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SELECTION OF DEN SITES BY BLACK BEARS IN THE SOUTHERN APPALACHIANS

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We evaluated selection of den sites by American black bears (*Ursus americanus*) in the Pisgah Bear Sanctuary, western North Carolina, by comparing characteristics of dens at 53 den sites with availability of habitat characteristics in annual home ranges of bears and in the study area. We also tested whether den-site selection differed by sex, age, and reproductive status of bears. In addition, we evaluated whether the den component of an existing habitat model for black bears predicted where bears would select den sites. We found bears selected den sites far from gravel roads, on steep slopes, and at high elevations relative to what was available in both annual home ranges and in the study area. Den-site selection did not differ by sex or age, but it differed by reproductive status. Adult females with cubs preferred to den in areas that were relatively far from gravel roads, but adult females without cubs did not. The habitat model overestimated the value of areas near gravel roads, underestimated the value of moderately steep areas, and did not include elevation as a predictor variable. Our results highlight the importance of evaluating den selection in terms of both use and availability of den characteristics.

Key words: bears, dens, habitat quality, roads, southern Appalachian Mountains, *Ursus americanus*

Understanding den-site selection by American black bears (*Ursus americanus*) is important for effective conservation of bears (Hellgren and Vaughan 1989; Linnell et al. 2000). Studies on den selection have focused largely on den type (e.g., tree dens, rock dens, etc.—Jonkel and Cowan 1971; Lindzey and Meslow 1976) and whether den type varies by sex and age of bears (Gaines 2003; Johnson and Pelton 1980; Klenzendorf et al. 2002), or whether topography (e.g., slope, elevation, etc.) at den sites varies by sex of the bears (Seryodkin et al. 2003) or among den types (Johnson and Pelton 1980; Ryan and Vaughan 2004; White et al. 2001). Relatively few studies have evaluated use of den sites by bears relative to the availability of the habitat features characterizing those sites, which is necessary to determine whether bears demonstrate selection. Martorello and Pelton (2003) and Oli et al. (1997) compared microhabitat at dens with that at random sites (Martorello and Pelton 2003) or sites without tree dens (Oli et al. 1997). Johnson and Pelton (1981) and Seryodkin et al. (2003) compared characteristics at den sites with those at random sites in the study area. Kasbohm et al. (1996) and Gaines (2003) compared categorical data at den sites (e.g., forest cover type) with their availability in the study area. The objective of our research was to evaluate den-site selection by bears in the Pisgah Bear Sanctuary (PBS), located in western North Carolina, by comparing characteristics of dens at known den sites with the availability of these characteristics within annual home ranges of bears and within the study area.

Bears in PBS have been shown to use a wide variety of den types (e.g., tree dens, rock cavities, brush piles in clear-cuts, and open depressions—Powell et al. 1997), indicating den type may not be as important to den selection as other variables. Zimmerman (1992) hypothesized steep slopes may be important to den-site selection because steep areas provide seclusion and drainage. Although studies have shown black bears to den on steep sites (Aune 1994; Huygens et al. 2001; LeCount 1983; Novick et al. 1981; Seryodkin et al. 2003; Tietje and Ruff 1980), we found only 1 study that evaluated whether slope at den sites differed from what was available in the study area (Seryodkin et al. 2003). If steep slopes are important to den selection by black bears, we predicted bear

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dens in PBS would be located in steep areas at a greater frequency than predicted by the availability of steep slopes in home ranges and within the study area.

Proximity to human disturbance also has been hypothesized to be important to den-site selection (Gaines 2003; Goodrich and Berger 1994; Oli et al. 1997; Rogers 1987) because disturbance can increase overwinter weight loss (Tietje and Ruff 1980) and reduce reproductive success because of abandonment of cubs (Linnell et al. 2000). Studies have shown that bears select den sites in areas away from roads (Gaines 2003; Huygens et al. 2001; Mitchell et al. 2005), but no study has included estimates of availability of habitat near roads. Assuming that use of areas near different types of roads (i.e., paved roads, gravel roads, and gated roads) varies inversely with traffic volume (Beringer et al. 1989; Brody 1984; Brody and Pelton 1989), we predicted that bears would prefer to den in areas further away from paved roads but closer to gravel and gated roads, relative to their availability.

Alternatively, bears may select den sites with respect to types of roads as a function of the predictability of human disturbance on roads. Linnell et al. (2000) hypothesized that bears would be more likely to den in areas where human disturbance is predictable. We tested 2 predictions of this hypothesis by evaluating den-site selection with respect to paved and gravel roads. In PBS, the primary paved road is the Blue Ridge Parkway, which provides leisurely motoring opportunities for tourists. Motorists who are sightseeing along the Blue Ridge Parkway rarely wander more than a few meters from their vehicles. Therefore, human use of paved roads in PBS is predictably high but human use of areas near paved roads is predictably low. Alternatively, gravel roads in PBS are used not only as scenic byways but also for accessing hiking and biking trails, campsites, and hunting or poaching sites. A motorist driving along a gravel road in PBS might stop at a trailhead, a campsite, a hunting site, or might not stop at all. Therefore, human use of gravel roads, and areas near gravel roads, are both relatively unpredictable. If the hypothesis of Linnell et al. (2000) is true, we predicted that bears would den closer to paved roads and farther from gravel roads, relative to the availability of these areas.

In addition to the predictability of human disturbance, the intensity of human disturbance may also influence the behavior of bears. Orlando (2003) found black bears in Florida avoided otherwise suitable habitat near highways where traffic noise was predictably high. In PBS, traffic noise along paved roads is high relative to that along gravel roads, but motorists traveling along gravel roads are more likely than motorists traveling on paved roads to get out of vehicles and use areas near roads for hiking, biking, and so on. Therefore, the intensity of human use of areas near gravel roads is predictably high compared to that near paved roads. If the intensity of noise affects den selection, we predicted PBS bears would den farther from paved roads. If intensity of human use of areas near roads affects den selection, we predicted PBS bears would den farther from gravel roads.

Our 2nd objective was to evaluate whether den-site selection differed by sex, age, or reproductive status of bears. Previous studies have shown females use tree dens more than do males (Johnson and Pelton 1981; Klenzendorf et al. 2002), adults den at higher elevations compared to juveniles (Mitchell et al. 2005; White et al. 2001), and females with cubs select den types similarly to females without cubs (Klenzendorf et al. 2002). However, none of the previous studies compared differences in characteristics of dens used by bears that differ in sex, age, or reproductive status relative to the availability of these characteristics.

Our final objective was to test an existing model of habitat quality for bears with respect to its ability to predict high-quality den sites. Previously, Zimmerman (1992) developed a spatially explicit model of habitat quality that incorporated 3 life requirements: foods used by bears, den sites, and escape cover. The overall model was tested using annual home ranges of bears in PBS (Mitchell et al. 2002; Powell et al. 1997; Zimmerman 1992), but the den-site component of the model has not been rigorously evaluated. We used known den sites to evaluate the efficacy of the den-site component of the habitat model.

Materials and Methods

Study area.—We conducted our study in PBS in North Carolina (35°17′N, 82°47′W) during 1981–2002. PBS (235 km^2) was located within the Pisgah National Forest, where topography was mountainous with elevations ranging from 650 m to 1,800 m above sea level. The region was considered a temperate rain forest, with annual rainfall approaching 250 cm/year (Powell et al. 1997).

Roads in PBS included 48.5 km of paved roads, 65.7 km of gravel roads, and 200.3 km of gated roads (Continuous Inventory Stand Condition database—United States Department of Agriculture Forest Service 2001). The Blue Ridge Parkway, administered by the National Park Service, transected the north-central portion of PBS, United States Highway 276 bounded the western edge of PBS, and State Road 151 (a paved road) ran though a small portion of PBS. Several gravel roads ran through parts of PBS, 1 of which (Forest Road 1206) bisected PBS. By 2000, more than 80 gated roads ran throughout PBS.

Trapping bears and collecting location data.—We captured bears in PBS from May through mid-August 1981–2002 (except 1991 and 1992) using Aldrich foot snares modified for safety (Johnson and Pelton 1980) or barrel traps. We immobilized captured bears using a combination of approximately 200 mg ketamine hydrochloride (Wyeth Holdings Corporation, Carolina, Puerto Rico) + 100 mg xylazine hydrochloride (Phoenix Pharmaceutical, Inc., St. Joseph, Missouri) /90 kg of body mass (Cook 1984) or 5 mg/kg Telazol (Fort Dodge Animal Health, Fort Dodge, Iowa) administered with a blow dart or pole syringe. We determined the sex of captured bears, then tattooed and attached 2 ear tags to each immobilized bear and extracted a 1st premolar to determine age (Willey 1974). Bears were considered to be adult when >3 years of age; 2-year-old females that bred and produced cubs the following winter also were considered to be adults. Most captured bears were fitted with motion-sensitive radiotransmitter collars (Telonics, Inc., Mesa, Arizona; Sirtrak, Havelock North, New Zealand). Bears were handled in a humane manner and all procedures complied with both guidelines approved by the American Society of Mammalogists (Animal Care and Use Committee 1998) and the requirements of the Institutional Animal Care and Use Committees for Auburn University (IACUC 0208-R-2410) and North Carolina State University (IACUC 00-018).

From May each year until the bears denned (except 1991 and 1992), we located collared bears using telemetry receivers (Telonics Inc.; Lotek, Newmarket, Ontario, Canada; Sirtrak) and a truck-mounted, 8-element Yagi antenna. The high elevation of the Blue Ridge Parkway allowed unobstructed line-of-sight with the majority of the study area, reducing the likelihood of signal error due to interference from terrain. Locations were estimated by triangulating compass bearings taken from a minimum of 3 separate locations within 15 min (Zimmerman and Powell 1995). Bears were located every 2 h for 8, 12, or 24 consecutive hours and sampling was repeated every 32 h to standardize bias from autocorrelation (Swihart and Slade 1985).

To estimate telemetry error, each observer regularly estimated locations of test collars. Zimmerman and Powell (1995) evaluated telemetry error for our study using test collar data and determined the median error to be 261 m. Error did not differ significantly among observers.

Estimating home ranges.—We used the fixed-kernel estimator (program KERNELHR—Seaman et al. 1998), with bandwidth determined by cross validation, to estimate annual home ranges of bears. The kernel estimator depicts use of space by a bear as a utility distribution (i.e., the probability that a bear will be found within a given cell of a grid that encompasses all location estimates—Worton 1989). A minimum of 20 locations was used for home-range estimates (Seaman and Powell 1996), and a grid size of 250 m was used for kernel estimation to match the resolution of our telemetry data. For analyses, home ranges were defined as the area containing 95% of the estimated utility distribution. We estimated annual home ranges because we wanted to evaluate den-site selection based on resources available to bears throughout the year.

Mapping roads.—We used a Geographic Information System (ArcView 3.2 and Spatial Analyst 2.0; ESRI, Redlands, California) to map the distribution of roads in PBS for each year 1981–2001. We partitioned roads into 3 types (paved, gravel, or gated—Brody 1984; Powell et al. 1997) and developed a road map for each type of road for each year 1981–2001. Information about road type and date of construction were provided by United States Department of Agriculture Forest Service at the Pisgah Ranger District, North Carolina.

Collecting data on dens.—We tracked radiocollared bears to their dens during most winters 1981–2002. To determine reproductive status of adult females, we visited accessible dens in February and March and immobilized females using a combination of approximately 200 mg ketamine hydrochloride + 100 mg xylazine hydrochloride/90 kg of body mass (Cook 1984) or Telazol (5 mg/kg) administered with a pole syringe. Adult females were categorized as adults with cubs (i.e., cubs were born during the winter after den selection that occurred during fall), adults with yearlings (i.e., cubs from the previous year that accompanied an adult female into her den), or adults with no cubs or yearlings.

We classified dens in trees or snags as tree dens, for which we measured diameter at breast height (dbh) in centimeters. We classified dens in rocks or caves as rock dens. We classified dens on the ground or in depressions without noticeable cover as open ground dens. We classified dens on the ground with some cover (e.g., under brushpiles, under logs, etc.), dens in holes under trees, and dens in holes dug in the ground as covered ground dens.

Den characteristics: den sites versus home ranges.—We used a geographic information system to map values of slope across PBS at a 30-m resolution. For each known den site, we estimated the slope value to be that for the 30-m cell within which that den was located. For each bear that had a known den site, we estimated availability of slope in its home range as the mean slope of all 30-m cells within its annual home range. Because elevation (Mitchell et al. 2005; White et al. 2001) and distance to streams (Johnson and Pelton 1981) also may be important to selection of den sites by bears, we used the same methods to estimate elevation and distance to streams for each den site as well as mean elevation and mean distance to streams within corresponding annual home ranges. Our stream layer included both low-lying streams as well as waters that flowed down mountainsides into flatter, downslope riparian areas.

To test whether topography at known den sites differed from mean topography within home ranges, we matched topographic variables (slope, elevation, and distance to streams) at each den site with mean values of topographic variables in corresponding annual home ranges and conducted paired *t*-tests ($\alpha = 0.10$). We used the paired *t*-test because our data were continuous, because we wanted to control for individual variability, and because we wanted to retain information on den characteristics that would otherwise be lost if we categorized data into groups. We graphed residuals against predicted values to test for normality and constant variance.

To test whether proximity to roads influenced den-site selection, we mapped each known den site in a geographic information system, overlaid each road map (paved, gravel, and gated), and calculated distances of dens to roads by type of road. For each bear that had a known den site, we estimated availability of distance to roads in home ranges as the mean distance to roads of all 30-m cells within its annual home range. We matched distance to roads at each den site with mean distance to roads in the annual home range and conducted paired *t*-tests, by type of road. We also evaluated whether proximity of dens to roads differed by type of road by modeling proximity of dens to roads as a function of type of road. Using Akaike's information criterion, with an adjustment for small sample bias (AIC_c—Akaike 1973; Anderson et al. 1994), we compared the ability of this model to explain the data relative to the ability of the null model (i.e., intercept-only model).

We also evaluated correlations between slope, elevation, distance to paved roads, distance to gravel roads, distance to gated roads, and distance to streams at den sites (Proc Correlation—SAS Institute Inc. 2000).

Den characteristics: den sites versus study area.—To evaluate whether topography at known den sites differed from that available in the study area, we grouped continuous data on

Table 1.—The den component of Zimmerman's (1992) model of habitat quality for black bears in the southern Appalachian Mountains. The overall den value is a function of conterminous forest (D_1), understory (D_2), slope (D_3), and availability of large trees (D_4). Den value = $\{[(D_1 + D_2)/2](D_3 + D_4)\}^{0.5}$ when $\{[(D_1 + D_2)/2](D_3 + D_4)\}^{0.5} < 1.0$. Den value = 1.0 when $\{[(D_1 + D_2)/2](D_3 + D_4)\}^{0.5} \geq 1.0$.

Den model component	Value	x
D_1 (conterminous forests)	0.0	$x^a \leq 200$
	$0.00098x - 0.20$	$200 < x^a < 1{,}225$
	1.0	$x^a > 1{,}225$
D_2 (understory)	$0.0333x$	$x^b < 30$
	1.0	$x^b \geq 30$
D_3 (slope)	Tan(x)	$x^c \leq 45$
	1.0	$x^c > 45$
D_4 (large trees)	$0.564(\log x) - 0.352$	$x^d \leq 250$
	1.0	$x^d > 250$

[a] Distance to roads in meters.
[b] Area covered in rhododendron and laurel plants.
[c] Slope in degrees of terrain.
[d] Number of large trees > 90 cm dbh.

slope, elevation, and distance to streams into categories (e.g., slope categories; < 10°, 10–15°, 15–20°, etc.) and compared the frequency of categories at known den sites with the frequency of categories available in PBS using chi-square goodness of fit tests with adjusted confidence intervals (e.g., slope had 6 categories so $\alpha = 0.10/6 = 0.016$). We did not use paired *t*-tests because although we had estimates of variance for mean values of each topographic variable at the den sites (n = 53 den sites), we did not have estimates of variance for mean values of topographic variables for the study area (n = 1 study area). To evaluate whether distances of dens to roads differed from distances of 30-m cells in the study area, we grouped distances of dens from roads into 6 categories (< 1,000 m, 1,000–1,500 m, 1,500–2,000 m, 2,000–2,500 m, 2,500–3,000 m, and < 3,000 m) and compared the frequency of categories of known den sites with the frequency of categories available in PBS using chi-square goodness of fit tests with adjusted confidence intervals.

Sex, age class, and reproductive status.—To determine if selection of den sites differed by sex or age, we compared use of characteristics of den sites with availability of these characteristics in annual home ranges using paired *t*-tests, by sex and age class. To determine if selection of den sites differed by reproductive status of adult females (i.e., adult females with and without cubs), we compared use of characteristics of den sites with availability of these characteristics in annual home ranges for adult females using paired *t*-tests, by reproductive status. We defined adult females with cubs to be those females that bore cubs during the winter in which they selected a den. For example, if a female bore cubs during February 1990, then we considered its winter den during 1989–1990 to be a reproductive den.

Many previous studies investigating use of dens or den sites by black bears did not evaluate use of dens relative to the availability of different habitat features. Nevertheless, we were interested in comparing our findings to some of these previous studies, and did so by evaluating selection of den sites by bears of different ages and sex using logistic regression with the Newton–Raphson optimization technique (Proc Logistic—SAS Institute Inc. 2000). Using sex as the response variable, we developed a suite of models using age class as a categorical predictive variable and slope, elevation, distance to roads (paved, gravel, and gated), and distance to streams as continuous predictive variables. We considered the intercept-only model to be the null model. We used AICc for model selection and we considered models with ΔAIC value < 2.0 to have substantial support (Burnham and Anderson 2002). We also estimated model likelihoods and model weights, which provide strength of evidence for model selection. We used Hosmer and Lemeshow goodness of fit statistics to test for model fit. We used a similar approach to evaluate whether selection of den sites differed by reproductive status of adult females.

To determine if type of den (e.g., tree dens, rock dens, etc.) differed among bears by sex and age, we used chi-square goodness of fit with adjusted confidence intervals.

Evaluating the den component of the habitat model.—Using the Den Value algorithm from Zimmerman's (1992) habitat model (Table 1), we used a geographic information system to map den values for every 30-m cell within PBS during each year 1981–2001. We estimated D_2 (understory in rhododendron and laurel plants) and D_4 (large trees) for each 30-m cell based on field data collected on percent understory and number of large trees (M. J. Reynolds-Hogland, in litt.). For each known den site, we considered its den value to be that which was estimated for the 30-m cell within which the den was located. For each bear that had a known den site, we estimated the mean den value within its annual home range during the year that corresponded to use of that den site.

To test if den values at known den sites differed from den values within annual home ranges, we matched den values at each den site with mean den values in the corresponding annual home range and conducted paired *t*-tests to control for variability among individual bears. We graphed residuals against predicted values to test for normality and constant variance.

To test whether den values at known den sites differed from den values available in the study area, we grouped den values into 10 equal categories (e.g., 0.0–0.1, 0.1–0.2, etc.) and compared the frequency of categories at known den sites with the frequency of categories available in PBS using the chi-square goodness of fit test with adjusted confidence intervals.

Zimmerman's (1992) den component of the habitat model predicts the capacity of areas to provide den resources, with values ranging between 0 and 1. Therefore, we grouped den values for den sites into 10 equal categories, calculated the frequency of den value categories, and regressed the frequency of den value categories for den sites with den value category (Proc Regression—SAS Institute Inc. 2000). If the den model predicted high-quality den sites, then the frequency of den value categories for den sites should increase as den value category increases. A better approach would be to compare den values for known den sites with den values for nonden sites, but we could not determine nonden sites with accuracy.

Individual components of Zimmerman's (1992) den model included forest contiguity (D_1), area in understory (D_2), slope

Table 2.—Results of paired *t*-tests: topography (slope, elevation, and distance to streams), proximity to roads (paved, gravel, and gated), and den values at den sites compared to mean topography, road distance, and den values in annual home ranges for 53 black bears in the Pisgah Bear Sanctuary in western North Carolina. Den values were estimated using the den component of Zimmerman's (1992) habitat model.

Variable	Mean difference[a]	90% *LCL*[b]	90% *UCL*[c]	*P*-value
Slope (°)	3.66	2.27	5.05	0.001
Elevation (m)	111.28	54.61	167.95	0.002
Distance to streams (m)	63.68	30.73	96.63	0.002
Distance to paved roads (m)	−65.40	−279.10	148.34	0.611
Distance to gravel roads (m)	188.68	4.49	372.88	0.092
Distance to gated roads (m)	32.54	−90.31	155.39	0.659
Den value	0.00	−0.02	0.03	0.839

[a] Mean difference between variable value at den site and mean value of variable in annual home range. Positive differences indicate variable value at den site was larger than that in home range.
[b] *LCL* = lower confidence limit.
[c] *UCL* = upper confidence limit.

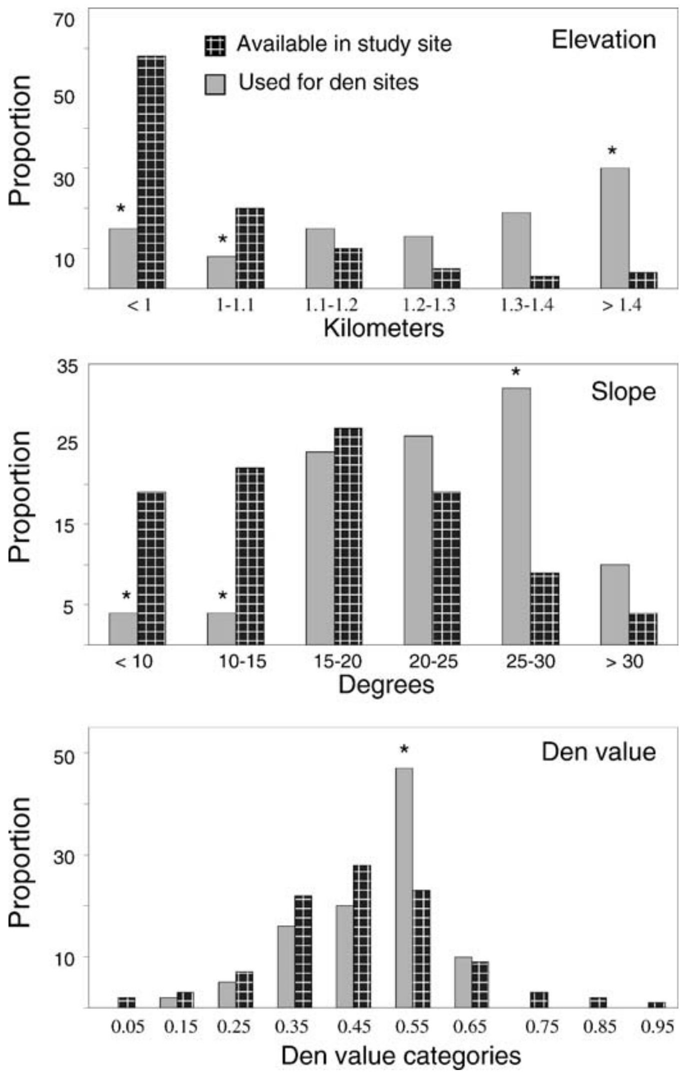

Fig. 1.—Frequency of elevation, slope, and den value categories used at dens of American black bears (*Ursus americanus*; $n = 53$) compared with frequency of categories available in Pisgah Bear Sanctuary in western North Carolina. Den values were estimated using the den component of Zimmerman's (1992) habitat model. An asterisk indicates use differed from availability ($P < 0.01$).

of terrain (D_3), and availability of large trees (D_4; Table 1). Forest contiguity is often a function of distance to roads, so we examined distances of known dens to paved, gravel, and gated roads compared to mean distance of 30-m cells from roads in home ranges and in the study area. We did not compare understory or number of large trees at den sites with availability in home ranges and in the study area because the equations to estimate availability of understory and large trees had relatively low predictive power (M. J. Reynolds-Hogland, in litt.). To provide some information regarding large trees, we calculated mean dbh of trees when trees were used as dens.

Results

Of the 102 females and 141 males we captured during 1981–2002, we collared 79 females and 83 males. We radiotracked 63 bears to their dens, including 32 adult females, 13 juvenile females, 13 adult males, and 5 juvenile males. We had sufficient location data (i.e., ≥ 20 locations) to estimate corresponding annual home ranges for 53 bears, including 28 adult females, 10 juvenile females, 13 adult males, and 2 juvenile males.

Den characteristics: den sites versus home ranges.—Results of paired *t*-tests showed that slope, elevation, distance to gravel roads, and distance to streams were greater at known den sites compared to that available within annual home ranges (Table 2). Errors were normally distributed and variance was constant. At den sites, there was a positive correlation between slope and elevation ($P = 0.005$), slope and distance to streams ($P = 0.002$), and elevation and distance to streams ($P = 0.002$). There was a negative correlation between elevation and distance to paved roads ($P = 0.01$), and distance to streams and distance to gravel roads ($P = 0.02$). There was no correlation between slope and distance to paved roads ($P = 0.83$), slope and distance to gravel roads ($P = 0.83$), elevation and distance to gravel roads ($P = 0.94$), or distance to streams and distance to paved roads ($P = 0.22$).

Proximity to roads by type of road.—The top-ranked model included type of road as a variable. Mean distance of dens to gravel roads was 2,146 m (90% confidence interval [90% *CI*] = 1,899–2,393 m), whereas mean distance of dens to paved and gated roads was 1,035 (90% *CI* = 743–1,327 m) and 755 m (90% *CI* = 622–888 m), respectively.

Den characteristics: den sites versus study area.—Overall, bear dens were found on steeper slopes ($\chi^2 = 41.95$, *d.f.* = 5, $P < 0.0001$; Fig. 1), at higher elevations ($\chi^2 = 36.5$, *d.f.* = 5, $P < 0.0001$; Fig. 1), closer to paved roads ($\chi^2 = 24.92$, *d.f.* = 5, $P < 0.0001$; Fig. 2), and farther from gravel roads ($\chi^2 = 36.45$, *d.f.* = 5, $P < 0.0001$; Fig. 2) than predicted by the distributions of these characteristics in the study area.

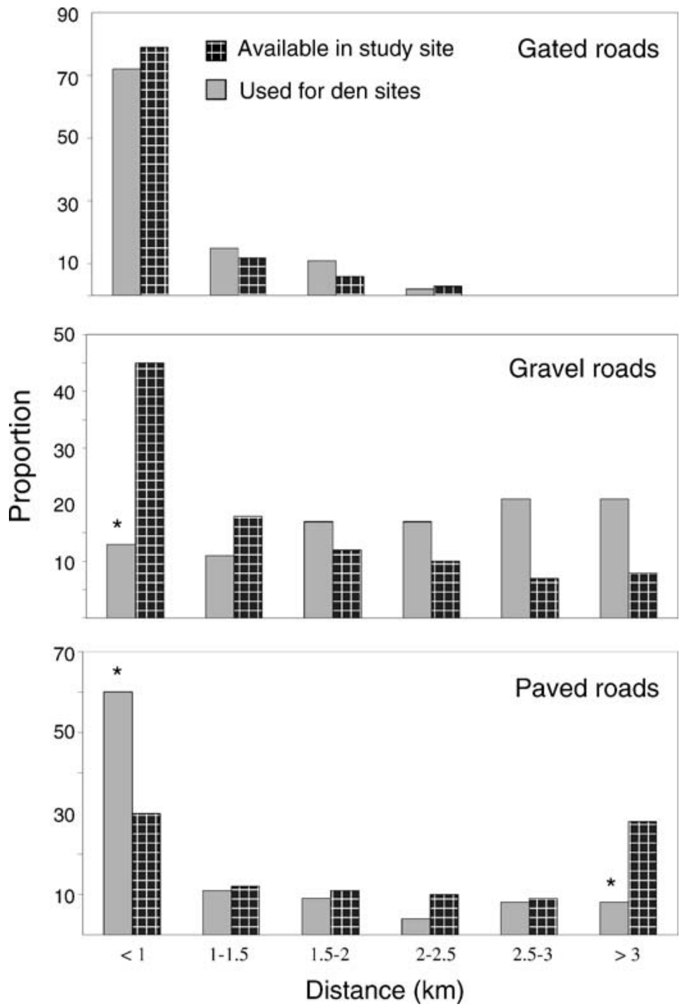

FIG. 2.—Frequency of road (paved, gravel, or gated) distance categories used at dens of American black bears (*Ursus americanus*; $n = 53$) compared with frequency of road distance categories available in Pisgah Bear Sanctuary in western North Carolina. An asterisk indicates use differed from availability ($P < 0.01$).

Sex and age class.—Adult females used 14 tree dens, 4 rock dens, 2 open ground dens, and 9 covered ground dens. Adult males used 3 tree dens, 6 rock dens, and 2 open ground dens. Juvenile females used 3 tree dens and 4 rock dens. Juvenile males used 5 tree dens and 1 rock den. Adult females used covered ground dens, but other bears did not. Adults used open ground dens but juveniles did not. The proportion of rock and tree dens used by bears did not differ between sex or age class (90% *CI*s for the difference between proportions contained zero).

When availability of characteristics at known den sites was compared with availability of these characteristics in annual home ranges of bears that differed by sex and age class (i.e., paired *t*-tests), we found no differences that related to sex and age class. We also examined differences in characteristics of den sites of bears in different sex and age classes using logistic regression so that we could compare our results with those from previous studies that did not include estimates of availability of these habitat characteristics. Based on logistic regression analysis, 2 models had ΔAIC_c values < 2.0. The top-ranked model was the null model and the 2nd-ranked model included elevation ($\Delta AIC_c = 0.90$). As strength of evidence for model selection, the model weight for the top-ranked model was 0.27, indicating the top-ranked model was only 1.6 times more likely to be selected over the 2nd-ranked model (model weight = 0.17), which was not sufficient to differentiate among models (Burnham and Anderson 2002). Mean elevation for den sites of males was 1,338 m (90% CI = 1,259–1,416 m), whereas mean elevation for den sites of females was 1,253 m (90% CI = 1,197–1,308 m). Results of goodness-of-fit tests (Hosmer and Lemeshow $\chi^2 = 7.61$, $d.f. = 9$, $P > 0.57$) indicated data were not overdispersed.

Reproductive status.—Of the 28 dens for adult females, 11 belonged to adult females with cubs, 1 belonged to an adult female with yearlings, and 16 belonged to adult females that had neither cubs nor yearlings. Based on paired *t*-tests, distance from known dens to gravel roads was greater than the mean distance to gravel roads in annual home ranges for adult females with cubs, but not for adult females without cubs or yearlings (Table 3). Slope, elevation, and distance to streams were greater at known den sites compared to mean slope, elevation, and distance to streams in annual home ranges for adult females without cubs or yearlings, but not for adult females with cubs. Distance of known dens to paved roads was less than the mean distance of dens to paved roads in annual home ranges for adult females without cubs or yearlings, but not for adult females with cubs.

We also compared differences in characteristics of den sites used by adult females with and without cubs using logistic regression so that we could compare our results with those from previous studies that did not include an evaluation of the availability of different habitat features relative to den use and selection of den sites. Based on results of logistic regression, 2 models had ΔAIC_c values < 2.0. The top-ranked model included slope as a variable and the 2nd-ranked model was the null model ($\Delta AIC_c = 0.41$). As strength of evidence for model selection, the model weight for the top-ranked model was 0.34, indicating it was only 1.2 times more likely to be selected over the null model (model weight = 0.28), which was not sufficient to differentiate among models (Burnham and Anderson 2002). Results of goodness of fit (Hosmer and Lemeshow $\chi^2 = 4.03$, $d.f. = 7$, $P > 0.77$) indicated data were not overdispersed.

Evaluation of the den component of the habitat model.—Mean den values at known den sites ranged from 0.17 to 0.65. Based on paired *t*-tests, den values at known den sites did not differ from mean den values within annual home ranges (Table 2). Errors were normally distributed and variance was constant. Use of den value categories was disproportionate to availability of den value categories in the study area ($\chi^2 = 37.98$, $d.f. = 9$, $P < 0.0001$; Fig. 1). Results of regression analysis, based on 58 dens, showed the frequency of den value categories for den sites increased as den value category increased, but only up to den value category 0.60–0.70 ($F = 3.82$, $d.f. = 1, 6$, $P = 0.10$; $r^2 = 0.43$). No dens had den values > 0.70. The sample size for the regression analysis differed from that for most other analyses, which used only those den sites for which we could estimate home ranges ($n = 53$). The regression analysis did not

TABLE 3.—Results of paired *t*-tests: topography (slope, elevation, and distance to streams), proximity to roads (paved, gravel, and gated), and den values at den sites compared to mean topography, road distance, and den values in annual home ranges for adult females with cubs ($n = 11$) and adult females without cubs ($n = 16$) in the Pisgah Bear Sanctuary in western North Carolina. Den values were estimated using the den component of Zimmerman's (1992) habitat model.

Reproductive status	Variable	Mean difference[a]	90% *LCL*[b]	90% *UCL*[c]	*P*-value
Without cubs or yearlings	Slope (°)	4.80	2.51	7.01	0.002
	Elevation (m)	92.76	11.15	174.36	0.065
	Distance to streams (m)	55.55	2.24	108.86	0.088
	Distance to paved roads (m)	−426.30	−760.10	−92.46	0.040
	Distance to gravel roads (m)	16.36	−407.50	440.23	0.950
	Distance to gated roads (m)	−20.38	−184.20	143.39	0.831
	Den value	0.14	−0.02	0.05	0.537
With cubs	Slope (°)	0.96	−2.58	4.49	0.636
	Elevation (m)	19.97	−76.90	116.83	0.718
	Distance to streams (m)	43.56	−42.38	129.51	0.382
	Distance to paved roads (m)	249.65	−184.20	683.49	0.324
	Distance to gravel roads (m)	218.21	31.99	404.43	0.059
	Distance to gated roads (m)	−70.12	−404.10	263.87	0.713
	Den value	0.012	−0.03	0.06	0.657

[a] Mean difference between variable value at den site and mean value of variable in annual home range. Positive differences indicate variable value at den site was larger than that in home range.
[b] *LCL* = lower confidence limit.
[c] *UCL* = upper confidence limit.

require home-range estimates so we included all known den sites for which we could estimate den values ($n = 58$). We collected data on dbh for 14 tree dens; mean dbh = 99 cm (90% *CI* = 91–106 cm).

DISCUSSION

Topography and proximity to gravel roads were important to selection of den sites by bears in PBS. Compared to availability in both annual home ranges and in the study area, bears selected den sites on relatively steep slopes, at high elevations, and in areas that were relatively far from gravel roads. Although gravel roads are often associated with low elevations and low slopes in some regions, gravel roads in PBS occurred in areas with high elevations and slopes as well as in areas with low elevations and slopes. We found no correlation between distance of dens to gravel roads and elevation or between slope and distance of dens to gravel or paved roads. In a previous study, we found that habitat selection by bears at PBS for areas near gravel and paved roads was not confounded by slope (Reynolds-Hogland and Mitchell 2007). It was unlikely, therefore, that bears denned in areas away from gravel roads strictly to avoid low elevations and low slopes.

Compared to availability in home ranges, dens were located relatively far from streams. Distance of dens to streams was positively correlated with slope and elevation, so bears may have denned in areas away from streams to avoid relatively low elevations and low slopes. Alternatively, bears may have chosen to den far from streams to minimize mortality due to predation. Riparian areas are important travel corridors for mammalian predators (Beier 1993; Hilty and Merenlender 2004) so assuming large male bears use riparian areas, and because females enter dens earlier (Hellgren and Vaughan 1989; Oli et al. 1997) or emerge later (Kasbohm et al. 1996) than do males, females that den farther from streams may decrease their risk of predation by large male bears.

Roads.—Our results did not support the hypothesis that proximity of dens to roads varies inversely with traffic volume. Traffic volume was highest on paved roads and lowest on gated roads, but mean distance of dens to paved roads did not differ from mean distance of dens to gated roads. However, mean distance of dens to gravel roads was higher than mean distance of dens to paved and gated roads. In addition, distance of dens to gravel roads was greater than mean distance to gravel roads within annual home ranges (Table 2) and bears avoided areas within 1,000 m of gravel roads relative to availability within the study area (Fig. 2).

Our results regarding distance of dens to paved roads provided evidence in support of the hypothesis of Linnell et al. (2000), which posits that bears will be more likely to den in areas where human disturbance is predictable. Dens should have been located relatively close to paved roads and relatively far from gravel roads if the ''disturbance predictability'' hypothesis was true. Assuming ''close'' is defined as areas within 1 km (Linnell et al. 2000), bear dens in PBS were located close to paved roads but not close to gravel roads (Fig. 2). Distance of dens to paved roads did not differ from mean distance to paved roads in annual home ranges (Table 2), indicating bears did not avoid areas near paved roads when selecting den sites. On the contrary, bears in PBS preferred to den in areas close to paved roads relative to availability in the study area (Fig. 2). Our results corroborated those of Klenner and Kroeker (1990) and Tietje and Ruff (1983), who reported black bears denned close to regularly traveled roads in Canada. Our results differed from Orlando (2003), who found black bears in Florida avoided otherwise suitable habitat within 100–500 m of highways, probably due to the intensity of noise. Noise along paved roads in PBS (e.g., Highway 276, Blue Ridge Parkway, State Road

151, etc.) was likely less intense than along busy highways in Florida because paved roads in PBS curved excessively, requiring motorists to drive relatively slowly.

Our results regarding distance of dens to gravel roads (Tables 2 and 3; Fig. 2) supported both the hypothesis of Linnell et al. (2000) and the intensity of use hypothesis. Human disturbance on gravel roads was relatively unpredictable, but only because motorists traveling on gravel roads might stop at trailheads, camping sites, or hunting sites, or they may not stop at all. However, the intensity of human use near gravel roads was high relative to that near paved roads. How a bear determines where it will den relative to different road types likely depends on its experience with encountering many humans near gravel roads and few humans near paved roads. Future research could focus on understanding the degree to which predictability and intensity of human use affect selection of den sites by bears.

How bears select den sites in late fall may be influenced by their behavior during the rest of the year. Previously, we found females at PBS avoided areas near gravel roads more than they avoided areas near paved roads during both summer and fall (Reynolds-Hogland and Mitchell 2007). We hypothesized 2 reasons to explain our findings for fall. Bears may have avoided areas near gravel roads during fall to avoid nonlethal human contact, such as hikers, campers, bikers, and legal hunters of white-tailed deer (*Odocoileus virginianus*) and small game. Alternatively, bears may have avoided areas near gravel roads to minimize risk of mortality due to poaching. Although bears were legally protected in PBS, poaching occurred in bear sanctuaries in North Carolina (Beringer et al. 1989; Brody and Pelton 1989). Of the 240 bears in PBS that we tagged during 1981–2001, 5 were reported killed by vehicle collisions, 43 were reported hunted, and 19 were known to be poached or possibly poached (North Carolina Wildlife Resources Commission, in litt.). These numbers underestimate illegal harvests if illegally killed bears were either unreported or if hunters registered bears that were illegally killed in PBS as legal harvests, which has been a concern among residents living near PBS.

Poachers in PBS likely use gravel roads to access bears because doing so lowers their risk of detection by enforcement officers or other drivers who may report them to enforcement officers. If bears avoided areas near gravel roads to avoid risk of mortality due to poaching, then use by bears of areas near gravel roads should have had survival consequences. We found females that were known to have survived avoided areas near gravel roads, whereas females that were known to have been poached or hunted did not avoid areas near gravel roads (Reynolds 2006). At the population level, we found annual survival increased during years when females avoided areas near gravel roads (Reynolds 2006). Our results indicate that poaching may have influenced responses of bears to gravel roads during fall, which may have subsequently influenced selection of den sites during late fall.

In terms of fitness, the behavioral response of females to gravel roads during fall had survival consequences (Reynolds 2006) and results from our study show that selection of den sites by females, with respect to gravel roads, may have had reproductive consequences. Adult females with cubs selected dens in areas that were far from gravel roads, relative to what was available to them in their home ranges (Table 3). Alternatively, distance of dens from gravel roads did not differ from mean distance to gravel roads in home ranges for adult females without cubs or yearlings (Table 3). Preferred natal hibernacula likely occur in areas with a combination of physical characteristics such as suitable temperature, shelter, and vegetation, each of which could be a function of topography and distance to streams. however, adult females with cubs did not select or avoid areas based on slope, elevation, or distance to streams (Table 3). Based on the variables we considered, distance to gravel roads was the only criterion that affected selection of den sites by adult females with cubs.

Because humans use areas near gravel roads during late fall and winter for hunting legal game and hiking, bears that den near gravel roads may be disturbed. Disturbance of dens may affect reproductive success negatively by increasing abandonment of cubs (Linnell et al. 2000) and overwinter weight loss (Tietje and Ruff 1980). Humans who use areas near gravel roads in PBS may induce abandonment of dens, similar to that documented by Goodrich and Berger (1994) and Tietje and Ruff (1980), who reported abandonment of dens when black bears were disturbed by approaching investigators. Abandonment of dens by pregnant females may deplete fat reserves below that necessary to produce cubs (Tietje and Ruff 1980). Selecting den sites away from gravel roads, therefore, may decrease risk of reproductive failure.

The difference we found in selection of den sites between adult females with cubs and adult females without cubs or yearlings was detectable only when we included estimates of both use and availability of characteristics of den sites. This result highlights the importance of examining selection of den sites in terms of both use and availability. We found only 2 studies that examined differences in characteristics of den sites related to reproductive status of bears (Hightower et al. 2002; Klenzendorf et al. 2002). Neither study found a difference in selection of den type, but neither study evaluated selection of den type in terms of use and availability.

Distance of dens to gravel roads differed from availability in home ranges (Table 1) and in the study area (Fig. 2), and distance of dens to gravel roads was greater than the mean distance to gravel roads in home ranges of adult females with cubs (Table 3), which supports the hypothesis that human disturbance may be one of the strongest forces affecting selection of den sites by black bears (Rogers 1987). Both black bears (Gaines 2003; Mitchell et al. 2005) and brown bears (Ciarniello et al. 2005; Petram et al. 2004) have been shown to den in remote areas, but no study has explicitly tested whether proximity of dens to roads affects overwinter survival and reproductive success, which could be the focus of future research.

Sex and age class.—We found no differences in den characteristics between sex and age, which corroborated findings by Gaines (2003), who found distance from roads and elevation at den sites were similar for males and females. Our results conflicted with findings by White et al. (2001) and Mitchell et al. (2005), who found elevation at den sites differed among age classes. Other studies found that females used tree dens more often than did males (Johnson and Pelton 1981; Klenzendorf et al. 2002), but examination of our data did not corroborate this finding. Availability of large tree dens likely differed between the Great Smoky Mountains and PBS, which may help explain why our results differed from findings by Johnson and Pelton (1981).

Black bears may use areas for den sites that they rarely visit during the rest of the year. Male bears in Manitoba (Klenner and Kroeker 1990) and subadult males in Alberta (Tietje and Ruff 1980) denned in areas beyond their summer home ranges, but females in both studies denned in areas within their summer home ranges. These results indicate that habitat features that provided quality den sites for males may not have been used on a regular basis during other parts of the year. Alternatively, Tietje and Ruff (1980) hypothesized subadult males denned in areas beyond their home ranges, where there are relatively few clues to their presence, and where risk of predation by large male black bears was reduced. In PBS, 16 (30%) of the 53 dens for which we had home-range data were located in areas outside summer home ranges. Of the 38 dens of females, 10 (26%) were located in areas outside annual home ranges. Of the 15 dens of males, 6 (40%) were located in areas outside annual home ranges.

Den component of the habitat model.—Our results regarding the den component of Zimmerman's (1992) habitat model were mixed. Den values (estimated using the habitat model; Table 1) at den sites did not differ from mean den values available within annual home ranges (Table 2). These results suggest bears did not prefer areas with high den values based on what was available to them within their home ranges. Based on availability of den values in the study area, however, bears preferred areas with den values between 0.5 and 0.6. Moreover, results of regression analysis showed the frequency of den sites generally increased as den value category increased. These results indicate the den component of the habitat model captured at least part of the functional relationship between habitat and den value, but it could be improved.

Distance to gravel roads, slope, and elevation were important to selection of den sites based on availability in home ranges (Table 2) and in the study area (Figs. 1 and 2), so the way these variables were modeled for the den component should be reevaluated. The habitat model assumed areas > 1,225 m from all roads provide high-quality den sites (Table 1), but we found den proximity to roads depended on road type. PBS bears preferred to den in areas < 1,000 m from paved roads, but they avoided denning in areas < 1,000 m from gravel roads (Fig. 2). Mean den distance to gravel roads was 2,145 m, indicating the habitat model overestimated den values for areas near gravel roads. The hypothesized relationship between proximity to roads and den value based on Zimmerman's (1992) habitat model is presented in Fig. 3. On a scale of 0 to 1, areas that are within 1,000 m of gravel roads are hypothesized to have a den value = 0.78. Our results indicate that this relationship should be modified.

We present 1 possible modification to Zimmerman's (1992) habitat model for black bears in Fig. 3. No den was located closer than 322 m from gravel roads, so we defined the den value to be zero when distance to gravel roads was <322 m. Because we did not know the optimal distance of dens to gravel roads, we used the mean distance of dens to gravel roads (2,145 m ± 126 *SE*) to define the upper asymptote for gravel roads. Bears in PBS preferred denning in areas < 1,000 m from paved roads and they showed no preference or avoidance for areas < 1,000 m from gated roads as den sites. No den was located closer than 16 m from paved roads and mean distance of dens to paved roads was 1,035 m ± 149 *SE*, so we used these values to define the lower and upper asymptotes for paved roads. No den was located closer than 54 m from gated roads and mean distance of dens to gated roads was 755 m ± 68 *SE*, so we used these values to define the upper and lower asymptotes for gated roads.

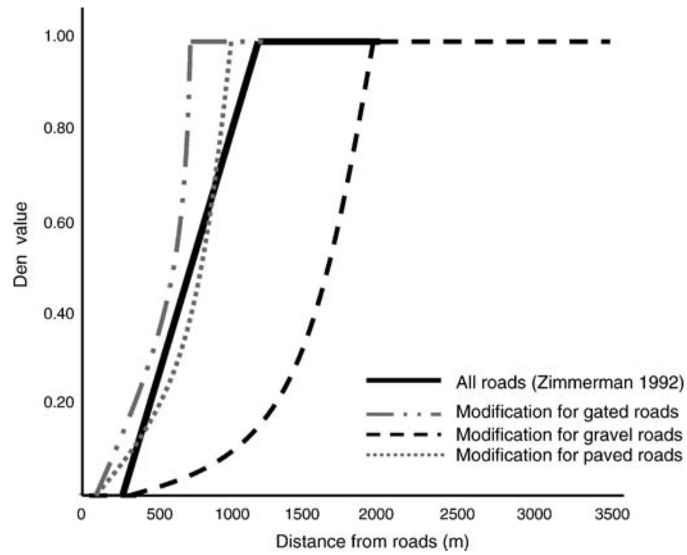

Fig. 3.—Hypothesized relationships between distance of dens of American black bears (*Ursus americanus*) to roads (m) and den value. The solid line represents the relationship for all types of roads as hypothesized by Zimmerman (1992) for the den component of the habitat model. The dashed lines represent proposed modifications to the relationship based on findings from this paper.

The habitat model assumed areas with slopes > 45° have the highest den value because human access is limited on these areas (Table 1). We found mean slope for den sites was 23.5°, indicating the habitat model underestimated the value of moderately steep slopes. Based on the equation for slope, the den value for areas with 23.5° slope is only 0.43 (i.e., tan(23.5) = 0.43; Table 1). We recommend that the slope equations for the den component of the habitat model be adjusted downward to reflect the den value of areas with slopes < 45°. The habitat model did not incorporate elevation as a possible predictor, but we found bears preferred to den at elevations > 1,400 m and avoided denning at elevations < 1,100 m (Table 2; Fig. 1). Therefore, we recommend that an elevation equation, which reflects our results, is included in the den component of the habitat model. Subsequently, the adjusted habitat model should be tested using data from dens that are independent of those we used to explore the efficacy of the den component of the habitat model.

The habitat model assumed areas with large trees provided quality den sites for bears. We did not estimate number of large trees in PBS, but we did find that tree dens were relatively large (mean dbh = 99 cm ± 4.5 *SE*), indicating large trees were probably important to bears that denned in trees.

Conclusions and Conservation Implications

Our results highlight the importance of considering both use and availability of characteristics of den sites to understand selection of den sites by black bears. Had we considered only use of characteristics of den sites, we would have surmised that selection of den sites did not differ by reproductive status of bears. Moreover, we would have concluded that bears do not select steep sites for denning. Mean slope at den sites in PBS (23.5°) was not steep relative to mean slope at dens of black bears in Alaska (mean slope = 35°—Schwartz et al. 1987), California (mean slope = 49°—Novick et al. 1981), or Tennessee (mean slope = 31°—Wathen et al. 1986), but mean slope at den sites in PBS was steep relative to mean slope available in home ranges (Table 2) and in the study area (Fig. 1).

Gravel roads, where human use was unpredictable and where intensity of human use was high, appeared to influence den selection by black bears in PBS. These findings have conservation implications for managers who use timber harvesting as a tool to improve bear habitat. Although harvesting trees can increase availability of soft mast (i.e., fleshy fruits—Clark et al. 1994; Mitchell et al. 2002; Perry et al. 1999; Reynolds-Hogland et al. 2006), a food important to fitness of bears (Elowe and Dodge 1989; Reynolds-Hogland et al., in press; Rogers 1976, 1987), harvested stands are usually spatially associated with gravel roads. Habitat use of areas near gravel roads had negative survival consequences for females during fall (Reynolds 2006) and adult females with cubs avoided areas near gravel roads for denning, which indicates gravel roads had a negative effect on habitat quality for bears in PBS. Therefore, managers must consider the trade-offs associated with timber harvesting in terms of increased habitat quality due to increased bear foods in summer as well as decreased habitat quality due to the negative effects of gravel roads on habitat use in fall and for dens.

Importantly, inferences from our study regarding gravel and paved roads may not be relevant to areas where bear hunting is legal or where vehicle collision is a major source of mortality for bears. In such regions, areas near paved roads might have high intensity of human use relative to areas near gravel roads. Similarly, bears may choose to den in areas away from paved roads in exurban subdivisions where human use of areas near paved roads may be relatively unpredictable.

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