual production of natural foods affected the bears' willingness to approach paved roads and houses. Bears' use of feeding sites is high when natural foods are scarce (Mansfield 2007; Rogers 2011) and some of the feeding sites in our Eagles Nest study area were close to roads and close to houses where bears were not fed. The Minnesota Department of Natural Resources maintains online access to its annual indices of production of important bear foods in major sections of the state. During July–August, bears' main foods included wild sarsaparilla berries (*Aralia nudicaulis*), blueberries (*Vaccinium* spp.), raspberries (*Rubus idaeus*), juneberries (*Amelanchier* spp.), and cherries (*Prunus virginiana*, *P. pennsylvanica*). During late August–September, main foods were dogwood berries (*Cornus* spp.), hazelnuts (*Corylus cornuta*), and acorns of red oak (*Quercus rubra*; Noyce and Coy 1990; Noyce and Garshelis 1997).

The Eagles Nest study site provided data for three additional variables for our regression models (ground cover, nearby food, and horizontal limb for sites with a refuge tree). Thus, we next developed three model statements using data from

Eagles Nest only, each with five variables, adding variables for ground cover and nearby food, and followed the same reduction process. Finally, using data for bed and control sites at Eagles Nest having refuge trees, we developed three model statements with six variables, adding a variable for a tree having a sturdy, horizontal limb.

After testing for differences between bed sites and control site, we followed the same progression of tests for differences between bed sites chosen by bear families vs. lone female bears.

Finally, we tested for the effect of the month of the year on distributions of variables for bed sites of families vs. those of lone females. We used regression analyses on the monthly differences (April through October) in the values of the upland–lowland, coarse-bark tree and canopy closure variables for families vs. those for lone bears. For example, we tested whether the proportion of bed sites of bear families that were upland minus the proportion of bed sites for lone females that were upland converged on zero.

We collected data in concordance with annual permits from the Minnesota Department of Natural Resources and consistent with the American Society of Mammalogists' guidelines for using wild mammals in research (Sikes et al. 2016).

Results

The mean number of SPOT locations per bear per year was 4,319 ± 3,079 locations (±*SD*), for a total of 267,784 locations over 5 years at Eagles Nest. All mean GPS locations of test collars were within 3 m of our GoogleEarth locations. GPS locations for the test collars ranged, however, up to 300 m from the GoogleEarth locations. The closest 25% of GPS locations were all within 9 ± 4 m (±*SD*) of the test locations; the closest 50% were within 14 ± 6 m; the closest 75% were within 24 ± 11 m; and the closest 90% were within 36 ± 11 m.

Our selection criteria resulted in 132 bed sites (81%) used overnight and 31 bed sites (19%) used during the day. For the 101 bed sites at our Eagles Nest study area, which were chosen at random with respect to time of year, 20 of 21 bed sites used during the day were used during autumn, when bears were becoming less active. These 101 bed sites were used an average of 3.7 ± 3.5 (±*SD*) times each (range 2–23) by our GPS monitored bears in different years and seasons. Generally, they were reused by the same bear (79.2%), but occasionally by daughters (11.9%), nieces (5.9%), and even cousins (2.0%). Sixteen sites did not have distinct beds.

An Eagles Nest bear bed was usually a round to oval depression on the forest floor approximately averaging 39 ± 9 (*SD*) cm in length, 30 ± 7 cm in width and 3 ± 2 cm in depth. At some bed sites, the bears had scraped litter or loose vegetation onto the sites (Fig. 2). The bears at the Kawishiwi study area sometimes slept for many hours but also slept for short periods, then sat up or walked around near the bed, and then slept for another short period. Thus, bears both slept and rested at bed sites.

The distributions of upland vs. lowland areas (Eagles Nest 66% upland, Kawishiwi 94%), presence of a white pine refuge tree (Eagles Nest 16% with white pine, Kawishiwi 39%), and canopy closure (Eagles Nest 0.57 ± 0.16, Kawishiwi 0.48 ± 0.18) differed between control sites at our two study areas (MANOVA; $F = 32.2$, d.f. = 3). The difference in upland vs. lowland was caused by Eagles Nest having more area in lowland conifer, shrub and spruce-fir land cover and less in mixed conifer-hardwood and upland hardwood. Bears' bed sites at different distances from houses where bears were fed did not differ with respect to environmental characteristics for any model ($F = 0.24$, d.f. = 95, $P > 0.05$). Thus, for all further tests using data from both study areas, we blocked by study area but did not have to include interaction terms with distances from roads or houses.

For the tests of Hypothesis 1 (Table 1), all female black bears (families plus lone females, both study sites) were more likely than expected to select bed sites in lowland habitats (47% vs. 25% for control sites) with high canopy closure (0.60 ± 0.11 vs. 0.54 ± 0.18), and close to a refuge tree (70% vs. 40%), specifically a tree with coarse bark (57% vs. 13%), and a white pine for a single species (30% vs. 5%; Table 1). The difference in upland vs. lowland was caused by bears selecting bed sites in lowland conifer, spruce-fir, and ash land covers and less in mixed conifer-hardwood, open, shrub, and upland hardwood (Fig. 3). Bears selected bed sites near white cedars and white pines but avoided small aspens, birches, balsam firs, red maples, and jack and red pines (Fig. 4).

Female black bears in just the Eagles Nest study area were also more likely than expected to select bed sites in lowland habitats (60% vs. 35%) with high canopy closure (0.62 ± 0.09 vs. 0.56 ± 0.17) and close to a refuge tree (68% vs. 51%), specifically a tree with coarse bark (55% vs. 18%), and a white pine for a single species (23% vs. 5%; Fig. 5; Table 1). The difference in upland vs. lowland was caused by bears selecting beds sites in lowland conifer, spruce-fir, and ash land covers and less in mixed conifer-hardwood, open, shrub, and upland hardwood. Bears selected bed sites near white cedars and white pines but avoided small aspens, birches, balsam firs, red maples, and red pines.

For bed and control sites with a refuge tree, 79% of the refuge trees at beds sites had a sturdy, horizontal limb but no trees at control sites did (Fig. 5; Table 1).

The proportion of bed sites near roads (0.04) and near houses of nonfeeders (0.06) did not differ from the proportions expected given their home ranges (roads: proportion in home range = 0.04, $F = 1.39$, d.f. = 1; houses: proportion in home range = 0.05; $F = 0.08$, d.f. = 1). The proportion of bed sites for bear families that were near roads (0.03) and were near houses of nonfeeders (0.07) did not differ from the proportions for lone females (roads: proportion lone females = 0.04; $F = 0.07$, d.f. = 1; houses: proportion lone females = 0.01 $F = 2.20$, d.f. = 1). The proportions of beds that were near roads and houses of nonfeeders were not affected by annual or seasonal food production (Fig. 6; roads: $F = 0.61$, d.f. = 1; houses: $F = 0.28$, d.f. = 1).

For tests of Hypothesis 2 (Table 1) across both study areas, black bear families were more likely than lone females to select bed sites close to a refuge tree (80% vs. 58%), specifically a tree with coarse bark (66% vs. 45%), and a white pine for a single species (42% vs. 15%; Table 1). In contrast to our prediction, however, bear families selected sites in upland (55%) more than did lone females (37%). The difference in upland vs. lowland was caused by bear families avoiding lowland conifer land covers and also avoiding shrub areas (Fig. 3). Compared with lone females, families selected bed sites near ashes and white pines but avoided white cedars, balsam firs, and spruces.

Just at Eagles Nest, black bear families were more likely than lone females to select bed sites with refuge trees (78% vs. 56%), especially a white pine (32% vs. 13%), and less likely to choose a site near food (70% vs. 81%). The relationship of bed site choices to nearby food was not simple. Bear families coming out of their dens were most likely to choose bed sites near food but that likelihood decreased through their active season (*F* = 2.76, d.f. = 5), while lone females appeared most likely to choose bed sites near food during autumn, though not significantly so (*F* = 1.32, d.f. = 5). Upland vs. lowland, canopy closure, ground cover, and presence of a horizontal limb did not affect the significance of the difference in bed site choice by families vs. lone females.

For Hypothesis 3 (Table 1), black bear families did not select bed sites more like those of lone females as their active seasons progressed and cubs grew and matured. Tests of changes in bed sites in uplands vs. lowlands, next to trees with coarse bark, and white pines showed no significant convergence.

Discussion

We collected data from 163 bed sites that female black bears at two study areas in northern Minnesota (101 and 62 bed sites per study area) had used for resting or sleeping during their active season. Bears used the bed sites most often during nighttime (>80%), and most daytime use occurred during autumn. We tested three suites of hypotheses related to how female black bears choose bed sites.

Consistent with the basic biological knowledge that animals base behavioral decisions on their physical condition, environmental conditions, and resources, female black bears in northeastern Minnesota were selective in their choices of bed sites. In general, female black bears preferred to bed in lowland areas and close to large trees with coarse bark, especially white pines (Fig. 5). These results support our premise that bears choose bed sites based, at least in part, on safety. Although female black bears did choose sites with denser canopies than at control sites, the difference was small and may not be biologically significant (Fig. 5).

Bear families were about 1.5H more likely than lone females to choose bed sites near coarse-barked trees and 2.8H more likely to choose white pines. These results support the observation of Rogers and Lindquist (1992) that female black bears with cubs prefer to bed near white pines, though our results are more general in showing that females chose trees with coarse bark. We hypothesize that, across the species range, females with cubs choose refuge trees preferentially for coarse bark that facilitates climbing by cubs.

Our female black bears in general selected refuge trees with sturdy, horizontal limbs, which can support a lone female or a bear family without them having to maintain holds on the tree trunk. In contrast to our expectation, however, female black bears with cubs did not preferentially choose bed sites near trees with sturdy horizontal branches compared to lone females.

Also, in contrast to our expectation, choices of bed sites by female black bears were not affected by proximity to roads and to houses where they were not fed. In addition, the proximity of bed sites to roads and houses of non-feeders did not differ between bear families and lone females. One might argue that

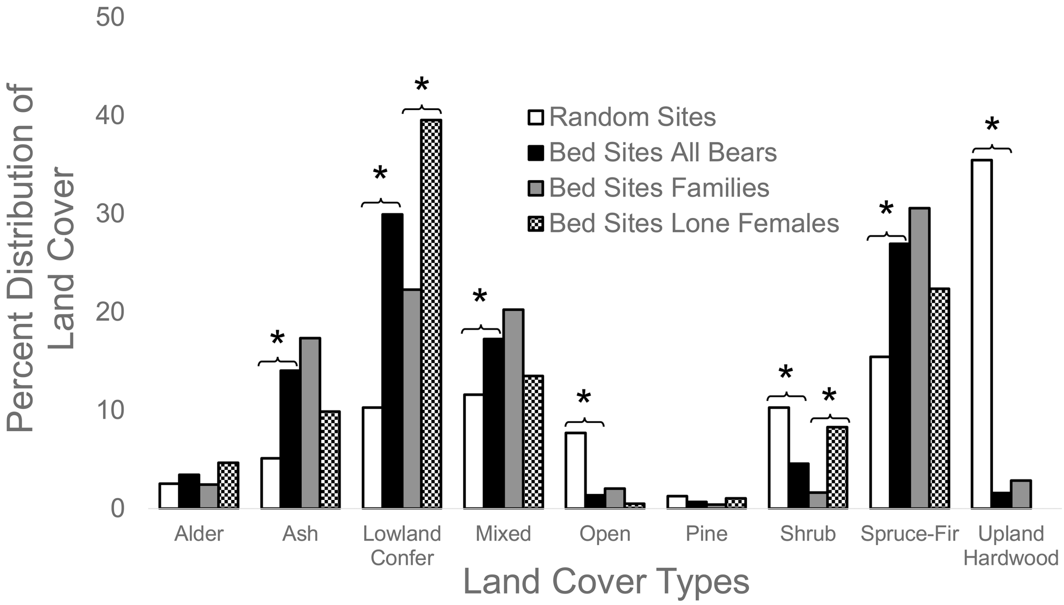

Fig. 3.—Distribution across land cover categories of control sampling sites and bed sites of all female black bears studied, just females with cubs (families), and just lone females.

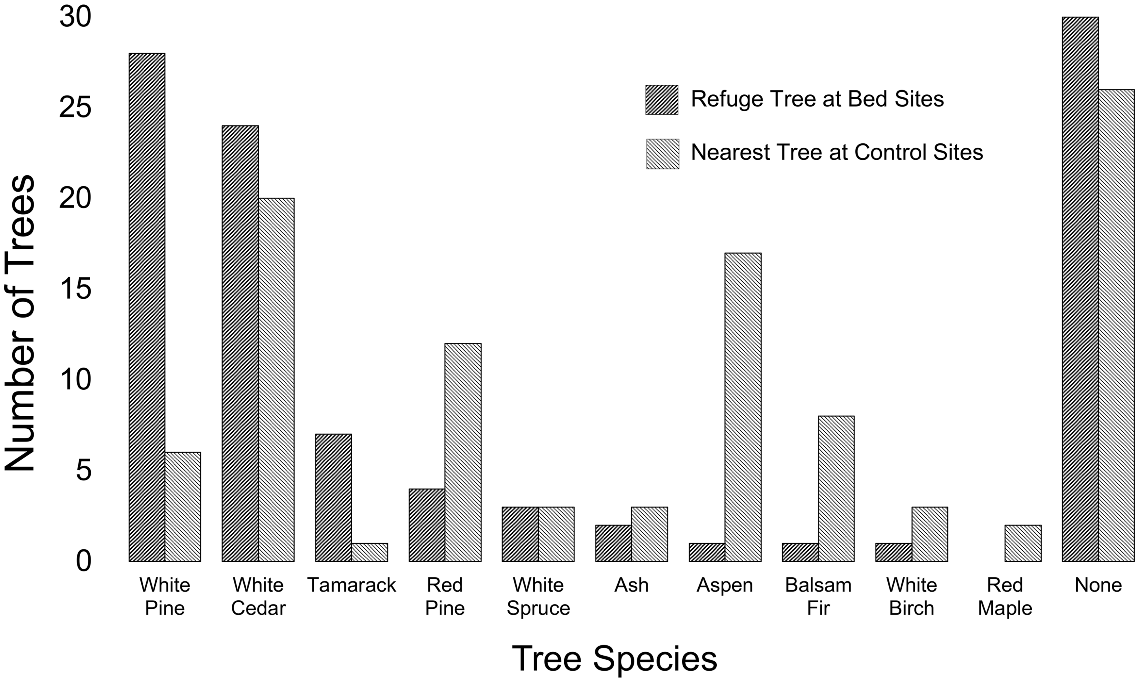

Fig. 4.—Distributions of trees of different species at bed sites (“refuge” trees) and at control sites.

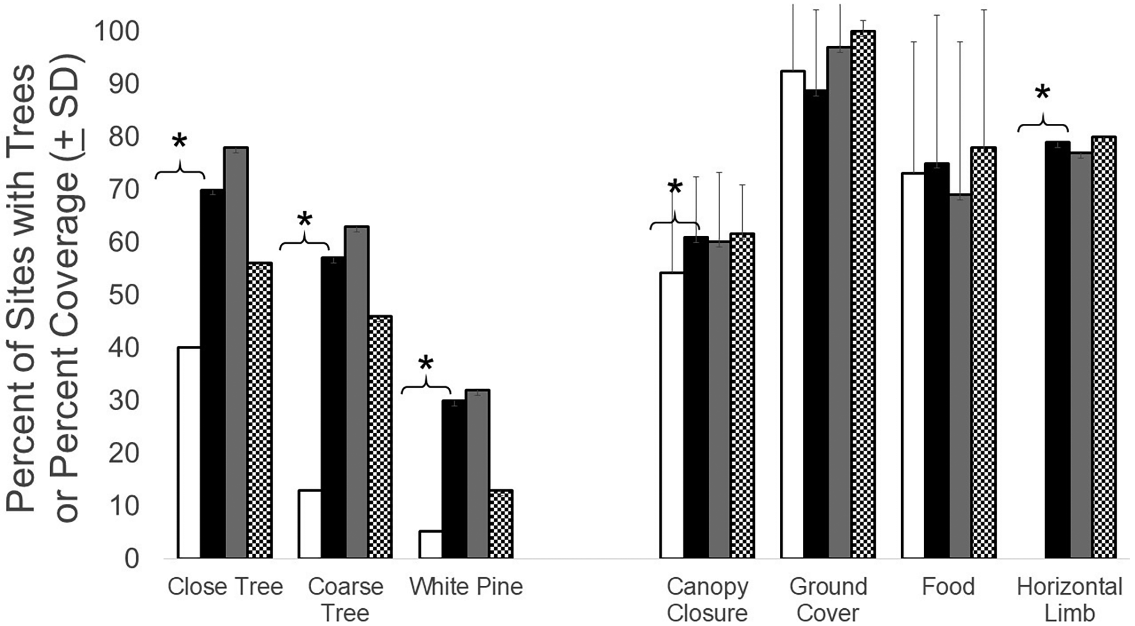

Fig. 5.—Percent of control sampling sites and bed sites of all female black bears studied, just females with cubs (families), and just lone females with respect to having a nearby tree (refuge tree), a nearby tree with coarse bark, a nearby white pine, and with respect to percent canopy closure, percent of the sampling or bed area with ground cover, percent with woody debris, and percent of open water. Legend as in Fig. 3.

bears in our study site, by being habituated to certain people, were pre-selected not to be afraid of roads and people at houses where bears were not fed. In contrast, however, these bears did not spend more time than expected near houses of nonfeeders. Given that houses in the Eagles Nest community are clustered along the shores of lakes, any bear choosing to bed in the proximity of a house where bears are fed would de facto be bedding near houses where bears are not fed. In the early spring, mothers do not bring their cubs to the houses that feed but, rather, leave them at bed sites nearby (Rogers and Mansfield unpublished data). By late spring, cubs accompanied mothers to feeding stations, but families still needed to bed nearby to accommodate the limitations of traveling with young cubs.

Finally, as the bears’ active season progressed, female black bears with cubs did not select bed sites more like those of lone females. This result contrasts with the observation of Rogers and Lindquist (1992) that females with cubs are less choosy in late summer and autumn when their cubs are large. Given this

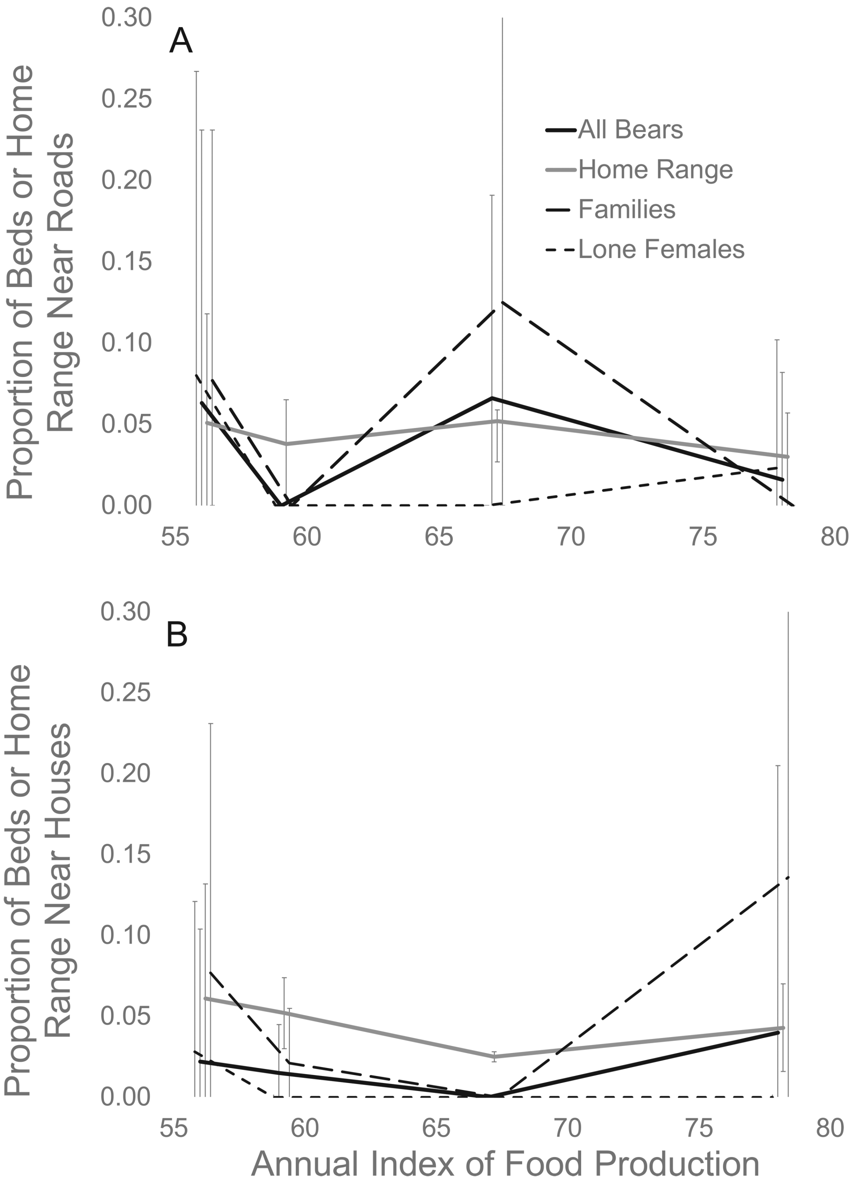

Fig. 6.—Percent of control sampling sites and bed sites of all female black bears studied, just females with cubs (families), and just lone females that were (A) near roads and (B) near houses where bears were not fed in years with different productivities of wild foods.

lack of convergence of behaviors, we hypothesize that black bear cubs do not become sufficiently able to avoid danger to change their mothers' behaviors. This continued maternal protection throughout their first summer likely increases cub survival. As the active season progressed, mother bears decreased their choice of bed sites near food, while, at the same time, lone females appeared most interested in bed sites near food in autumn. This pattern makes sense. In spring, when food is scarce, mother bears are responsible for all of the food for their cubs. Thus, being near food is critically important. As the summer progresses, food becomes more abundant and cubs eat more on their own. Lone females, in contrast, must prepare for their upcoming pregnancies and for nursing cubs in dens in the coming winter.

Black bears are highly adaptable and range over diverse habitats throughout North America. Although various species of large coarse-barked trees exist within much of the black bear range, portions of their range lack large trees with coarse bark. Given the strong preference of female black bears to bed near large trees that we documented in northern Minnesota, where do they rest in habitats lacking such trees? We hypothesize that female black bears depend heavily on other behaviors that provide safety for themselves and cubs, such as choosing bed sites with broad smell-sheds, hearing-sheds and, to a lesser degree, broad view-sheds. This hypothesis warrants testing with data from portions of the black bear range without coarse-barked, large-diameter trees.

Clearly, black bears are not alone in choosing sleeping and resting sites that confer safety (Powell and Brander 1977; Altmann 1980; Holler 1999; Baker and Hill 2003; Creel et al. 2005). Although the locations on landscapes and the physical characteristics of many mammals' rest sites have been well studied (Zielinski et al. 2004; Creel et al. 2005; Raley et al. 2012;

Thompson et al. 2012; Virgós et al. 2012), why an individual mammal chooses a particular rest or bed site at a particular time has not been well investigated. We had hypothesized that black bears would choose to rest near sites with food nearby, which was the case (75% of bed sites near food) but did not affect bears' choices because food is widespread across northern Minnesota (73% of control sites near food). When a bear finishes a foraging bout and chooses to rest for 2 h or more, seeking a site with a refuge tree is most important.

Thus, preferences for bed sites appear related more to safety than to protection from weather, despite adult black bears being large carnivorans with few predators in our study areas. Wolves curl up and sleep near a kill but black bears seek safety. We understand this as a variation on the "life-dinner principle" because safety, even when danger is relatively low, trumps the hassle of hiking to a safe place to sleep.

Acknowledgments

We thank John Borchardt for writing the initial code to find clusters of telemetry locations, Shirley Starks for developing the app for entering field data, and Marcella Rose for assisting with data collection. Greg Wilker recorded data while following bears at our Kawishiwi study site. Aaron Facka, Melissa Reynolds-Hogland and Nicholas Gould provided helpful comments on early drafts of our manuscript.

Conflict of Interest

None declared.

Literature Cited

Altmann J. 1980. Baboon mothers and infants. Harvard University Press.

Altmann S.A. 1998. Foraging for survival: yearling baboons in Africa. University of Chicago Press, Chicago.

Altmann S.A., Altmann J. 1970. Baboon ecology. University of Chicago Press, Chicago.

Amo L., Caro S.P., Visser M.E. 2011. Sleeping birds do not respond to predator odour. PLoS One 6:e27576.

Baker B.W., Hill E.P. 2003. *Beaver castor canadensis*. In: Feldhamer G.A., Thompson B.C., Chapman J.A., editors. Wild mammals of North America. Johns Hopkins University Press, Baltimore, MD; p. 288–310.

Baldellou, M., Henzi P. 1992. Vigilance, predator detection and the presence of supernumerary males in vervet monkey troops. Animal Behaviour 43:451–461.

Bard S.M., CainIII J.W. 2020. Investigation of bed and den site selection by American black bears (*Ursus americanus*) in a landscape impacted by forest restoration treatments and wildfires. Forest Ecology and Management 460:117904.

Baruch-Mordo S., Wilson K.R., Lewis D.L., Broderick J., Mao J.S., Breck S.W. 2014. Stochasticity in natural forage production affects use of urban areas by black bears: implications to management of human-bear conflicts. PLoS One 9:e85122.

Beckmann J.P., Berger J. 2003. Rapid ecological and behavioural changes in carnivores: the responses of black bears (*Ursus americanus*) to altered food. Journal of Zoology 261:207–212.

Benson-Amram S., Dantzer B., Stricker G., Swanson E.M., Holekamp K.E. 2016. Brain size predicts problem-solving ability in mammalian carnivores. Proceedings of the National Academy of Sciences of the United States of America 113:2532–2537.

Carpenter C.R. 1934. A field study of the behavior and social relations of howing monkeys (Alouatta palliata). Comparative Psychology Monographs.

Cattet M., Boulanger J., Stenhouse G., Powell R.A., Reynolds-Hogland M.J. 2008. An evaluation of long-term capture effects in urside: implications for wildlife welfare and research. Journal of Mammalogy 89:973–990.

Chirichella R., Mustoni A., Zibordi F., Armanini M., Caliari A., Apollonio M. 2019. Rent a room in the Alps: winter den site preference of native and reintroduced brown bears. Mammal Research 64:213–222.

Cirelli C., Tononi G. 2008. Is sleep essential? PLoS Biology 6:e216.

Creel S., Winnie Jr. J., Maxwell B., Hamlin K., Creel M. 2005. Elk alter habitat selection as an antipredator response to wolves. Ecology 86:2287–3397.

DelGuidice G.D. 2000. Natural history of deer in Minnesota. In: Mech L.D., editor. The wolves of Minnesota: howl in the heartland. Voyageur Press, Stillwater, Minnesota; p. 116–118.

DeVore I. 1963. Mother-infant relations in free-ranging baboons. In: Rheingold H.L., editor. Maternal behavior in mammals. John Wiley & Sons, Hoboken, New Jersey, USA; p. 305–335.

Dissel S., Angadi V., Kirszenblat L., Suzuki Y., Donlea J., Klose M., Koch Z., English D., Winsky-Sommerer R., van Swinderen B., et al. 2015. Sleep restores behavioral plasticity to Drosophila mutants. Current Biology 25:1270–1281.

Ditmer M.A., Rettler S.J., Fieberg J.R., Iaizzo P.A., Laske, T.G., Noyce K.V., Garshelis D.L. 2018. American black bears perceived the risks of crossing roads. Behavioral Ecology 29:667–675.

Gais S., Born J. 2004. Declarative memory consolidation: mechanisms acting during human sleep. Learning & Memory (Cold Spring Harbor, NY) 11:679–685.

Garrison E.P., McCown J.W., Oli M.K. 2007. Reproductive ecology and cub survival of Florida black bears. The Journal of Wildlife Management 71:720–727.

Gilbert B.K. 2019. One of us. Friesen Press, Victoria, British Columbia, Canada.

Goodall J. 1963. Feeding behavior of wild chimpanzees. Symposia of the Zoological Society of London 10:39–47.

Gould N.P. 2020. Ecology of American black bears in an urban environment. Dissertation, North Carolina State University, Raleigh.

Gray C.A., Hooker M.J., Chamberlain M.J. 2016. Reproduction and denning ecology of the central Georgia American black bear population. Ursus 27:67–77.

Hamilton W.D. 1971. Geometry for the selfish herd. Journal of Theoretical Biology 31:295–311.

Holler N.R. 1999. Oldfield mouse (Peromyscus polionotus). In: Wilson D.E., Ruff S., editors. The Smithsonian book of North American mammals. Smithsonian Institution Press, Washington, DC; p. 580–582.

Johnson H.E., Breck S.W., Baruch-Mordo S., Lewis D.L., Lackey C.W., Wilson K.R., Mao J.S., Beckmann J.P. 2015. Shifting perceptions of risk and reward: dynamic selection for human development by black bears in western United States. Biological Conservation 178:164–172.

Jonkel C.J., Cowan I.M. 1971. The black bear in spruce-fir forest. Wildlife Monographs 27:318–324.

Karelus D.L., McCown J.W., Scheik B.K., van de Kerk M., Bolker B.M., Oli M.K. 2019. Incorporating movement patterns to discern habitat selection: black bears as a case study. Wildlife Research 46:76–88.

Lima S.L., Rattenborg N.C., Lesku J.A., Amlaner C.J. 2005. Sleeping under the risk of predation. Animal Behaviour 70(4):723–736.

Mansfield S.A. 2007. Effects of supplemental food on weights and reproductive success of black bears in northeastern Minnesota. Master's thesis, Antioch University New England, Keene, New Hampshire, USA.

Maser C., Anderson R.G., Cromack Jr. K., Williams J.T., Martin R.E. 1979. Dead and down woody material. In: Thomas J.W., editor. Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington. U.S. Department of Agriculture, Forest Service, Agriculture Handbook No. 553; p. 78–95.

Mech L.D. 1988. The arctic world: Living with the pack. Voyageur Press, Stillwater, Minnesota, USA.

Mech L.D., Cluff H.D. 2011. Movements of wolves at the northern extreme of the species' range, including during four months of darkness. PLoS One 6:e25328.

Merkle J.A., Robinson H.S., Krausman P.R., Alaback P. 2013. Food availability and foraging near human developments by black bears. Journal of Mammalogy 94:378–385.

Merrick N.J. 2014. Among chimpanzees: field notes from the race to save our endangered relatives. Beacon Press, Boston, USA.

Nelson M.E. 2000. Deer movements, populations, and predation by wolves. In: Mech L.D., editor. The wolves of Minnesota: howl in the heartland. Voyageur Press, Stillwater, Minnesota, USA; p. 118–120.

Noyce K.V., Coy P.L. 1990. Abundance and productivity of bear food species in different forest types of northcentral Minnesota. International Conference on Bear Research and Management 8:169–181.

Noyce K.V., Garshelis D.L. 1997. Influence of natural food abundance on black bear harvests in Minnesota. Journal of Wildlife Management 61:1067–1074.

Pelton M.R. 2003. Black bear *Ursus americanus*. In: Feldhamer G.A., Thompson B.C., Chapman J.A., editors. Wild mammals of North America. Johns Hopkins University Press, Baltimore, Maryland, USA; p. 547–555.

Pennisi E. 2021. The simplest of slumbers. Science 374:526–529.

Powell R.A. 2005. Evaluating welfare of black bears (*Ursus americanus*) captured in foot snares and handled in winter dens. Journal of Mammalogy 86:1171–1177.

Powell R.A., Brander R.B. 1977. Adaptations of fishers and porcupines to their predator-prey system. In: Phillips R.L., Jonkel C., editors. Proceedings of the 1975 Predator Symposium. Montana Forest & Conservation Experiment Station, University of Montana, Missoula, USA; p. 45–53.

Powell R.A., Zimmerman J.W., Seaman D.E. 1997. Ecology and behaviour of North American black bears: home ranges, habitat and social organization. Chapman & Hall, London, United Kingdom.

Raley C.M., Lofroth E.C., Truex R.L., Yaeger J.S., Higley J.M. 2012. Habitat ecology of fishers in western North America: a new synthesis. In: Aubrey K.B., Zielinski W.J., Raphael M.G., Proulx G., Buskirkn S.W., editors. Biology and conservation of martens, sables and fishers: a new synthesis. Cornell University Press, Ithaca, New York, USA; p. 231–254.

Reynolds-Hogland M.J., Mitchell M.S. 2007. Effects of roads on habitat quality for bears in the southern Appalachians: a long-term study. Journal of Mammalogy 88:1050–1061.

Reynolds-Hogland M.J., Mitchell M.S., Brown D., Powell R.A. 2007. Den site selection by black bears in the Southern Appalachians. Journal of Mammalogy 88:1062–1073.

Rogers L.L. 1987. Effects of food supply and kinship on social behavior, movements, and population growth of black bears in northeastern Minnesota. Wildlife Monographs 51:1–72.

Rogers L.L. 1995. White pine use by female black bears in northeastern Minnesota. Abstracts of the 10th International Conference on Bear Research and Management, Anchorage, Alaska, USA.

Rogers L.L. 2011. Does diversionary feeding create nuisance bears and jeopardize public safety?. Human-Wildlife Interactions 5:287–295.

Rogers L.L., Lindquist E.L. 1992. Supercanopy white pine and wildlife. In: Stine R.A., Baughman M.J., editors. White Pine Symposium Proceedings NR-BU-6044. Minnesota Extension Service, University of Minnesota, St Paul, Minnesota, USA; p. 39–43.

Rogers L.L., Mech L.D. 1981. Interactions of wolves and black bears in northeastern Minnesota. Journal of Mammalogy 62:434–436.

Rogers L.L., Wilker G.W. 1992. How to obtain behavioral and ecological data from free-ranging, researcher habituated black bears. Bears: Their Biology and Management 8:321–327.

Rößler D.C., De Agrò M., Biundo E., Shamble P.S. 2021. Hanging by a thread: Unusual nocturnal resting behavior in a jumping spider. Frontiers in Zoology 18: 23. https://doi.org/10.1186/s12983-021-00410-3. Accessed 2021 Nov 4.

Sapolsky R.M. 2001. A primate's memoir: a neuroscientist's unconventional life among the baboons. Scribner, New York, New York, USA.

Sikes R.S., and the Animal Care and Use Committee of the American Society of Mammalogists. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. Journal of Mammalogy 97:663–688.

Silverman B.W. 1986. Density estimations for statistics and data analysis. Chapman and Hall, London, United Kingdom.

Sober E. 2008. Evidence and evolution: the logic behind the science. Cambridge University Press.

Stringham S.F., Rogers L.L. 2017. Fear of humans by bears and other animals (Anthropophobia): how much is natural?. Journal of Behavior 2:1009.

Thompson I.D., Fryxell J., Harrison D.J. 2012. Improved insights into use of habitat by American martens. In: Aubrey K.B., Zielinski W.J., Raphael M.G., Proulx G., Buskirk S.W., editors. Biology and conservation of martens, sables and fishers: a new synthesis. Ithaca, New York, USA: Cornell University Press; p. 209–230.

Virgós E., Zalewski A.J., Rosalino, L.M., Mergey M. 2012. Habitat ecology of Martes species in Europe. In: Aubrey K.B., Zielinski W.J., Raphael M.G., Proulx G., Buskirk S.W., editors. Biology and conservation of martens, sables and fishers: a new synthesis. Ithaca, New York, USA: Cornell University Press; p. 255–268.

Vyazovskiy V.V., Cirelli C., Pfister-Genskow M., Faraguna U., Tononi G. 2008. Molecular and electrophysiological evidence for net synaptic potentiation in wake and depression in sleep. Nature Neuroscience 11:200–208.

Walker M.P., Stickgold R. 2004. Sleep-dependent learning and memory consolidation. Neuron 44:121–133.

Xie L., Kang H., Xu Q., Chen M.J., Liao Y., Thiyagarajan M., O'Donnell J., Christensen D.J., Nicholson C., Iliff J.J., et al. 2013. Sleep drives metabolite clearance from the adult brain. Science 342:373–377.

Zielinski W.J., Truex R.L., Schmidt G.A., Schlexer F.V., Schmidt K.N., Barrett R.H. 2004. Resting habitat selection by fishers in California. Journal of Wildlife Management 68:475–482.

Submitted 01 July 2020. Accepted 12 November 2021.

Associate Editor was Jack Hopkins.