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Source: Ursus, 2024(35e18) : 1-17

Published By: International Association for Bear Research and Management

URL: https://doi.org/10.2192/URSUS-D-23-00017R1

Denning ecology of an at-risk American black bear population in a unique habitat on the Bruce Peninsula, Ontario, Canada

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Abstract: The American black bear (*Ursus americanus*) population on the Bruce Peninsula in southern Ontario, Canada, is small (~300 bears), genetically isolated from the closest bears in other parts of Ontario because of geography and urban development, and it is at risk because of habitat loss. The Bruce Peninsula is underlain by dolostone, and soils over much of the Peninsula are shallow. The bedrock is karstic with extensive networks of rock fissures and underground drainage systems created by solutional processes. During the nondenning season bears select dense mixed forest and dense deciduous forest stands. From May 1998 to February 2004, we documented the habitat requirements of denning black bears on the Bruce Peninsula and described the characteristics of winter dens in this unique substrate. Thirteen of 30 (43%) dens were located in dense mixed forests, 12 of 30 (40%) were located in dense coniferous forests, and 4 of 30 (13%) were located in dense deciduous forests. Eighty-one percent of dens (25 of 31) were within rock crevices often >2 m deep and ending in a subsurface chamber. Of the remaining dens, 3 were excavated, 2 were under brush piles, and 1 was under a large boulder on a steep talus slope. Twenty-one of 29 dens were located with potential sanctuary trees (>30 cm diameter at breast height) within 30 m of the den. Population viability analysis determined the most effective management action that would ensure persistence of black bears on the Peninsula to be conserving habitat outside of Bruce Peninsula National Park. The importance of dense mixed and dense coniferous stands for denning shown in this study emphasizes that point.

Key words: American black bear, Bruce Peninsula, denning, den site characteristics, habitat selection, karst, Ontario, *Ursus americanus*

DOI: 10.2192/URSUS-D-23-00017R1 ***Ursus 35:article e18 (2024)***

American black bears (*Ursus americanus;* hereafter, black bear) spend the winter in a den as a response to an ecological problem: the seasonal shortage of food. Parturient females spend the winter in a den in response to an additional problem: they give birth to altricial young weighing about 0.3 kg (Oftedal et al. 1993) between late December and mid-February during adverse weather conditions and must provide a safe environment for the cubs' early development (Clark et al. 2020). In northern portions of the range, such as Ontario, Canada, black bears may be in a den for 6–7 months (Kolenosky and Strathearn 1987), whereas in southern areas bears may den for about 3 months and males and nonparturient females may be active during much of the winter (Hellgren and Vaughan 1989, Wooding and Hardisky 1992, Hightower et al. 2002, Dobey et al. 2005, Mitchell et al. 2005). Nevertheless, across the range, secure winter dens are important to black bears, and they are essential to cub survival and the reproductive success of adult females because parturition and initial parental care occur there (Powell et al. 1997, Clark et al. 2020).

The population of black bears inhabiting the Bruce Peninsula of southern Ontario presents a conservation challenge. Constrained by water on 3 sides and concentrated development to the south, the population of black bears on the Bruce Peninsula may be genetically isolated from the larger, contiguous Ontario black bear population (Pelletier et al. 2012, 2017), likely numbers only about 300 individuals (Obbard et al. 2016), and is

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at risk of extirpation unless habitat outside Bruce Peninsula National Park is conserved and harvest from hunting is reduced (Howe et al. 2007). Habitat use by black bears on the Peninsula during the spring, summer, and autumn has been described (Obbard et al. 2010), and that study documented the importance of dense deciduous and dense mixed forest stands to bears on the Peninsula. However, the habitat requirements for winter denning on the Bruce Peninsula have not been previously described.

The Bruce Peninsula is underlain by dolostone (magnesium rich limestone) bedrock of Middle Silurian age (ca. 430 M yr BP; Cowell 1976, Ross et al. 1989). The bedrock is karstic with extensive networks of rock fissures created by solutional processes, many leading to underground drainage systems through sinkholes (Cowell 1976, Ross et al. 1989). Much of the Peninsula has bedrock exposed at or near the surface and soils are shallow (Hoffman and Richards 1954, Moreland 1996)—the combination of shallow soils underlain by porous dolomite is a marked contrast to areas where denning in other populations of black bears has been documented.

Small populations occupying isolated habitats, such as the black bears on the Bruce Peninsula, are susceptible to random demographic and genetic effects and to natural catastrophes and, as a result, have increased extinction probabilities (Shaffer and Samson 1985, Lande 1993, Lacy 2000). For bear populations, survival of adult females is important to population persistence, but reproductive output and recruitment of young into the population is critical to determining population growth rate (Oli and Dobson 2003, Beston 2011), especially for small populations (Hooker et al. 2015). Across their range, black bears use a variety of den sites including ground nests, brush piles, excavations, rock crevices, downed trees, hollow logs, the base of hollow trees, and elevated tree cavities (Kolenosky and Strathearn 1987, Hellgren and Vaughan 1989, Hayes and Pelton 1994, Oli et al. 1997, Powell et al. 1997, Garrison et al. 2007, Crook and Chamberlain 2010, Gray et al. 2017). Types of dens used by black bears vary among populations, and the denning period is critical to cub survival; therefore, it is important to develop population-specific denning habitat information to provide input for conservation and management. Conservation of the small population of black bears on the Bruce Peninsula depends in part on a full understanding of habitat requirements during all seasons (Howe et al. 2007).

The objectives of our study were to document the habitat requirements of denning black bears on the Bruce Peninsula and to describe the characteristics of winter dens. To meet these objectives, we examined the following: (1) habitat use at the den site level; (2) characteristics and type of den used in relation to reproductive status, sex, and age of bear; (3) location of den sites in relation to home ranges of neighboring bears; (4) fidelity of bears to den type; and (5) fidelity of offspring to maternal den type. We hypothesized that cover type and soil depth would influence specific densite choice. We also hypothesized that females with offspring would select smaller dens with presumably more thermally efficient properties than dens selected by other classes of bears.

Study area

This study was conducted from May 1998 to February 2004 on the Bruce Peninsula, which separates Lake Huron from Georgian Bay in southern Ontario and is the northern extension of the contiguous Niagara Escarpment (Fig. 1). The Peninsula (ca. 950 km^2) is characterized by a wide diversity of cover types: mixed forests, wetlands, alvars, agricultural lands (pastures and croplands), and shorelines (Suffling et al. 1995). At the north end of the Peninsula occur conifer and mixed conifer–deciduous forests, with small islands of pure deciduous forest that include hard mast–producing species (Young et al. 1996). Historically (Bennett 1992), and more recently (Suffling et al. 1995), the forest toward the north of the Peninsula had a higher component of conifers with deciduous species in higher proportion toward the south of the Peninsula. Bruce Peninsula National Park (BPNP; ~156 km^2), created in 1987, covers a considerable proportion of the north end of the peninsula south of Tobermory (Fig. 1). Pastures and croplands make up a small portion of the northern Peninsula but are extensive in the central to southern region.

The climate is continental, moderated by the Great Lakes, with long, moderate winters and short, cool summers (Moreland 1996). Mean air temperatures at Wiarton toward the south of the Peninsula are −6.3°C in January and 18.9°C in July (Climate Normals 1981–2010; https://climate.weather.gc.ca/climate_normals/). Extreme temperatures range from −35°C to 35°C. Average total rainfall for the area is 75.1 cm mainly during April to November, with a mean annual snowfall of 40.5 cm mainly during December–March; total precipitation averages 104.8 cm.

Fig. 1. Study area on the Bruce Peninsula, south-central Ontario, Canada, where we documented the habitat requirements of denning American black bears (*Ursus americanus*), 2000–2004. Insets show location of Ontario within Canada and study area within Ontario.

Dominant tree species include eastern white cedar (*Thuja occidentalis*), balsam poplar (*Populus balsamifera*), trembling aspen (*P. tremuloides*), sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), northern red oak (*Quercus rubra*), white pine (*Pinus strobus*), and spruce species (*Picea* spp.). Common understory species include dogwoods (*Cornus* spp.), balsam fir (*Abies balsamea*), choke cherry (*Prunus virginiana*), wild raspberry (*Rubus idaeus* spp.), bearberry (*Arctostaphylos uva-ursi*), and wild sarsaparilla (*Aralia nudicaulis*; Kaiser 1995, Suffling et al. 1995).

Methods

Summer captures

We live-captured bears in barrel or culvert traps from May 1998 to July 2003. Within BPNP, we selected trap site locations ($n = 25$) to avoid large gaps in the sampling pattern and so that all adult females had an equal opportunity of capture. Trap spacing was such that no point within the study area was >2 km from a trap site, which is less than the average radius of the home range of an adult female black bear in Ontario (Schenk et al. 1998). Outside the park, we located trap sites in accessible areas in a nonsystematic fashion to target known bears in the area.

Once captured, we chemically immobilized bears with an intramuscular injection of either Telazol® (Fort Dodge Laboratories, Inc., Fort Dodge, Iowa, USA) at 4–6 mg/kg based on estimated body mass (Gibeau and Paquet 1991), or a mixture of ketamine hydrochloride (Rogarsetic™; Rogar/STB, Inc., London, Ontario, Canada) at 4.5 mg/kg and xylazine hydrochloride (Rompun®; Bayer, Inc., Etobicoke, Ontario, Canada) at 2.0 mg/kg (Addison and Kolenosky 1979). We reversed xylazine hydrochloride with yohimbine hydrochloride (Antagonil®; Wildlife Pharmaceuticals Canada, Inc., Calgary, Alberta, Canada) at 0.2 mg/kg (Garshelis et al. 1987). We took standard morphometric measurements and extracted the first premolar tooth to determine age by counts of cementum annuli (Stoneberg and Jonkel 1966). Following recovery, we released most bears at the site of capture though a few individuals involved in human–bear conflict were relocated up to 5 km from the capture site. Handling procedures were approved annually by the Animal Care Committee of the Ontario Ministry of Natural Resources (Permit numbers 21-98 to 21-04) and followed guidelines of the Canadian Council on Animal Care (Canadian Council on Animal Care 2003) and the Animal Care and Use Committee of the American Society of Mammalogists (Sikes and Gannon 2011).

We fitted all adult females captured with very high frequency (VHF) radiocollars with a 2-hour delay mortality switch (Lotek Engineering Inc., Newmarket, Ontario, Canada). We focused on adult females because, in addition to fecundity, the most critical input parameters for modeling growth in bear populations, such as survival and age at first reproduction, are derived from females (Knight and Eberhardt 1985, Yodzis and Kolenosky 1986, Beston 2011), and parturient females select the dens that provide security to newborn cubs.

Den field work

We determined approximate locations of dens of radiocollared bears in late autumn or early winter each year using a combination of ground and aerial telemetry and standard telemetry techniques (White and Garrott 1990). For habitat analysis we determined exact locations of dens during winter handling using a handheld global positioning system (GPS) unit. We determined the reproductive status of individuals during winter den visits. During den visits, all bears older than cubs of the year were chemically immobilized with a combination of ketamine hydrochloride and xylazine hydrochloride at an approximate dosage of 4.5 mg/kg and 1 mg/kg, respectively, based on estimated body mass. We halved the xylazine hydrochloride dosage from the recommended summer dosage (Addison and Kolenosky 1979) because xylazine hydrochloride further depresses the respiration rate of the already depressed respiration rate of hibernating bears (Tøien et al. 2011). We replaced radiocollars of adult females as necessary and fitted yearlings with expandable radiocollars (Strathearn et al. 1984). At the end of handling, we returned bears to the den, placed them in a lateral recovery position, reversed xylazine hydrochloride with yohimbine hydrochloride (Garshelis et al. 1987), and closed up the den entrance with brush.

We noted den type (e.g., tree cavity, ground nest den, excavation, brush pile, blowdown tree, rock cavity, human-made structure) along with characteristics of the site (percent canopy closure, presence of sanctuary or refuge trees; Rogers and Lindquist 1992). In Minnesota, USA, sanctuary or refuge trees were large-diameter (>50 cm diameter breast height [dbh]) supercanopy white pines, which functioned as escape cover for young cubs in the period after emergence from the den in spring (Rogers and Lindquist 1992). In an Ontario study (Kolenosky and Strathearn 1987), refuge trees were 20–200 m from the den site. For our study, we designated candidate sanctuary trees as being >30 cm dbh and within 30 m of the den site. We measured several features of the den: den entrance (height and width), den tunnel (length, height, and width), and den chamber (length, height, and width), and noted the depth and components of bedding material in the den chamber (all measurements in cm). We also documented den entrance orientation (horizontal or vertical), and den entrance direction (compass heading).

For analysis of den characteristics, we assigned bears to their age class in autumn at the time of den selection. We considered all bears older than 4 years to be adults, subadults were 2–4 years, and independent yearlings were between 1 and 2 years of age. Small sample sizes required us to combine data for yearlings and subadults for analysis.

Table 1. Cover types and linear features used in American black bear (*Ursus americanus*) denning habitat analyses, and acronyms used in text, Bruce Peninsula, Ontario, Canada, 2000–2004.

Cover type or linear feature	Acronym
Dense coniferous forest	DCF
Dense deciduous forest	DDF
Dense mixed forest	DMF
Exposed rock	ER
Pasture and croplands	PCL
Marsh	MAR
Settlements and developed lands	SDL
Sparse forests	SF
Water	WAT
Roads	ROA
Snowmobile trail	SNO
Streams	STR

Analysis

Telemetry. We converted locations obtained via aerial telemetry from latitude and longitude coordinates to Universal Transverse Mercator (UTM) coordinates using Geographic Calculator™ (version 5.1) software (Blue Marble Geographics, Gardiner, Maine, USA). We estimated ground locations by the Lenth maximum likelihood estimation (MLE) technique (Lenth 1981) using Locate II software (Pacer 1990) and recorded them to the nearest meter as a UTM coordinate (Schenk et al. 1998).

Although point locations only serve to indicate a study animal's trajectory through space (Aebischer et al. 1993), inferences from habitat selection analysis at the den site level may be influenced by autocorrelation of telemetry locations. Therefore, we selected point locations for analysis that were separated by ≥12 hours to establish home range area and to examine the location of den sites within an individual's home range as well as relative to the home range of neighboring individuals.

Den habitats. Den site locations were displayed and analyzed using ArcView GIS™ 3.2a (Environmental Systems Research Institute, Inc. 1992–2000, Redlands, California, USA). We overlaid spatial coordinates of dens on an unsupervised satellite classification of the Peninsula collected from Landsat Thematic Mapper 7 on 26 September 1999. The image was classified into 20 cover types at 25-m pixel size (Geosphere Infomatic Services 1999). We reclassified these 20 cover types into 9 cover types (dense coniferous forests [DCF], dense deciduous forests [DDF], dense mixed forests [DMF], exposed rock [ER], marshes [MAR], pastures and croplands [PCL], settlement and developed lands [SDL], sparse forests [SF], water [WAT]) and 3 linear features (roads [ROA], snowmobile trail [SNO], and streams [STR]) by collapsing deciduous and coniferous swamps and open and treed bogs into a marsh cover type, and golf courses and airports into settlement and developed lands (Table 1).

We assessed the accuracy of the satellite classification (Obbard et al. 2010) by comparing site classification from the map to a field assessment of the same site using the field protocol of the southern Ontario ecological land classification (ELC) system (Lee et al. 1998). We then created a confusion matrix to assess the accuracy of the supervised image (Congalton and Green 1999) and determined the overall accuracy of the unsupervised satellite classification.

We used the Nearest Features v. 3.7a program (Jenness 2004) to determine distances between each location and each cover type and linear feature using ArcView GIS™ 3.2a (Environmental Systems Research Institute, Inc. 1992–2000).

Habitat availability. Habitat availability can be defined as the quantity accessible to the animal or population of animals in the environment (Alldredge et al. 1998). Almost all methods of habitat analysis compare habitat use with some measure of habitat availability (Aebischer et al. 1993). For this analysis, we defined available habitat as all cover types within each bear's home range and estimated habitat availability within a bear's home range by establishing the bounds of home ranges using the fixed-kernel home range utilization distribution (KHR; Worton 1989) with the least-square cross-validation (LSCV) technique smoothing parameter. The LSCV method produces estimates with small variance and bias (i.e., with sample size bias; Bowman 1985, Seaman et al. 1999). Fixed-kernel home range utilization distributions are used to assess an animal's probability of occurrence at each point in space, highlighting centers of activity (Millspaugh et al. 2000). We identified centers of activity to determine whether individuals denned within areas exclusively used by them, or in areas of overlap shared with other bears. Thus, we overlaid individual 50%, 75%, and 95% area contours to determine in what part of their home range bears selected a den site (i.e., in the center $\leq$50% KHR, or on the periphery $\geq$75%).

We developed KHR estimates for individual bears using the Animal Movement Analysis (with Spatial Analyst) extension (Hooge et al. 2001) in ArcView GIS™ 3.2a (Environmental Systems Research Institute, Inc. 1992–2000). We estimated habitat availability within each individual 95% KHR by generating 250 points from a uniform random distribution using the Random Point Generator v1.27 extension (Jenness 2001). Fixed-kernel home range utilization distributions were estimated for individuals that had a minimum of 20 and a maximum of 196 locations for their overall active season using the Animal Movement Extension (Hooge et al. 2001) in ArcView GIS™ 3.2a (Environmental Systems Research Institute, Inc. 1992–2000).

Habitat use. We used the distance-based approach founded on the distances of animal locations to all cover type categories (Conner and Plowman 2001, Conner et al. 2003) that was used by Obbard et al. (2010) to determine whether habitat selection occurred at the den site level. Each den site location determined via hand-held GPS was used to examine den-site selection relative to the availability of cover types and linear features within each individual home range. We considered all cover types within home ranges to be available habitat and habitat use was derived from the den site. For each bear, we determined the distance from each random point within the home range to the nearest representative of each cover type or linear feature, and calculated the average distance from each den site to each cover type and linear feature. This created a vector of mean distances (r_i) for each animal (i), representing expected values under a null hypothesis of no selection. Then we repeated this step using the actual distances from each den site (u_i). We created a vector of ratios (d_i) for each animal by dividing each element in u_i by the corresponding element in r_i. We calculated the mean of the d_i as ρ and calculated a multivariate analysis of variance (MANOVA) to determine whether ρ differed from a vector of 1s (null hypothesis of no selection). We considered habitat selection to occur if ρ differed from a vector of 1s. To determine which cover types were used disproportionately, each element within ρ was tested to determine whether it differed from 1 using a paired t-test. Finally, we used pairwise comparisons (Aebischer et al. 1993, Conner et al. 2003) to assess relative habitat preferences. We intersected KHR contours with the land cover map of the Peninsula and exported habitat attributes for each home range for analysis.

Den and site characteristics. We compared den dimensions (entrance height and width; tunnel height, width, and length; and chamber height, width, and length) among den types using a single-factor analysis of variance (ANOVA). We compared the cross-sectional area of den structures used by males and females with t-tests. We estimated the cross-sectional areas of den chambers using length $\times$ height. We compared the cross-sectional area of den entrances among den types using single-factor ANOVA. Multiple den sites were not documented for all individuals, so we did not conduct repeated measures tests. We assumed multiple observations of individuals across years to be independent because sample sizes were small. To avoid Type II error, we accounted for the lack of independence informally by choosing $\alpha = 0.10$. We calculated mean compass direction that den entrances faced and compared these across classes of bears using circular statistics (Zar 1999).

Results

General results

We fitted 9 adult females, 3 subadult females, and 3 subadult males with VHF radiotransmitters during the study and visited them in winter dens. Of these, all 15 bears were visited once in the den. In ensuing years, 7 of 15 were visited a second time (6 adult females; 1 subadult male), 5 of 15 were visited 3 times (5 adult females), 3 adult females were visited 4 times, and 1 adult female was visited in all 5 years from 2000 to 2004, yielding 31 den visits over the study. Typical of field studies, individual animals entered the study at different times. Ages of independent bears visited in dens ranged from 2 to 14 years. As a result of dropped collars and high mortality related to human–bear conflicts, few

Fig. 2. Examining the entrance to an occupied American black bear (*Ursus americanus*) den in a vertical fissure in the dolostone bedrock, Bruce Peninsula, Ontario, Canada. Photo credit: W. Waterton.

yearling and subadult bears carried radiocollars for a sufficient time to yield information on denning requirements of subadults. The logistics of handling bears in rock crevices did not allow us to obtain weights or den measurements for all individuals.

The analysis of the confusion matrix indicated that the overall accuracy of the unsupervised 1999 satellite classification was 88.5% (Obbard et al. 2010). Most conflicts between visited locations and the unsupervised classification occurred with DMF, which resulted in a user's accuracy of 41%. DMF was most commonly confused with DCF (10 of 22) followed by DDF (2 of 22) and MAR (1 of 22). All other cover types produced user's accuracy >85% (Obbard et al. 2010).

The study area was 26% DCF, 13.8% DDF, 22.1% DMF, 2.0% ER, 7.2% MAR, 14.8% PCL, 0.8% SDL, 10.1% SF, and 3.2% WAT, with 15.4 km of SNO and 417.51 km of ROA.

Den site characteristics

Of the dens examined, 81% (25 of 31) were within rock crevices (narrow vertical fissures $\geq$2 m deep in the dolostone bedrock (Fig. 2). These crevices were solutionally widened joints in the pavement bedrock (i.e., grikes or cleftkarren). The crevices typically ended in a subsurface chamber, which also resulted from solutional processes originally created by glacial meltwater and the flow of water from the draining of postglacial lakes, and more recently by rain and by meltwater from winter snowpack (Cowell 1976, Ross et al. 1989). Of the remaining dens, 3 were excavated, 2 were under brush piles, and 1 was under a large boulder on a steep talus slope on the Georgian Bay shore of the Peninsula (Table 2). Twenty percent (3 of 15 opportunities) of bears switched den types, and those switched from other den types to rock crevices in subsequent years. Nine of 11 females with cubs, 5 of 8 females with yearlings, 2 of 3 solitary females, and 5 of 7 yearlings constructed a den where sanctuary trees were within 30 m (Table 2). Potential sanctuary trees were eastern white cedar, red pine (*Pinus resinosa*), jack pine (*Pinus banksiana*), and white spruce (*Picea glauca*).

Forty-seven percent of all dens (14 of 30) faced west (226–315°), 23% (7 of 30) faced east (46–135°), 20% (6 of 30) faced south (136–225°), and 7% (2 of 30) faced north (316–45°). Circular mean angles of den entrance orientation for adult females with cubs, adult females with yearlings, subadults, and lone adult females were 81°, 166°, 21°, and 62°, respectively. Statistical comparison of den entrance orientation among classes of bears was not possible because of small sample sizes in some classes.

Den characteristics

Seventy-six percent of bears (22 of 29) raked leaves, twigs, or grass into their dens to line the bed in the den chamber. Only 10% (3 of 30) plugged or partially plugged their den entrances with forest litter. There was moderate evidence that more females than males lined dens ($t = -5.71$, $P = 0.012$), but no evidence of differences in proportion of dens lined among other classes of bears (Table 2).

There was no evidence that the cross-sectional area of entrances (height $\times$ width) differed among den types ($F_{3,27} = 0.84$, $P = 0.484$). There was no evidence that the cross-sectional area of den entrances used by females differed from that of dens used by males ($F_{1,29} = 0.25$, $P = 0.618$). Finally, there was no evidence ($F_{3,27} = 0.02$, $P = 0.995$) that the cross-sectional area of den

Table 2. Characteristics of American black bear (*Ursus americanus*) dens on the Bruce Peninsula, Ontario, Canada, 2000–2004.[a]

	Den type				Entrance orientation		Average entrance direction	Plugged[b]		Lining[b]		Sanctuary trees		Crown cover
Sex-age class	Rock crevice	Excavated	Brush	Under boulder	Horizontal	Vertical	Degrees	y	n	y	n	y	n	% ± SD
Female with yearling	6	2	0	1	1	8	166	0	9	7	2	5	3	54.2 ± 24.9
Female with cubs	11	1	0	0	4	8	81	2	9	9	3	9	2	48.9 ± 27.2
Solitary adult female	2	0	1	0	1	2	62	1	2	3	0	2	1	56.7 ± 20.8
Subadults	6	0	1	0	1	6	21	0	7	3	2	5	2	75.0 ± 17.3

[a]Sample sizes may vary between variables because of the difficulty of accessing some dens in rock crevices.
[b]y = yes, n = no.

entrances for females accompanied by cubs of the year ($\bar{x}$ = 130.5 cm^2, SE = 16.8, n = 12), differed from the cross-sectional area of den entrances for yearlings ($\bar{x}$ = 125.2 cm^2, SE = 32.1, n = 9), solitary adults ($\bar{x}$ = 134.0 cm^2, SE = 39.0, n = 3), or subadults ($\bar{x}$ = 134.4 cm^2, SE = 19.8, n = 5).

The mean diameter of den chambers was 177.6 cm (SE = 11.7, n = 27; Table 3). There was moderate evidence that diameters of den chambers differed among den types ($F_{3,23}$ = 4.70, P = 0.011). However, there was no evidence of differences in the diameter of den chambers used by male and female bears (t = 0.45, P = 0.653), or by different family types (i.e., females with cubs, females with yearlings, solitary females or subadults; $F_{3,23}$ = 0.49, P = 0.687).

There was very strong evidence that the cross-sectional areas of den chambers differed among den types ($F_{3,23}$ = 96.66, P < 0.001). The den located under a large boulder on a talus slope had a larger den chamber than dens in excavations, in rock crevices, or under brush. There was no evidence of a difference in chamber cross-sectional area among sex class (t = 0.25, P = 0.618) or family grouping ($F_{3,23}$ = 0.85, P = 0.477; Table 3). There was no evidence that den chamber area of females with yearlings ($\bar{x}$ = 3.97 m^2, SE = 2.51, n = 9) differed from those of females with cubs ($\bar{x}$ = 1.86 m^2, SE = 0.47, n = 12; t = −0.95, P = 0.355). Solitary adults had the third largest den chamber ($\bar{x}$ = 1.63 m^2, SE = 0.34, n = 3) followed by subadults ($\bar{x}$ = 0.67 m^2, SE = 0.50, n = 7).

Den locations within home range

Seven of 30 dens (23.3%) were located within the inner 50% home range area polygon, 16 of 30 (53%) were located outside the 50% utilization contour, but within the inner 95% area polygon, and 7 of 30 (23.3%) denned at distances beyond the inner 95% area polygon. There was no evidence that female bears with cubs denned within their inner 50% area polygon more often than did other classes of bears (P = 0.83).

Fifteen of 30 (50%) bears had other bears den within some portion of their active range. Of that group, 10 (67%) denned within the inner 95% area polygon, 8 (53%) denned within the 75% polygon, and only 3 (20%) denned within the 50% area polygon of another bear. Of the 3 individuals that denned within the 50% area polygon of another bear, 1 subadult denned within the inner 50% area polygon of his mother.

Den habitat

Of the 9 available cover types, 29 of 30 (97%) dens were within dense forest cover types, and the remaining den was in the pastures and cropland cover type. Thirteen of 30 (43%) dens were located in dense mixed forests, 12 of 30 (40%) were located in dense coniferous forests, and 4 of 30 (13%) were located in dense deciduous forests. We did not assign the den of the bear that denned in the talus slope on the Georgian Bay side of the peninsula to a cover type.

The analysis of distances ratios indicated that there was very strong evidence that black bear den locations differed from random locations ($F_{11,20}$ = 5.24, P < 0.001). Examination of distances to cover types in univariate space indicated that there was very strong evidence that black bear dens were found closer to DMF than expected (ρ_{dmf} = 0.44 ± 0.11 [$\bar{x}$ ± SE], t_{30} = 4.99, P < 0.001), and moderate evidence that dens were closer to SNO (ρ_{sno} = 0.72 ± 0.12, t_{30} = 2.43, P = 0.018) than expected. There was very strong evidence that dens were farther away from PCL (ρ_{pcl} = 1.874 ± 0.22, t_{30} = −4.00, P < 0.001) and

Table 3. Dimensions ($\bar{x}$ ± SD) of American black bear (*Ursus americanus*) dens, Bruce Peninsula, Ontario, Canada, 2000–2004.[a]

	Entrance			Tunnel				Chamber			
Sex-age class	*N*	Height (cm)	Width (cm)	*N*	Height (cm)	Width (cm)	Length (cm)	*N*	Height (cm)	Width (cm)	Length (cm)
Female with yearling	9	66.9 ± 30.5	63.6 ± 38.7	9	95.9 ± 91.3	67.9 ± 29.4	127 ± 51.1	9	70 ± 21.2	106.4 ± 61.9	166.9 ± 52.3
Female with cubs	12	72.1 ± 59.4	53.1 ± 46.2	12	41.2 ± 8.5	67.3 ± 31.9	116 ± 84.1	12	58.3 ± 11.8	137.7 ± 65.1	198.6 ± 227.3
Solitary adult female	3	84 ± 71.4	50 ± 25.9	3	32 ± 0	54 ± 3.6	162.3 ± 55.0	3	65 ± 7	117 ± 44.6	140.3 ± 18.6
Subadults	7	50.4 ± 27.7	72 ± 56.7	7	48.3 ± 23.1	52.2 ± 28.3	162.6 ± 83.5	7	37.3 ± 7.4	102.3 ± 69.0	123.7 ± 66.3

[a]Sample sizes may vary between variables because of the difficulty of accessing some dens in rock crevices.

ROA ($\rho_{roa} = 1.68 \pm 0.17$, $t_{30} = -3.91$, $P < 0.001$) than expected, and strong evidence that dens were farther away from SDL ($\rho_{sdl} = 1.32 \pm 0.10$, $t_{30} = -3.27$, $P = 0.002$) and STR ($\rho_{str} = 1.43 \pm 0.92$, $t_{30} = -2.52$, $P = 0.014$) than expected. There was no evidence of any difference between black bear den locations and random points with regard to distance to the other cover types: DCF ($\rho_{dcf} = 1.02 \pm 0.42$, $t_{30} = -0.05$, $P = 0.420$), DDF ($\rho_{ddf} = 1.23 \pm 0.17$, $t_{30} = -1.37$, $P = 0.177$), ER ($\rho_{er} = 1.11 \pm 0.11$, $t_{30} = -1.01$, $P = 0.318$), MAR ($\rho_{mar} = 1.10 \pm 0.18$, $t_{30} = -0.60$, $P = 0.553$), SF ($\rho_{sf} = 1.42 \pm 0.24$, $t_{30} = -1.75$, $P = 0.085$), and WAT ($\rho_{wat} = 1.13 \pm 0.13$, $t_{30} = -1.00$, $P = 0.321$).

A ranking of cover types based on the values of the elements in ρ indicated that DMF was used most, followed by SNO (Fig. 3). Pairwise comparisons (Table 4) of distance ratio associated with cover types provided moderate evidence that DMF was preferred over all cover types ($P < 0.05$) except DCF ($P = 0.146$) and SNO ($P = 0.116$). There was moderate evidence that SNO was preferred over all cover types ($P < 0.05$) except DCF ($P = 0.497$) and DMF ($P = 0.116$). There was moderate evidence that WAT was preferred over PCL ($P = 0.009$) and ROA ($P = 0.029$). There was moderate evidence that MAR was preferred over PCL ($P = 0.012$) and ROA ($P = 0.024$). There was moderate evidence that DDF was preferred over PCL ($P = 0.029$). There was strong evidence that ER was preferred over PCL ($P = 0.003$) and ROA ($P = 0.011$). There was moderate evidence that SDL was preferred over PCL ($P = 0.014$) and ROA ($P = 0.017$) and that STR was preferred over PCL ($P = 0.030$).

Discussion

Habitat use by black bears in the nondenning season is well-documented across the range including northern areas (Jonkel and Cowan 1971, Lindzey and Meslow 1977, Davis et al. 2006, Carter et al. 2010, Duquette et al. 2017) and the Bruce Peninsula population (Obbard et al. 2010). We showed that most bears on the Peninsula denned within dense forested cover types. Black bears showed preference for denning in mature forest stands elsewhere in northern populations (Tietje and Ruff 1980, Kolenosky and Strathearn 1987, Davis et al. 2012). At the den site level, bears on the Peninsula were found farther away from settlement and developed lands and farther from roads than expected, suggesting that even though bears had these features in their home range, they avoided them when selecting a den site.

Pairwise comparisons of distance ratios indicated that dense mixed forest stands and the snowmobile trail were preferred. Though there could be considerable disturbance on the snowmobile trail during winter, there would be no disturbance on the snowmobile trail at the time bears were selecting a den site. Rather than interpreting the pairwise comparison to suggest that bears showed preference for the snowmobile trail, it is more reasonable to conclude that the bears did not avoid the trail because there was no disturbance at the time a den site was selected. The snowmobile trail runs along the eastern side of the Peninsula, through the National Park and much of the undeveloped dense forests that occur there. Thus, bears are likely selecting to den in dense forested habitat rather than reacting positively to the snowmobile trail.

Twenty-one of 29 dens were located with potential sanctuary trees (Kolenosky and Strathearn 1987, Rogers and Lindquist 1992) within 30 m. We generally identified sanctuary trees as conifers (eastern white cedar, red pine, jack pine, and white spruce), all of which have rough bark that would enable young cubs to easily climb to safety (Hosie 1979). For example,

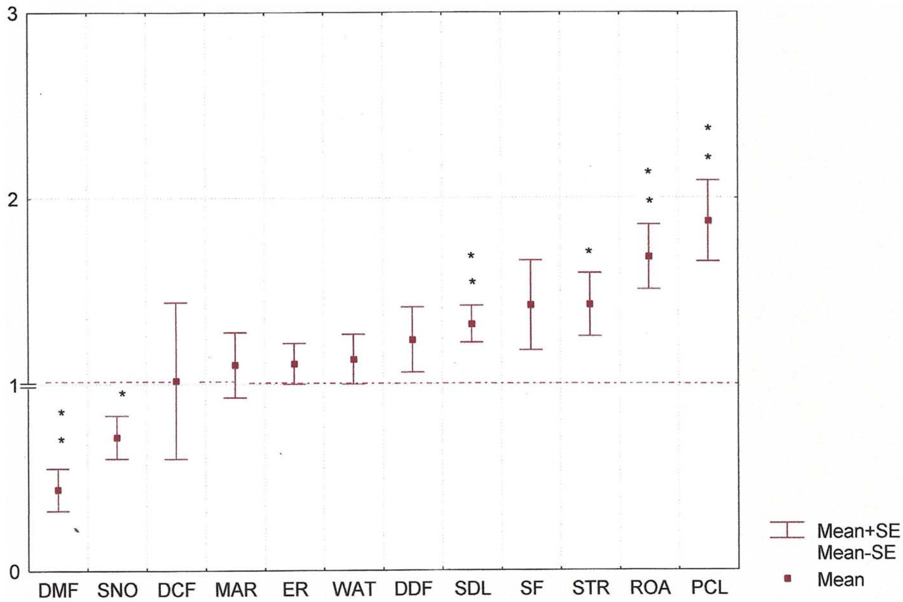

Fig. 3. Habitat rankings (most preferred [values $<$1.0] to least preferred [values $>$1.0]), based on average distances between American black bear (*Ursus americanus*) den site locations and a given habitat divided by the average random distance to the same habitat, Bruce Peninsula, Ontario, Canada (2000–2004). For habitats marked with *, there was moderate evidence that they differed significantly in relative preference (2-tailed test, $P < 0.05$). For habitats marked with **, there was strong evidence that they differed in relative preference (2-tailed test, $P < 0.01$).

eastern white cedar was documented in 90% of dense mixed forest ELC plots and in 100% of dense coniferous forest ELC plots in the study area (Coady 2005), cover types where 25 of 31 dens were located. Large diameter eastern white cedars have rough bark forming ridges on old trunks; though the trunk may be exposed for half the height of the tree when growing in a stand, stubs of dead branches remain much lower (Hosie 1979), thus providing secure resting sites for young cubs. Notably, 9 of 11 females with newborn cubs denned close to potential sanctuary trees. These findings emphasize the importance of dense forest stands to black bears on the Peninsula

Table 4. Simplified ranking matrix for American black bear (*Ursus americanus*) den site preferences (2000–2004; see Table 1) based on the distance between den site locations and a given habitat type or linear feature with the average random distance to the same habitat, Bruce Peninsula, Ontario, Canada.[a]

	WAT	MAR	DDF	DCF	DMF	SF	ER	SDL	PCL	ROA	STR	SNO
WAT					**							*
MAR					**							*
DDF					**							**
DCF												
DMF												
SF					**							*
ER					**							*
SDL					**							**
PCL	**	*	*		**		**	*			*	**
ROA	*	*			**		*	*				**
STR					**							**
SNO												

[a]Each habitat component in the column heading that is used more than a component in the row heading is represented by *($P < 0.05$) or **($P < 0.01$).

and highlight the value of dense coniferous stands as denning habitat. The importance of dense mixed-forest stands and dense deciduous forest stands as foraging areas from spring to autumn was previously identified (Obbard et al. 2010). Combined, empirical results of the current study and Obbard et al. (2010) confirm the assertion (Howe et al. 2007) that conserving habitat outside of Bruce Peninsula National Park would be the most effective management action to ensure persistence of this population of bears.

Most dens on the Bruce Peninsula were located in deep fissures in the dolostone, many of which were narrow vertical cracks that extended >2 m below ground level and ended in a rounded chamber. The typically shallow, sandy soils, underlain by porous dolomite, provide variable drainage patterns (Hoffman and Richards 1954, Ross et al. 1989). Despite the temperate climate with abundant precipitation (Moreland 1996), winter thaws do not appear to flood below-ground dens, thus making them ideal den sites. During den visits in late February, we occasionally found bears in the den with water dripping on them via seepage through the overhead dolostone (i.e., vertical drainage sensu Cowell [1976]). Nevertheless, we have no evidence that these underground dens flooded during spring thaw.

Black bear dens have been previously reported to be associated with various rock formations. Most dens were excavated under large solitary boulders or were in rockslide areas in Arizona, USA (LeCount 1983); in natural caves and rock piles in some areas in Alaska, USA (Schwartz et al. 1987); under large boulder piles on hillsides or in narrow rock caves in Coahuila, Mexico (Doan-Crider and Hellgren 1996); and in rock piles, caves, or excavated under rock formations in Big Bend National Park, Texas, USA (Mitchell et al. 2005). In Oregon, USA, most dens were in hollow standing trees or downed logs, but 15% were in caves or rock piles (Immell et al. 2013). A study in Virginia, USA, occurred in an area of karst topography (Klenzendorf et al. 2002). Even so, most bears in the Virginia study denned in trees; those that denned in rock cavities (27%) did so in above-ground crevices (S. Klenzendorf, WWF Deutschland, Berlin, Germany, personal communication, 15 Aug 2023). The Nimpkish valley of northern Vancouver Island, British Columbia, Canada, is another area of karst topography (H. Davis, Artemis Wildlife Consultants, Victoria, B.C., Canada, personal communication, 28 Dec 2023), but all black bear dens located were in or beneath large diameter trees or wooden structures derived from trees (i.e., logs, root boles, and stumps; Davis et al. 2012). To the best of our knowledge our study is the first to document black bears denning below ground in natural fissures in karst topography.

In many regions of the southeastern United States, black bears den in hollow logs or 5–20 m above ground in large-diameter (>80 cm dbh) trees in natural tree cavities that were formed by wind or lightning followed by natural decay (Pelton et al. 1980, Johnson and Pelton 1981). Above-ground cavities in tree dens are commonly used where spring flooding is a risk to hibernating bears (Hamilton and Marchinton 1980, Weaver and Pelton 1994). Such above-ground cavities in standing trees are used in many other areas and are assumed to have both security and thermal benefits over more exposed types of dens, especially with respect to protecting bears from winter rains rather than cold air temperatures (Johnson et al. 1978, Pelton et al. 1980, Lentz et al. 1983). Bears in forested areas of the northwestern United States and western Canada often den in the hollow base or above-ground cavity of large-diameter mature trees (Jonkel and Cowan 1971, Bull et al. 2000, Davis et al. 2012, Immell et al. 2013). No bears on the Bruce Peninsula denned in hollow trees likely because of the scarcity of suitable trees in the study area. Eastern white cedar growing in stands average 15 m in height and 30 cm diameter and rarely reach heights of 25 m and a diameter of 1 m (Hosie 1979). In addition, the widespread forest fires in the early 1900s (Hepburn 1969, Ross et al. 1989) contributed to the current largely second-growth nature of forest stands in the study area. Extensive amounts of slash left over from logging practices resulted in hotter fires; and, therefore, effects of the fires were long lasting (Hepburn 1969). It may be that few mature trees on the Peninsula are currently large enough in diameter to enable large hollow cavities to develop.

A few bears used excavated dens in areas of the Peninsula where soils are deeper. Excavated dens are commonly used across the range of black bears, especially in northern populations and where soils are deep and the winter climate is more severe (Fuller and Keith 1980, Tietje and Ruff 1980, Kolenosky and Strathearn 1987, Schwartz et al. 1987, Klenner and Kroeker 1990, Smith et al. 1994). Indeed, where soils are suitable, a high proportion of bears (>80%) may construct excavated dens (Tietje and Ruff 1980, Kolenosky and Strathearn 1987, Schwartz et al. 1987, Klenner and Kroeker 1990, Smith et al. 1994). In these areas, it is assumed that denning in an excavated den and adding bedding material provides greater protection from the extreme winter climate by reducing heat loss to the environment (Tietje and Ruff 1980). In the only other Ontario study, 89% of dens were excavated (Kolenosky and Strathearn 1987). That study was conducted in eastern Ontario within Ecoregion 5E, an area of deep soils (Crins et al. 2009). Deeper soils on the Peninsula are more common in what are now agricultural areas where, of course, the forest cover has been cleared (Hoffman and Richards 1954). Perhaps the mild winter climate of the Peninsula reduces the necessity for bears to winter in excavated dens, or it may be that most bears in the study area simply have limited access to suitable soils. Overall, our results support our hypothesis that cover type and soil depth influence choice of den site.

Contrary to our hypothesis that pregnant females would select a den that was smaller and presumably more thermally efficient, we found no difference in size of den entrances between females and males, nor between reproductive classes of females. Other studies of northern populations have found den entrances of males to be larger than those of other bears (Tietje and Ruff 1980, Kolenosky and Strathearn 1987, Schwartz et al. 1987, Smith et al. 1994). However, some of those studies included adult males (Tietje and Ruff 1980, Schwartz et al. 1987, Smith et al. 1994), and most dens were excavated in deep soils so male bears would have the ability to enlarge the den entrance as needed. Males in our study were yearlings or subadults so likely required smaller entrances than those of adult females. Adult males on the Peninsula may be unable to den in fissures in the dolostone because it is impossible for bears to enlarge these fissures. If they are going to reproduce successfully, pregnant females should be in better body condition in autumn prior to denning than are females accompanied by 10-month-old cubs, and so they would likely require a larger den entrance. Although there was much variation in entrance measurements, it may be that our small sample size in each category has hidden a real difference.

Also, contrary to our hypothesis, we found no difference between females and males in den chamber size. However, we caution again that the only males in our study were yearlings and subadults. It may be that adult males would occupy larger den chambers or would be unable to exploit narrow vertical fissures in the bedrock. We also found no difference in den chamber size between females with cubs and those with yearlings. In part, this may be due to bears being unable to alter the size of chambers in the bedrock. Nevertheless, parturient females did not select dens with smaller chambers than those occupied by other bears. In eastern Ontario, Kolenosky and Strathearn (1987) found that den chambers of family groups were larger than those of single bears. Almost all of these dens were excavated in deep soils so reproductive females would be able to enlarge the den chamber.

Most bears on the Peninsula lined their dens with leaves and other forest litter, and many included bark and small branches stripped from nearby cedar trees. Sixteen of 21 adult females accompanied by cubs or yearlings in the den had lined the den chamber. Five den sites were excavated or located underneath brush piles; and, in all but one case, den chambers were lined with cedar twigs and forest litter. The other excavated den was neither plugged nor lined but was moderately sheltered between 2 boulders and had 3 dug-out secondary chambers for 2 yearlings. Overall, more females than males lined their dens. When in the den, bears lose more heat via conduction to the substrate than via radiation to the air (Maxwell et al. 2011). By adding a layer of less conductive material such as forest litter and branches as bedding, bears likely increased the thermal efficiency of the den by reducing heat loss to the substrate. If lining the den chamber provides a thermal advantage by reducing heat loss to the substrate as suggested, then there appears to be strong selective pressure for reproductive females to do so. The high mortality rate of yearlings and subadults in conflict situations prevented us from comparing the natural reproductive success of females who lined dens with those that did not.

Re-use of the same den by the same bear is generally low: 4.8% in Pennsylvania (Alt and Gruttadauria 1984), 2.5% in Virginia (Klenzendorf et al. 2002), $<1\%$ in Alberta, Canada (Tietje and Ruff 1980), and no reuse in central Ontario (Kolenosky and Strathearn 1987) but can be higher—28% (7 of 15 cases) on Vancouver Island, British Columbia (Davis et al. 2012). On the Bruce Peninsula, there was no evidence that bears reused dens from previous years, even though most dens were in rock crevices that would persist from year to year. The lack of evidence of re-use of dens suggests that the availability of den sites is not a limiting factor on the Peninsula.

Not only does denning provide bears with protection from inclement weather (Lindzey and Meslow 1977, Johnson and Pelton 1980, Pelton et al. 1980, Lentz et al. 1983), but it may also provide protection from predators (Pelton et al. 1980). Black bears have been killed at their den site or in their den by grizzly bears (*U. arctos*; Ross et al. 1988, Smith and Follmann 1993, Boyd and Heger 2000), wolves (*Canis lupus*; Rogers and Mech 1981, Horejsi et al. 1984, Paquet and Carbyn 1986), and other black bears (Alt and Gruttadauria 1984, Tietje et al. 1986, Davis and Harestad 1996, Garrison et al. 2007). Typically, the black bears killed were subadults or adult females with newborn cubs; often the predator dug into excavated dens to attack the den resident or there was a light snowpack at the time and the denned bear was in an exposed den. Based on these studies, it seems reasonable to conclude that there is strong selective pressure for parturient females to choose a den that provides security against attacks by predators. Parturient females on the Bruce Peninsula appear to do so when selecting dens in fissures in the dolostone. The only wild canids on the Bruce Peninsula are coyotes (*C. latrans*; Wheeldon et al. 2013). It seems unlikely that coyotes would attempt to prey on black bears in their den, though they might if bears were in exposed dens. It seems more likely that selection favoring females that occupy secure dens is in response to historical mortality caused by wolves and other bears in other parts of the range.

The pattern of den location within home range on the Peninsula was unclear—53% of bears denned outside their 50% core area, but within the 95% utilization contour, 23% of bears denned within the 50% core area, and 23% denned outside the 95% contour. The pattern reported in other studies is conflicting. Kolenosky and Strathearn (1987) reported that almost three-quarters of bears in their study denned within the 50% core area. In contrast, in Alberta, females denned in the periphery of their home range (Tietje and Ruff 1980). Such behavior was explained as a strategy to avoid predation because there would be fewer signs of a bear's presence in the outer areas of a home range (Tietje and Ruff 1980). About three-quarters of our bears denned outside the core area, similar to the situation in Alberta (Tietje and Ruff 1980). Kolenosky and Strathearn (1987) suggested that den location may be related to the social status of the individual, with mature resident females being confident to den in the center of their ranges and less confident subadults and subordinate adults feeling safer along range peripheries. On the Bruce Peninsula, 5 of the 7 individuals that denned within their 50% area polygon were mature adult females. Adults may enhance their feeling of security by denning in sections of their range with which they are more familiar and have exclusive use, though not all bears did so. The other 2 individuals who denned within their 50% polygon were subadults in areas with high levels of human activity. These individuals may have been avoiding potential disturbance by humans.

A pattern of extensive home range overlap by adult females has been reported in a number of black bear studies (Powell 1987, Schenk et al. 1998). This pattern has been interpreted as resulting because of philopatry by subadult females and, therefore, male-biased dispersal by subadults (Costello et al. 2008). We did not know the genetic relationships of most of our study females but our data on den locations suggest a similar pattern of extensive home range overlap.

Management implications

Based on a population viability analysis, Howe et al. (2007) suggested that the most effective management action that would ensure persistence of black bears on the Peninsula would be to conserve habitat outside of BPNP. Results of the present study and those of Obbard et al. (2010) emphasize the importance of dense forest stands on the peninsula for bears in all seasons. Fragmentation of woodlots by clearing portions for construction of houses and other structures places bears in double jeopardy via the loss of foraging habitat and security cover and via the potential increase in human–bear conflict. Bears existing at the urban–wildland interface use the same habitat as bears farther away from urban areas, notably dense forest stands (Tri et al. 2016). Therefore, bears will continue to exploit preferred habitat that is close to human infrastructure provided the intensity of human use is low to moderate; this can lead to increased human–bear conflict and potential mortality of bears. Reducing the fragmentation and loss of intact forest stands should be a top land-use planning priority on the Peninsula.

Acknowledgments

We respectfully acknowledge that the land and water on which this study was conducted is the traditional territory of the Saugeen Ojibway Nation. We thank helicopter pilot D. Holtby and Aviation Services, Ontario Ministry of Natural Resources, for support of the winter field work. The following provided assistance during winter field work: T. Buckley, W. Lintack, D. Potter, J. Scheifley, J. Schosser, A. Smith, S. Sutton, and R. Williams. B. Pond and J. Schaefer provided advice on study design and statistical analysis. The Associate Editor and 2 anonymous referees provided helpful comments that enabled us to improve an earlier version of the manuscript. Funding was provided by the Wildlife

Research and Monitoring Section, Ontario Ministry of Natural Resources, by Parks Canada's Bruce Peninsula National Park and Fathom Five National Marine Park, and by a teaching assistantship to MBC from Trent University.

Literature cited

ADDISON, E.M., AND G.B. KOLENOSKY. 1979. Use of ketamine hydrochloride and xylazine hydrochloride to immobilize black bears (*Ursus americanus*). Journal of Wildlife Diseases 15:253–258.

AEBISCHER, N.J., P.A. ROBERTSON, AND R.E. KENWARD. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74:1313–1325.

ALLDREDGE, J.R., D.L. THOMAS, AND L.L. MCDONALD. 1998. Survey and comparison of methods for study of resource selection. Journal of Agricultural, Biological, and Environmental Statistics 3:237–253.

ALT, G.L., AND J.M. GRUTTADAURIA. 1984. Reuse of black bear dens in northeastern Pennsylvania. Journal of Wildlife Management 48:236–239.

BENNETT, K.D. 1992. Holocene history of forest trees on the Bruce Peninsula, southern Ontario. Canadian Journal of Botany 70:6–18.

BESTON, J.A. 2011. Variation in life history and demography of the American black bear. Journal of Wildlife Management 75:1588–1596.

BOWMAN, A.W. 1985. A comparative study of some kernel--based nonparametric density estimators. Journal of Statistical Computation and Simulation 21:313–327.

BOYD, D.K., AND E.E. HEGER. 2000. Predation of a denned black bear, *Ursus americanus*, by a grizzly bear, *U. arctos*. Canadian Field-Naturalist 114:507–508.

BULL, E.L., J.J. AKENSON, AND M.G. HENJUM. 2000. Characteristics of black bear dens in trees and logs in northeastern Oregon. Northwestern Naturalist 81:148–153.

CANADIAN COUNCIL ON ANIMAL CARE. 2003. CCAC guidelines on the care and use of wildlife. Canadian Council on Animal Care, Ottawa, Ontario, Canada.

CARTER, N.H., D.G. BROWN, D.R. ETTER, AND L.G. VISSER. 2010. American black bear habitat selection in northern Lower Peninsula, Michigan, USA, using discrete-choice modeling. Ursus 21:57–71.

CLARK, J.D., J.P. BECKMANN, M.S. BOYCE, B.D. LEOPOLD, A.E. LOOSEN, AND M.R. PELTON. 2020. American black bear (*Ursus americanus*). Pages 122–138 in M. Melletti and V. Penteriani, editors. Bears of the world: Ecology, conservation and management. Cambridge University Press, Cambridge, England, UK.

COADY, M.B. 2005. A distance-based analysis of seasonal habitat use and den site selection by American black bears (*Ursus americanus*) on the Bruce Peninsula, Ontario. Trent University, Peterborough, Ontario, Canada.

CONGALTON, R., AND K. GREEN. 1999. Assessing the accuracy of remotely sensed data: Principles and practices. CRC and Lewis Press, Boca Raton, Florida, USA.

CONNER, L.M., AND B.W. PLOWMAN. 2001. Using Euclidean distances to assess non-random habitat use. Pages 275–290 in J.J. Millspaugh and J.M. Marzluff, editors. Radio-tracking and animal populations. Academic Press, San Diego, California, USA.

———, M. SMITH, AND L.W. BURGER. 2003. A comparison of distance-based and classification-based analyses of habitat use. Ecology 84:526–531.

COSTELLO, C.M., S.R. CREEL, S.T. KALINOWSKI, N.V. VU, AND H.B. QUIGLEY. 2008. Sex-biased natal dispersal and inbreeding avoidance in American black bears as revealed by spatial genetic analyses. Molecular Ecology 17:4713–4723.

COWELL, D.W. 1976. Karst geomorphology of the Bruce Peninsula, Ontario. Thesis, McMaster University, Hamilton, Ontario, Canada.

CRINS, W.J., P.A. GRAY, P.W.C. UHLIG, AND M.C. WESTER. 2009. The ecosystems of Ontario, part 1: Ecozones and ecoregions. Science and Information Branch Technical Report TR-01, Ontario Ministry of Natural Resources, Peterborough, Ontario, Canada.

CROOK, A.C., AND M.J. CHAMBERLAIN. 2010. A multiscale assessment of den selection by black bears in Louisiana. Journal of Wildlife Management 74:1639–1647.

DAVIS, H., A.N. HAMILTON, A.S. HARESTAD, AND R.D. WEIR. 2012. Longevity and reuse of black bear dens in managed forests of coastal British Columbia. Journal of Wildlife Management 76:523–527.

———, AND A.S. HARESTAD. 1996. Cannibalism by black bears in the Nimpkish Valley, British Columbia. Northwest Science 70:88–92.

———, R.D. WEIR, A.N. HAMILTON, AND J.A. DEAL. 2006. Influence of phenology on site selection by female American black bears in coastal British Columbia. Ursus 17:41–51.

DOAN-CRIDER, D.L., AND E.C. HELLGREN. 1996. Population characteristics and winter ecology of black bears in Coahuila, Mexico. Journal of Wildlife Management 60:398–407.

DOBEY, S., D.V. MASTERS, B.K. SCHEICK, J.D. CLARK, M.R. PELTON, AND M.E. SUNQUIST. 2005. Ecology of Florida black bears in the Okefenokee–Osceola ecosystem. Wildlife Monographs 158.

DUQUETTE, J.F., J.L. BELANT, C.M. WILTON, N. FOWLER, B.W. WALLER, D.E. BEYER, N.J. SVOBODA, S.L. SIMEK, AND J. BERINGER. 2017. Black bear (*Ursus americanus*) functional resource selection relative to intraspecific competition and human risk. Canadian Journal of Zoology 95: 203–212.

FULLER, T.K., AND L.B. KEITH. 1980. Summer ranges, cover-type use, and denning of black bears near Fort McMurray, Alberta. Canadian Field-Naturalist 94:80–83.

GARRISON, E.P., J.W. MCCOWN, AND M.K. OLI. 2007. Reproductive ecology and cub survival of Florida black bears. Journal of Wildlife Management 71:720–727.

GARSHELIS, D.L., K.V. NOYCE, AND P.D. KARNS. 1987. Yohimbine as an antagonist to ketamine–xylazine immobilization in black bears. International Conference on Bear Research and Management 7:323–327.

Geosphere Infomatic Services. 1999. Bruce Peninsula satellite land classification and comparison 1993–1999. North-South Environmental Inc., Campbelville, Ontario, Canada.

Gibeau, M.L., and P.C. Paquet. 1991. Evaluation of Telazol® for immobilization of black bears. Wildlife Society Bulletin 19:400–402.

Gray, C.A., M.J. Hooker, and M.J. Chamberlain. 2017. Reproductive and denning ecology of the central Georgia American black bear population. Ursus 27:67–77.

Hamilton, R.J., and R.L. Marchinton. 1980. Denning and related activities of black bears in the coastal plain of North Carolina. International Conference on Bear Research and Management 4:121–126.

Hayes, S.G., and M.R. Pelton. 1994. Habitat characteristics of female black bear dens in northwestern Arkansas. International Conference on Bear Research and Management 9: 411–418.

Hellgren, E.C., and M.R. Vaughan. 1989. Denning ecology of black bears in a southeastern wetland. Journal of Wildlife Management 53:347–353.

Hepburn, G.F. 1969. The Bruce Peninsula bush fire of 1908. Bruce County Historical Society Year Book 1969:20–25.

Hightower, D.A., R.O. Wagner, and R.M. Pace III. 2002. Denning ecology of female American black bears in south central Louisiana. Ursus 13:11–17.

Hoffman, D.W., and N.R. Richards. 1954. Soil survey of Bruce County. Report No. 16 of the Ontario Soil Survey. Experimental Farm Service, Canada Department of Agriculture and the Ontario Agricultural College, Ottawa, Ontario, Canada.

Hooge, P.N., W.M. Eichenlaub, and E.K. Solomon. 2001. Using GIS to analyze animal movements in the marine environment. Pages 37–51 in G.H. Kruse, N. Bez, A. Booth, M. W. Dorn, S. Hills, R.N. Lipcius, D. Pelletier, C. Roy, S.J. Smith, and D. Witherell, editors. Spatial processes and management of marine populations: Proceedings of the symposium on spatial processes and management of marine populations, October 27–30, 1999, Anchorage, Alaska. University of Alaska Sea Grant College Program, Fairbanks, Alaska, USA.

Hooker, M.J., J.S. Laufenberg, A.K. Ashley, J.T. Sylvest, and M.J. Chamberlain. 2015. Abundance and density estimation of the American black bear population in central Georgia. Ursus 26:107–115.

Horejsi, B.L., G.E. Hornbeck, and M.R. Raine. 1984. Wolves, *Canis lupus,* kill female black bear, *Ursus americanus*, in Alberta. Canadian Field-Naturalist 98:368–369.

Hosie, R.C. 1979. Native trees of Canada. 8th edition. Fitzhenry & Whiteside, Don Mills, Ontario, Canada.

Howe, E.J., M.E. Obbard, and J.A. Schaefer. 2007. Extirpation risk of an isolated black bear population under different management scenarios. Journal of Wildlife Management 71: 603–612.

Immell, D., D.H. Jackson, and M.C. Boulay. 2013. Denning ecology of American black bears in the Cascade Mountains of western Oregon. Ursus 24:1–12.

Jenness, J. 2001. Random point generator (v. 1.3). U.S. Forest Service, Rocky Mountain Research Station, Flagstaff, Arizona, USA.

———. 2004. Nearest features with distances and bearings (v. 3.6). U.S. Forest Service, Rocky Mountain Research Station, Flagstaff, Arizona, USA.

Johnson, K.G., D.O. Johnson, and M.R. Pelton. 1978. Simulation of winter heat loss for a black bear in a closed tree den. Proceedings of the Eastern Black Bear Workshop 4:155–166.

———, and M.R. Pelton. 1980. Environmental relationships and the denning period of black bears in Tennessee. Journal of Mammalogy 61:653–660.

———, and ———. 1981. Selection and availability of dens for black bears in Tennessee. Journal of Wildlife Management 45:111–119.

Jonkel, C.J., and I.M. Cowan. 1971. The black bear in the spruce–fir forest. Wildlife Monographs 27.

Kaiser, J. 1995. The flora of the Bruce Peninsula National Park and vicinity, including the Tobermory islands. Parks Canada, Cornwall, Ontario, Canada.

Klenner, W., and D.W. Kroeker. 1990. Denning behavior of black bears (*Ursus americanus*) in western Manitoba. Canadian Field-Naturalist 104:540–544.

Klenzendorf, S.A., M.R. Vaughan, and D.D. Martin. 2002. Den-type use and fidelity of American black bears in western Virginia. Ursus 13:39–44.

Knight, R.R., and L.L. Eberhardt. 1985. Population dynamics of Yellowstone grizzly bears. Ecology 66:323–334.

Kolenosky, G.B., and S.M. Strathearn. 1987. Winter denning of black bears in east-central Ontario. International Conference on Bear Research and Management 7: 305–316.

Lacy, R.C. 2000. Considering threats to the viability of small populations using individual-based models. Ecological Bulletins 48:39–51.

Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. American Naturalist 142:911–927.

LeCount, A.L. 1983. Denning ecology of black bears in central Arizona. International Conference on Bear Research and Management 5:71–78.

Lee, H., W. Bakowsky, J. Riley, J. Bowles, M. Puddister, P. Uhlig, and S. McMurray. 1998. Ecological land classification for southern Ontario. Ontario Ministry of Natural Resources, North Bay, Ontario, Canada.

Lenth, R.V. 1981. On finding the source of a signal. Technometrics 23:149–154.

LENTZ, W. Mac, R.L. MARCHINTON, AND R.E. SMITH. 1983. Thermodynamic analysis of northeastern Georgia black bear dens. Journal of Wildlife Management 47:545–550.

LINDZEY, F.G., AND C.E. MESLOW. 1977. Home range and habitat use by black bears in southwestern Washington. Journal of Wildlife Management 41:413–425.

MAXWELL, R.K., J. THORKELSON, L.L. ROGERS, AND R.B. BRANDER. 2011. The field energetics of winter-dormant black bear (*Ursus americanus*) in northeastern Minnesota. Canadian Journal of Zoology 66:2095–2103.

MILLSPAUGH, J.J., G.C. BRUNDIGE, R.A. GITZEN, AND K.J. RAEDEKE. 2000. Elk and hunter space-use sharing in South Dakota. Journal of Wildlife Management 64:994–1003.

MITCHELL, F.S., D.P. ONORATO, E.C. HELLGREN, J.R. SKILES, JR., AND L.A. HARVESON. 2005. Winter ecology of American black bears in a desert montane island. Wildlife Society Bulletin 33:164–171.

MORELAND, F.W. 1996. The vegetation of Bruce Peninsula National Park and Fathom Five National Marine Park. Resource description and analysis. Parks Canada, Cornwall, Ontario, Canada.

OBBARD, M.E., M.B. COADY, B.A. POND, J.A. SCHAEFER, AND F.G. BURROWS. 2010. A distance-based analysis of habitat selection by American black bears (*Ursus americanus*) on the Bruce Peninsula, Ontario, Canada. Canadian Journal of Zoology 88:1063–1076.

———, E.J. HOWE, C.J. KYLE, J. HASELMAYER, AND J. SCHEIFLEY. 2016. Estimating the abundance of American black bears (*Ursus americanus*) on the Bruce Peninsula. Science and research technical report TR-13. Ontario Ministry of Natural Resources, Peterborough, Ontario, Canada.

OFTEDAL, O.T., G.L. ALT, E.M. WIDDOWSON, AND M.R. JAKUBASZ. 1993. Nutrition and growth of suckling black bears (*Ursus maritimus*) during their mothers' winter fast. British Journal of Nutrition 70:59–79.

OLI, M.K., AND F.S. DOBSON. 2003. The relative importance of life-history variables to population growth rate in mammals: Cole's prediction revisited. American Naturalist 161:422–440.

———, H.A. JACOBSON, AND B.D. LEOPOLD. 1997. Denning ecology of black bears in the White River National Wildlife Refuge, Arkansas. Journal of Wildlife Management 61:700–706.

PACER. 1990. Locate II manual. Version 1.3. Pacer Software, Truro, Nova Scotia, Canada.

PAQUET, P.C., AND L.N. CARBYN. 1986. Wolves, *Canis lupus,* killing denning black bears, *Ursus americanus*, in the Riding Mountain National Park area. Canadian Field-Naturalist 100:371–72.

PELLETIER, A., M.E. OBBARD, M. HARNDEN, S. MCCONNELL, E. J. HOWE, F.G. BURROWS, B.N. WHITE, AND C.J. KYLE. 2017. Determining causes of genetic isolation in a large carnivore (*Ursus americanus*) population to direct contemporary conservation measures. PLoS ONE 12:e0172319.

———, ———, K. MILLS, E.J. HOWE, F.G. BURROWS, B.N. WHITE, AND C.J. KYLE. 2012. Delineating genetic groupings in continuously distributed species across largely homogeneous landscapes: A study of American black bears (*Ursus americanus*) in Ontario, Canada. Canadian Journal of Zoology 90:999–1014.

PELTON, M.R., L.E. BEEMAN, AND D.C. EAGAR. 1980. Den selection by black bears in the Great Smoky Mountains National Park. International Conference on Bear Research and Management 4:149–151.

POWELL, R.A. 1987. Black bear home range overlap in North Carolina and the concept of home range applied to black bears. Ursus 7:235–242.

———, J.W. ZIMMERMANT, AND D.E. SEAMAN. 1997. Ecology and behavior of North American black bears: Home ranges, habitat and social organization. Chapman and Hall, London, England, UK.

ROGERS, L.L., AND E.L. LINDQUIST. 1992. Supercanopy white pine and wildlife. Pages 39–43 in R.A. Stine, editor. White pine symposium: History, ecology, policy and management. Minnesota Extension Service, University of Minnesota, St. Paul, Minnesota, USA.

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

ROSS, P.I., G.E. HORNBECK, AND B.L. HOREJSI. 1988. Late denning black bears killed by grizzly bear. Journal of Mammalogy 69:818–820.

ROSS, S.L., ENVIRONMENTAL RESEARCH LTD., MOSQUIN BIO-INFORMATION LTD., AND HORLER INFORMATION INC. 1989. Bruce Peninsula National Park biophysical inventory. A data collection and description of climate, geology, soils, terrain, primary and understory vegetation, and physical and chemical characteristics of the lakes and rivers in BPNP. Parks Canada, Cornwall, Ontario, Canada.

SCHENK, A., M.E. OBBARD, AND K.M. KOVACS. 1998. Genetic relatedness and home-range overlap among female black bears (*Ursus americanus*) in northern Ontario, Canada. Canadian Journal of Zoology 76:1511–1519.

SCHWARTZ, C.C., S.D. MILLER, AND A.W. FRANZMANN. 1987. Denning ecology of three black bear populations in Alaska. International Conference on Bear Research and Management 7:281–291.

SEAMAN, D.E., J.J. MILLSPAUGH, B.J. KERNOHAN, G.C. BRUNDIGE, K.J. RAEDEKE, AND R.A. GITZEN. 1999. Effects of sample size on kernel home range estimates. Journal of Wildlife Management 63:739–747.

SHAFFER, M.L., AND F.B. SAMSON. 1985. Population size and extinction: A note on determining critical population sizes. American Naturalist 125:144–152.

SIKES, R.S., AND W.L. GANNON. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 92:235–253.

SMITH, M.E., AND E.H. FOLLMANN. 1993. Grizzly bear, *Ursus arctos*, predation of a denned adult black bear, *U. americanus*. Canadian Field-Naturalist 107:97–99.

———, J.L. HECHTEL, AND E.H. FOLLMANN. 1994. Black bear denning ecology in interior Alaska. International Conference on Bear Research and Management 9:513–522.

STONEBERG, R.P., AND C.J. JONKEL. 1966. Age determination of black bears by cementum layers. Journal of Wildlife Management 30:411–414.

STRATHEARN, S.M., J.S. LOTIMER, G.B. KOLENOSKY, AND W.L. LINTACK. 1984. An expanding break-away radio collar for black bear. Journal of Wildlife Management 48: 939–942.

SUFFLING, R., T. CLARKE, M. EVANS, L. LAMB, S. MAY, I. MCKENZIE, AND A. RAMUNAS. 1995. Vegetation change and vegetation management in the Bruce Peninsula National Park and environs. Parks Canada, Cornwall, Ontario, Canada.

TIETJE, W.D., B.O. PELCHAT, AND R.L. RUFF. 1986. Cannibalism of denned black bears. Journal of Mammalogy 67: 762–766.

———, AND R.L. RUFF. 1980. Denning behavior of black bears in boreal forest of Alberta. Journal of Wildlife Management 44:858–870.

TØIEN, Ø., J. BLAKE, D.M. EDGAR, D.A. GRAHN, H.C. HELLER, AND B.M. BARNES. 2011. Hibernation in black bears: Independence of metabolic suppression from body temperature. Science 331:906–909.

TRI, A.N., J.W. EDWARDS, M.P. STRAGER, J.T. PETTY, C.W. RYAN, C.P. CARPENTER, M.A. TERNENT, AND P.C. CARR. 2016. Habitat use by American black bears in the urban–wildland interface of the Mid-Atlantic, USA. Ursus 27: 45–56.

WEAVER, K.M., AND M.R. PELTON. 1994. Denning ecology of black bears in the Tensas River basin of Louisiana. International Conference on Bear Research and Management 9:427–433.

WHEELDON, T.J., L.Y. RUTLEDGE, B.R. PATTERSON, B.N. WHITE, AND P.J. WILSON. 2013. Y-chromosome evidence supports asymmetric dog introgression into eastern coyotes. Ecology and Evolution 3:3005–3020.

WHITE, G.C., AND R.A. GARROTT. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, California, USA.

WOODING, J.B., AND T.S. HARDISKY. 1992. Denning by black bears in northcentral Florida. Journal of Mammalogy 73: 895–898.

WORTON, B.J. 1989. Kernel methods for estimating the utilization distribution in home- range studies. Ecology 70:164–168.

YODZIS, P., AND G.B. KOLENOSKY. 1986. A population dynamics model of black bears in east-central Ontario. Journal of Wildlife Management 50:602–612.

YOUNG, V.H., R.E. ELLIOTT, E. HOFSTEDE, J. DOBBYN, AND R.E. HARRIS. 1996. Bruce Peninsula National Park mammal inventory. Vol. IV. Final report. Canadian Parks Service file no. CR92-26. Parks Canada, Cornwall, Ontario, Canada.

ZAR, J.H. 1999. Biostatistical analysis. Fourth edition. Prentice Hall, Inc., Upper Saddle River, New Jersey, USA.

Received: September 6, 2023
Accepted: March 25, 2024
Associate Editor: T. Smith