Journal of Mammalogy, 88(4):1050–1061, 2007

EFFECTS OF ROADS ON HABITAT QUALITY FOR BEARS IN THE SOUTHERN APPALACHIANS: A LONG-TERM STUDY

Melissa J. Reynolds-Hogland* and Michael S. Mitchell

School of Forestry and Wildlife Sciences, 602 Duncan Drive, Auburn University, Auburn, AL 36849, USA (MJR-H)
United States Geological Survey, Alabama Cooperative Fish and Wildlife Research Unit, Auburn University, Auburn, AL 36849, USA (MSM)
Present address of MSM: United States Geological Survey, Montana Cooperative Wildlife Research Unit, University of Montana, Natural Sciences Building Room 205, Missoula, MT 59812, USA

We tested the hypothesis that gravel roads, not paved roads, had the largest negative effect on habitat quality for a population of American black bears (*Ursus americanus*) that lived in a protected area, where vehicle collision was a relatively minimal source of mortality. We also evaluated whether road use by bears differed by sex or age and whether annual variation in hard mast productivity affected the way bears used areas near roads. In addition, we tested previous findings regarding the spatial extent to which roads affected bear behavior negatively. Using summer and fall home ranges for 118 black bears living in the Pisgah Bear Sanctuary in western North Carolina during 1981–2001, we estimated both home-range–scale (2nd-order) and within-home-range–scale (3rd-order) selection for areas within 250, 500, 800, and 1,600 m of paved and gravel roads. All bears avoided areas near gravel roads more than they avoided areas near paved roads during summer and fall for 2nd-order selection and during summer for 3rd-order selection. During fall, only adult females avoided areas near gravel roads more than they avoided areas near paved roads for 3rd-order selection. We found a positive relationship between use of roads by adults and annual variability in hard mast productivity. Overall, bears avoided areas within 800 m of gravel roads. Future research should determine whether avoidance of gravel roads by bears affects bear survival.

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

Understanding how roads affect habitat quality for populations of wild animals is a growing concern among scientists (Kerley et al. 2004; Mumme et al. 1998; Reed et al. 1996; Wielgus and Vernier 2003), policy makers (United Nations 1999), and resource managers (United States Department of Agriculture Forest Service 2003). Habitat quality is the capacity of an area to provide resources necessary for survival and reproduction, relative to the capacity of other areas (Van Horne 1983). For American black bears (*Ursus americanus*), roads may affect survival by increasing mortality risk due to hunting, poaching, and vehicle collisions (Brody and Pelton 1989; Brody and Stone 1987; Hamilton 1978; Pelton 1986). Alternatively, roads may affect bear survival and reproduction positively by providing travel corridors (Brody and Pelton 1989; Hellgren et al. 1991; Manville 1983; Young and Beecham 1986). In addition, foods used by bears may grow along roadsides (Beringer et al. 1989; Brody 1984; Carr and Pelton 1984; Hellgren et al. 1991; Manville 1983), which could affect bear survival and reproduction positively.

How roads affect habitat quality for bears depends, in part, on traffic volume associated with roads. Roads with relatively high traffic volume (e.g., highways and other paved roads) have high risk of vehicle collision, which may help explain why bears avoided areas near paved roads in Maryland (Fecske et al. 2002), North Carolina (Beringer et al. 1989; Brody 1984; Brody and Pelton 1989), Tennessee (Quigley 1982), and Virginia (Garner 1986). Alternatively, roads with relatively low traffic volume (e.g., gravel roads, gated roads, and abandoned roads) may provide travel corridors, which may help explain why bears preferred areas near gravel or gated roads in Michigan (Manville 1983), Idaho (Young and Beecham 1986), North Carolina (Beringer et al. 1989; Brody 1984; Brody and Pelton 1989; Hellgren et al. 1991), and Tennessee (Carr and Pelton 1984).

That black bears have also been shown to avoid roads with relatively low traffic volume (Clark et al. 1993; Garner 1986;

* *Correspondent: meljor1@yahoo.com*

Heyden and Meslow 1999; Quigley 1982) indicates that traffic volume alone is insufficient to explain how roads affect habitat quality for bears. The source (or sources) of mortality that has the most impact on a bear population also must be considered. If vehicle collision is a primary source of mortality for a bear population, then roads with high traffic volume should have the largest negative effect on habitat quality. Alternatively, if hunting is a primary source of bear mortality, then roads that provide hunter access should have the largest negative effect on habitat quality. If poaching is a primary source of mortality for bears in a protected area, then roads that provide inconspicuous access for poachers should have the largest negative effect on habitat quality.

The behavioral response of bears to roads may differ by sex. Because males travel relatively widely (Garshelis and Pelton 1981; Powell et al. 1997; Smith and Pelton 1990; Young and Ruff 1982), males are more vulnerable to hunters (Bunnell and Tait 1985; Garshelis 1989) presumably because males encounter areas near roads relatively frequently. However, extensive travel by males does not necessarily mean males use areas near roads more than do females. Empirical evidence to test this hypothesis is sparse. Of the 15 studies we found that evaluated road use by black bears, only 3 compared road use by sex. Two studies found that females avoided areas near roads more than did males (Quigley 1982; Young and Beecham 1986), but the other study found no sex difference (Brody and Pelton 1989).

How bears respond behaviorally to roads also may differ by age, especially for males, because juvenile males not only travel extensively when dispersing (Kane 1989; Rogers 1987) but they may also seek areas away from adult males (Schwartz and Franzmann 1991), who may exclude juveniles from using high-quality areas (Garshelis and Pelton 1981). Alternatively, road avoidance may be a learned behavior. If so, and if roads affect habitat quality negatively, older bears of both sexes should avoid areas near roads more than do juveniles (Brody and Pelton 1989). Only 2 studies on black bears have compared road use between adults and juveniles (Brody and Pelton 1989; Quigley 1982), the results of which were conflicting.

The way roads affect habitat quality for bears may vary with the availability of hard mast (acorns and nuts), a food that is available in fall that is important to bear reproduction and population growth (Costello et al. 2003; Eiler et al. 1989; Elowe and Dodge 1989; Pelton 1989; Reynolds-Hogland et al., in press; Rogers 1976, 1987). Theoretically, bears should show risky behavior with respect to roads during years when hard mast productivity is low, whereas they should show risk-averse behavior during years when hard mast productivity is high. We define risk differently from definitions used to understand risk-averse and risk-prone behavior (i.e., the risk of poor foraging returns—Caraco et al. 1990; Krebs and Davies 1993). For this study, risk is the potential for mortality. To survive winter and ensure reproductive success, bears must acquire sufficient stores of energy during fall (Beecham 1980; Elowe and Dodge 1989). During years when hard mast productivity is below that required by bears for winter survival or to ensure reproductive success, bears should be more willing to accept mortality risk, associated with using areas near roads, to find alternative foods in the fall.

The way roads affect habitat quality of a given area, and the way bears respond behaviorally to roads, may depend on the area's proximity to roads. Quigley (1982) and Clark et al. (1993) found bears avoided areas < 200 m from roads in the Great Smoky Mountains and bears avoided areas < 240 m from roads in Arkansas, respectively. Alternatively, Carr and Pelton (1984) found bears in the Great Smoky Mountains preferred areas < 200 m from gravel roads. Rudis and Tansey (1995) predicted areas < 800 m from all roads would affect habitat quality negatively, but Hellgren et al. (1991) found bears in the Great Dismal Swamp in North Carolina preferred areas < 800 m from nonpaved roads. Mitchell et al. (2002), Powell et al. (1997), and Zimmerman (1992) predicted areas < 1,600 m from roads, especially paved roads, would affect habitat quality negatively for bears in western North Carolina. These previous findings and predictions can be considered a priori hypotheses, each of which can be tested simultaneously (Chamberlain 1897), which should yield strong inferences (Platt 1964).

The 1st objective of our research was to evaluate how paved and gravel roads affected habitat quality for a population of black bears that lived in a protected area where vehicle collision was a relatively minimal source of mortality. Our study population lived in Pisgah Bear Sanctuary (PBS) in western North Carolina and has been the focus of ongoing research since 1981. Of the 226 bears in PBS that we tagged during 1981–2001, 5 were reported killed by vehicle collisions, 43 were killed by hunters, 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 (R. A. Powell, pers. comm.). Because vehicle collision appears to be a small source of mortality for PBS bears relative to poaching, we hypothesized that paved roads would have a small effect on habitat quality relative to the effect of gravel roads. Therefore, we predicted PBS bears would avoid areas near gravel roads more than they would avoid areas near paved roads.

Our 2nd objective was to test if behavioral response of bears to roads differed by sex or age. We predicted PBS adults would avoid areas near gravel roads more than would PBS juveniles and that the difference would be most pronounced for males. Our 3rd objective was to test if annual variability of hard mast influenced the way bears responded behaviorally to roads. We hypothesized bears would show risky behavior with respect to roads during years when hard mast productivity was low and that they would show risk-averse behavior during years when hard mast productivity was high. Our final objective was to evaluate previous findings and predictions regarding the spatial extent to which roads affected bear behavior negatively. We predicted that bears would avoid areas within 1,600 m of gravel roads.

Materials and Methods

Study area.—We conducted our study in PBS in North Carolina (35°17′N, 82°47′W) during 1981–2001. The PBS

(235 km^2) was located within the Pisgah National Forest, where topography was mountainous with elevations ranging from 650 to 1,800 m above sea level. The region was considered a temperate rainforest, with annual rainfall approaching 250 cm/year (Powell et al. 1997).

Eighty-eight percent of PBS was composed of oak (*Quercus*) and oak–hickory (*Quercus* and *Carya*). Cove hardwoods (*Liriodendron tulipifera*, *Magnolia*, and *Betula*) and pine–hemlock (*Pinus rigida*, *P. strobus*, *P. virginiana*, and *Tsuga canadensis*) constituted approximately 4.5% and 3% of PBS, respectively. Subcanopy and understory species (*Rhododendron*, *Kalmia*, etc.) and a mixture of other species (*Corylus*, *Liquidambar styraciflua*, etc.) constituted the remaining portions of the PBS (Continuous Inventory Stand Condition database—United States Department of Agriculture Forest Service 2001).

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, which was administered by the United States 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 the northern portion of PBS. Several gravel roads ran through parts of PBS, one of which (Forest Road 1206) bisected PBS (Fig. 1). By 2000, more than 80 gated roads ran throughout PBS.

Bears were legally protected from hunting in PBS. Even so, bears were killed in and adjacent to PBS, as they were in other bear sanctuaries in North Carolina (Beringer et al. 1989; Brody and Pelton 1989). Other hunting (e.g., deer, turkey, etc.) was legal in PBS.

Trapping bears and collecting location data.—We captured bears in PBS from May through mid-August during 1981–2001 (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 (Fort Dodge Animal Health, Fort Dodge, Iowa) + 100 mg xylazine (Phoenix Pharmaceutical, Inc., St. Joseph, Missouri) hydrochloride/90 kg of body mass (Cook 1984) or Telazol (Wyeth Holdings Corporation, Carolina, Puerto Rico) administered with a blow dart or pole syringe. We sexed, weighed, measured, tattooed, and attached 2 ear tags to each immobilized bear and extracted a 1st premolar to determine age using cementum annuli (Willey 1974). Bears were considered to be adult when >3 years of age; 2-year-old females who 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 (0208-R-2410) and North Carolina State University (00-018).

From May each year until the bears denned (except for 1991 and 1992), we located collared bears using telemetry receivers

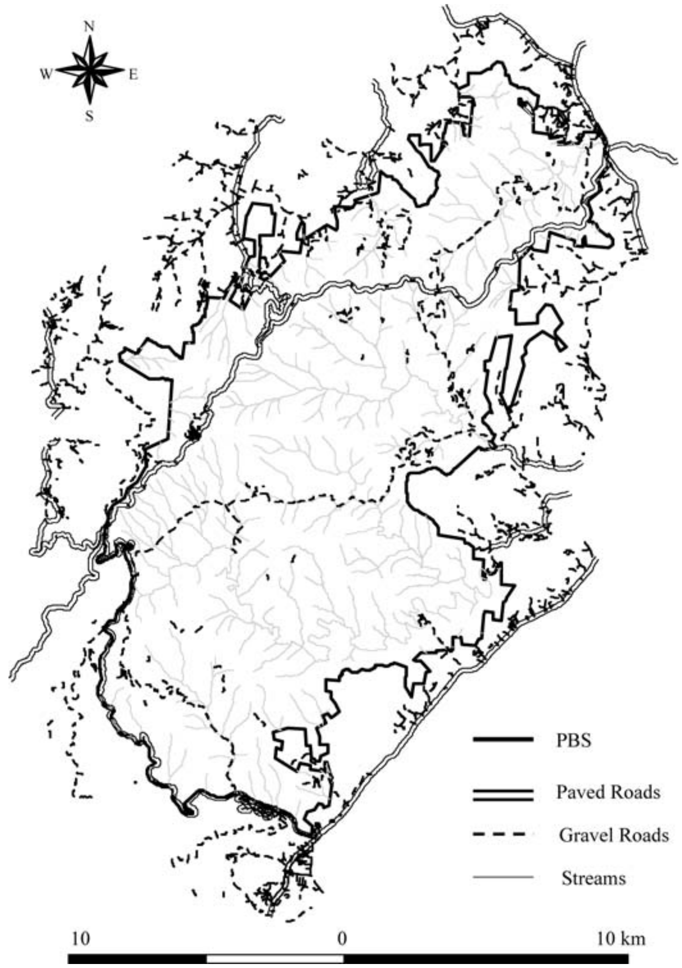

FIG. 1.—Pisgah Bear Sanctuary, North Carolina, with paved roads, gravel roads, and streams.

(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 for a 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). When practicable, we located bears every 2 h for 8 consecutive hours. We repeated sampling every 32 h to standardize bias from autocorrelation within 8-h sampling periods and to eliminate bias between periods (Powell 1987; 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 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 were used for home-range estimates (Noel 1993; 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 did not pool seasonal data because to do so could mask potential effects of roads on behavior of bears that differed by seasons. Negative effects of roads associated with increased mortality due to hunting and poaching should be most pronounced during fall when nonbear hunting is legal inside the sanctuary and bear hunting is legal outside the sanctuary. Alternatively, potential positive effects of roads associated with foods (i.e., berries) that grow along roadsides should be most pronounced during summer when berry plants are highly productive. Therefore, we estimated home ranges in both summer and fall. We defined the summer season as the period between June 1 and August 31 and the fall season as the period between September 1 and the time when bears entered their dens.

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 road type 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.

Using a geographic information system, we placed 4 vector buffers around each road during each year. Each buffer distance represented a previous finding regarding the spatial extent to which roads affected bear behavior: 250-m buffers (Carr and Pelton 1984; Clark et al. 1993; Quigley 1982), 800-m buffers (Hellgren et al. 1991; Rudis and Tansey 1995), and 1,600-m buffers (Mitchell et al. 2002; Powell et al. 1997; Zimmerman 1992). We also used 500-m buffers as an intermediate distance between 250 and 800 m.

Estimating habitat selection.—For each season during each year, we estimated habitat selection for each road type (paved, gravel, and gated) at each buffer distance (250 m, 500 m, 800 m, and 1,600 m) for each individual bear. We mapped each seasonal 95% kernel home range in a geographic information system and overlaid the road map corresponding to the year in which the home range was estimated. For each home range, we indexed preference for each road type at each buffer distance using Ivlev's (1961) electivity index modified to make it symmetrical with respect to zero:

$$E_i = \frac{2 \times (\text{use of habitat } i - \text{availability of habitat } i)}{1 + (\text{use of habitat } i + \text{availability of habitat } i)},$$

where E_i is the index of preference for habitat i. We modified Ivlev's electivity index ((use of habitat i − availability of habitat i)/(use of habitat i + availability of habitat i)) because Ivlev's electivity index overestimates E_i when use and availability of habitat i are very low. For example, E_i based on the Ivlev's electivity index equals 0.33 when use of habitat $i = 0.02$ and availability of habitat $i = 0.01$. Alternatively, E_i using the modified Ivlev's electivity index equals 0.019, which is more representative. Values of E_i can range from −1 to +1. We considered positive values of E_i to indicate preference and negative values of E_i to indicate avoidance (Powell et al. 1997).

We estimated both 2nd-order selection (i.e., home-range selection—Johnson 1980) and 3rd-order selection (habitat selection within home ranges). Currently, no objective biologically based means of defining habitat availability for 2nd-order selection exists (Mitchell et al. 2002). Because we were interested in the bear population living within PBS, we used availability of habitat i within PBS to define availability for 2nd-order selection (Mitchell and Powell 2003; Mitchell et al. 2002). PBS comprised all habitat *i*s and, to our knowledge, nothing precluded bears from using all habitat *i*s within PBS. For 3rd-order selection, availability of habitat i was calculated as the proportion of habitat i located within the 95% home range.

For both orders of selection, use of habitat i was calculated as the proportion of total kernel density probabilities that was located within habitat i. Kernel density probabilities were in raster format at a 250-m grain, whereas each habitat i was a vector buffer around a road. We mapped buffers using vector format because roads in PBS did not follow a grid. A kernel density probability j was considered to be located within habitat i when at least 50% of raster cell j was located within habitat i. Home ranges that contained no habitat i were not included in analyses for 3rd-order selection because to do so would bias estimates of electivity. For bears that had multiple seasonal home ranges, we calculated mean preference for each road type at each buffer distance for each season. For example, if we had 2 summer home ranges for 1 bear, we calculated preference for each road type at each buffer distance by estimating the mean for 2 summers.

Our method for evaluating 2nd-order selection differed somewhat from the traditional approach, which compares availability of habitat i within a home range to availability of habitat i within a designated area (e.g., a study area). We evaluated use of habitat i within a home range (i.e., proportion of total kernel density probabilities that was located within habitat i) relative to availability of habitat i within the study area (Mitchell and Powell 2003; Mitchell et al. 2002; Powell et al. 1997; Zimmerman 1992) because we were interested in understanding how animals selected habitat i when establishing home ranges. Knowing how much of habitat i is located within a home range yields little information about how or if habitat i is used, which is necessary to understand whether habitat i is selected. For example, the home range of an animal may comprise large amounts of habitat i, but if the animal does not use habitat i then habitat i was not selected for the home range.

We did not use a continuous measure of distance to roads via a regression-based analysis because our aim was to test previous a priori findings regarding the spatial extent to which roads affected habitat selection. Importantly, determining whether individuals demonstrate habitat selection requires evaluating habitat use relative to habitat availability. Categorical approaches, such as Ivlev's electivity index, provide a way to evaluate habitat selection in terms of both habitat use and habitat availability, whereas most regression-based approaches do not. We did not use logistic regression because we were not interested in evaluating habitat variables at telemetry locations versus habitat variables at random points. The distances to roads we used (i.e., 250 m, 500 m, 800 m, and 1,600 m) were not arbitrary. We specifically chose buffer distances based on findings from previous studies that evaluated behavioral response of bears to roads. We considered each buffer distance an a priori hypothesis.

Road type, sex, age class, and road distance.—To test whether road type, sex, age class, or buffer distance affected road use by PBS bears, we developed a suite of models for electivity index (E) for each order of selection (2nd and 3rd orders) during each season (summer and fall). We considered individual variables (i.e., road type, sex, age class, and buffer distance) as well as all possible interactions among variables (Proc GLM—SAS Institute Inc. 2002). We used Akaike's information criterion (AIC—Akaike 1973; Anderson et al. 1994) to rank the models in terms of their ability to explain the data. 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.

Controlling for slope.—Bears have been shown to prefer areas with steep slopes (Clark et al. 1993; Garner 1986; Heyden and Meslow 1999; Powell and Mitchell 1998; Unsworth et al. 1989), which could confound our analyses regarding preference for road types. In PBS, areas near paved roads, especially the Blue Ridge Parkway, were steep relative to areas near gravel and gated roads (M. J. Reynolds-Hogland, in litt.) so any differences in habitat selection for road types may be influenced by slope. To test if slope affected habitat selection among road types, we estimated mean slope within each buffer around each road type for each individual home range in fall. For each buffer distance for each order of selection (2nd and 3rd), we developed a suite of models to explain mean E during fall using slope, road type, sex, age class, and all possible combinations among individual variables. We used AIC to rank the models and we estimated model likelihoods and model weights. To determine the relative importance of each model variable j, we summed Akaike weights across all models in which the model variable j occurred (Burnham and Anderson 2002).

Because slope differed among buffer distances for both paved and gravel roads (M. J. Reynolds-Hogland, in litt.), we controlled for these differences by testing whether slope confounded the effects of road type by buffer distance. We ran 2 analyses to test our hypotheses. The 1st analysis was used to test whether road use differed by road type, sex, age class, or buffer distance, where buffer distance was considered a variable. The 2nd analysis was used to test whether slope confounded the effects of road type, where buffer distance was considered a level.

Hard mast productivity and road use.—We estimated annual variability in hard mast productivity using an annual index of hard mast production for the Pisgah National Forest (North Carolina Wildlife Resources Commission). North Carolina Wildlife Resources Commission measured mast production of red oak, white oak, hickory, and beech trees and calculated an index of production for most years 1983–2001 by species and for all species combined (Warburton 1995). We used the annual index for all species combined. To test if a relationship existed between road use by black bears and annual variability in productivity of hard mast, we used least squares regression (Proc REG—SAS Institute Inc. 2000) to model mean E in fall as a function of productivity index of hard mast by sex and age class.

Results

Of the 97 females and 129 males we captured during 1981–2001, we collared 75 females and 81 males. We collected sufficient location data ($\geq$ 20 locations per season per bear) to estimate both summer and fall home ranges for 118 bears (41 adult females, 29 adult males, 25 juvenile females, and 23 juvenile males).

The top-ranked model for 2nd-order selection during summer included buffer distance, road type, and sex (Table 1). The 2nd-ranked model included buffer distance, road type, sex, and age class. The AIC weight for the top model was 0.73 and that for the 2nd-ranked model was 0.16, indicating the top model was 4.5 times more likely to be selected over the 2nd-ranked model. The top-ranked model for 2nd-order selection during fall included buffer distance, road type, and sex. The 2nd-ranked model included buffer distance, road type, sex, and age class. The AIC weight for the top-ranked model was 0.64 and that for the 2nd-ranked model was 0.22, indicating the top-ranked model was only 2.9 times more likely to be selected over the 2nd-ranked model, which was not sufficient to discriminate among models (Burnham and Anderson 2002). The top-ranked model for 3rd-order selection during summer included buffer distance, road type, and the interaction between sex and age class. The top-ranked model was 2.5 times more likely to be selected over models without the interaction between sex and age class. The top-ranked model for 3rd-order selection during fall included only buffer distance and road type. The AIC weight for the top-ranked model was 0.78 and that for the 2nd-ranked model was 0.09, indicating the top model was at least 8.6 times more likely to be selected over all other models.

Road type.—Road type helped explain both orders of selection during both summer and fall (Table 1). For 2nd-order selection, all bears (except juvenile males in fall) avoided areas near gravel roads more than they avoided areas near paved roads at all buffer distances during both summer and fall (Fig. 2).

For 3rd-order selection, adult bears avoided areas near gravel roads more than they avoided areas near paved roads at all buffer distances during summer (Fig. 3). Behavioral response of juvenile bears was similar to that of adults, except juvenile males did not avoid gravel roads more than they avoided paved roads at 250-m buffer distance and juvenile females did not avoid gravel roads more than they avoided paved roads at 1,600-m buffer distance. During fall, adult females avoided

Table 1.—Model rankings for mean electivity index (preference), based on 2nd- and 3rd-order selection during summer and fall, for a population of black bears in Pisgah Bear Sanctuary, North Carolina, during 1981–2001.

Selection order	Season	Model[a]	ΔAIC[b]	Model likelihood	Model weight
2nd	Summer	Buffer × road type, sex	0.00	1.00	0.73
		Buffer × road type, age, sex	2.98	0.23	0.16
		Buffer × road type, age	3.79	0.15	0.10
		Buffer, road type	53.88	0.00	0.00
2nd	Fall	Buffer × road type, sex	0.00	1.00	0.64
		Buffer × road type age, sex	2.07	0.35	0.22
		Buffer × road type, age × sex	4.72	0.09	0.06
		Buffer × road type	5.71	0.06	0.04
3rd	Summer	Buffer, road type, age × sex	0.00	1.00	0.49
		Buffer × road type	1.78	0.41	0.20
		Buffer × road type, sex, age	2.38	0.30	0.15
		Buffer, road type, age	3.79	0.15	0.07
3rd	Fall	Buffer × road type	0.00	1.00	0.78
		Buffer × road type, age, sex	4.24	0.12	0.09
		Buffer, road type	5.30	0.07	0.06
		Buffer, road type, sex	6.59	0.04	0.03

[a] Only the top 4 models for each analysis are shown.
[b] AIC = Akaike's information criterion.

areas within 500–1,600 m of gravel roads more than they avoided areas near paved roads (Fig. 3). Adult males avoided areas within 1,600 m of gravel roads more than they avoided areas within 1,600 m of paved roads, but juvenile males and females did not avoid areas near gravel roads more than they avoided areas near paved roads at any distance. Bears neither preferred nor avoided areas near gated roads at all buffer distances (95% confidence intervals included zero).

Slope was likely a confounding factor for 2nd-order selection, but not for 3rd-order selection. Both slope and road type were included in the top-ranked models for 2nd-order selection at each buffer distance (Table 2) and the summed AIC weight for slope was equal to the summed AIC weight for road type (Table 3). For 3rd-order selection, models with slope ranked lower than models without slope at all buffer distances except 1,600 m (Table 2) and the summed AIC weight for road type was larger than that for slope at all buffer distances except 1,600 m (Table 3). Because adult females were the only bears that avoided areas near gravel roads more than they avoided areas near paved roads during fall (Fig. 3), we reran the slope analyses using 3rd-order selection in fall by only adult females. Results were similar to those using all bears, except the importance of road type was more pronounced.

Sex and age class.—Both sex and age class helped explain preference for areas near roads. Sex helped explain 2nd-order selection during summer and fall as well as 3rd-order selection during summer (Table 1). Age class helped explain 2nd-order selection during fall and 3rd-order selection during summer (Table 1). For both 2nd- and 3rd-order selection during summer, adult females avoided areas within 250–800 m of gravel roads more than did adult males (Figs. 2 and 3). For 3rd-order selection during summer, adult females avoided areas within 250–500 m of paved roads more than did juvenile females (Fig. 3). For 2nd-order selection during fall, adult females avoided areas within 250–500 m of gravel roads more than did adult and juvenile males (Fig. 2). Though neither sex nor age class were included in the top-ranked model for 3rd-order selection during fall (Table 1), only adult females avoided areas near gravel roads more than they avoided areas near paved roads (Fig. 3).

Hard mast productivity and road use.—The index of annual hard mast productivity for Pisgah National Forest was lowest during 1997 (index = 1.22) and highest during 1995 (index = 4.22). For 2nd-order selection, results of least-squares regression showed there was a positive relationship between E and annual productivity of hard mast, but only for adults. Adult females increased use of areas within 250–800 m of paved roads in the fall as annual hard mast productivity increased (for 250-m buffer: $P = 0.002$, $r^2 = 0.24$, slope = 0.12). Adult males increased use of areas within 250 m of paved roads ($P = 0.08$, $r^2 = 0.10$, slope = 0.56) and within 250 m of gravel roads ($P = 0.09$, $r^2 = 0.09$, slope = 0.04) in the fall as annual hard mast productivity increased.

Similar to 2nd-order selection, there was a positive relationship between E and annual productivity of hard mast for adults for 3rd-order selection. Adult females increased use of areas within 250–500 m of paved roads in the fall as annual hard mast productivity increased (for 250–m buffer: $P = 0.007$, $r^2 = 0.19$, slope = 0.049), whereas adult males increased use of areas within 250–800 m of gravel roads in the fall as annual hard mast productivity increased (for 250-m buffer: $P = 0.04$, $r^2 = 0.16$, slope = 0.040).

Distance from roads.—Distance from roads helped explain both orders of selection during both summer and fall (Table 1). For example, adult females avoided areas within 250 m, 500 m, and 800 m of gravel roads more than they avoided areas within 1,600 m of gravel roads for 3rd-order selection during summer (Fig. 3). Overall, bears avoided areas $< 1,600$ m from gravel roads for 2nd-order selection during summer and fall (Fig. 2). For 3rd-order selection during summer, adult females and adult males avoided areas ≤ 800 m from gravel roads and juvenile females avoided areas ≤ 500 m from gravel roads (Fig. 3). For

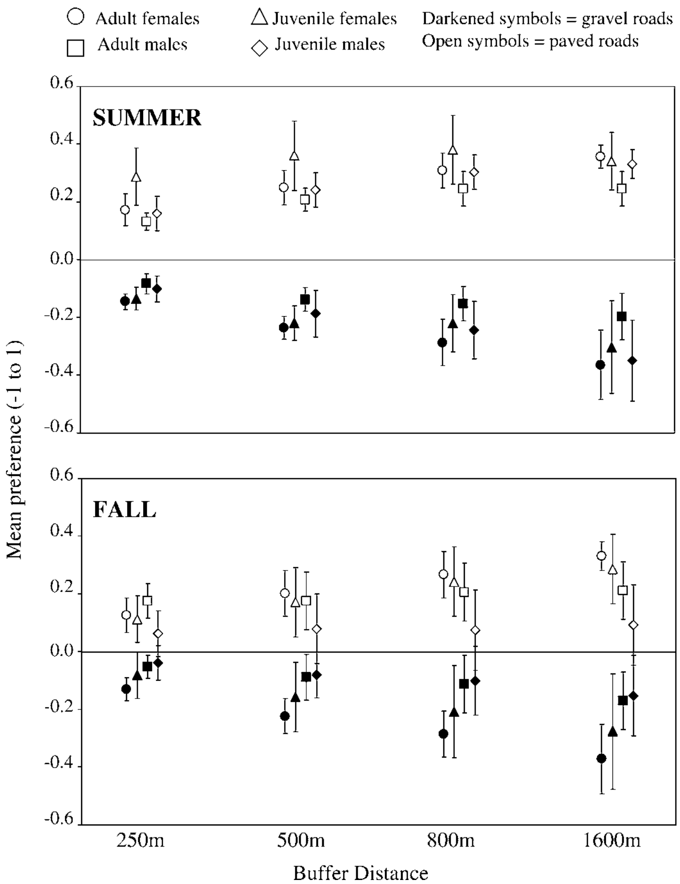

FIG. 2.—Mean electivity index (*E*; preference) during summer and fall for 2nd-order selection, with 95% confidence intervals, for areas within 250, 500, 800, and 1,600 m of paved and gravel roads by adult female, adult male, juvenile female, and juvenile male bears in Pisgah Bear Sanctuary in western North Carolina during 1981–2001.

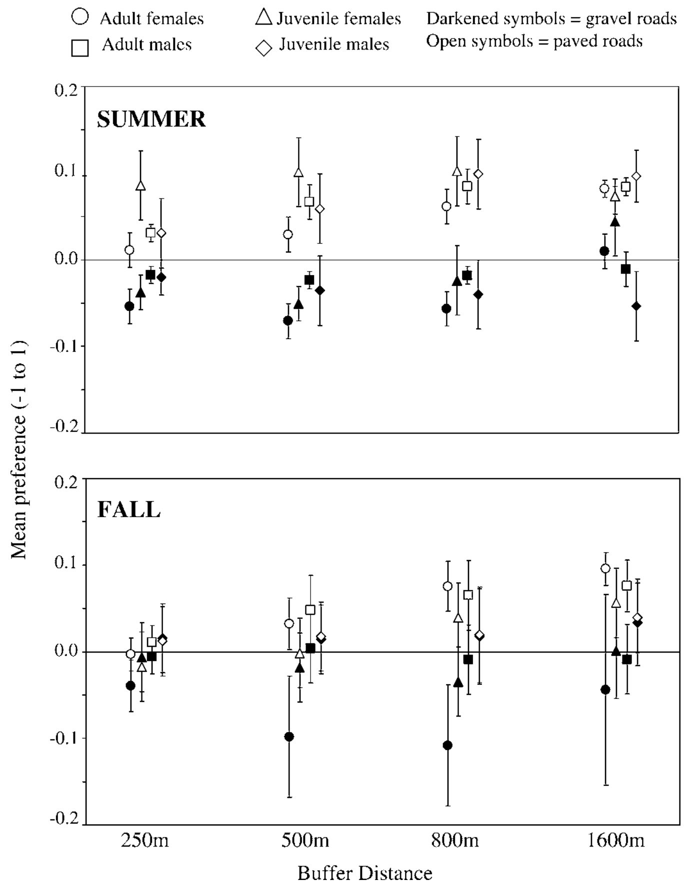

FIG. 3.—Mean electivity index (*E*; preference) during summer and fall for 3rd-order selection, with 95% confidence intervals, for areas within 250, 500, 800, and 1,600 m of paved and gravel roads by adult female, adult male, juvenile female, and juvenile male bears in Pisgah Bear Sanctuary in western North Carolina during 1981–2001.

3rd-order selection during fall, adult females avoided areas ≤ 800 m from gravel roads (Fig. 3).

DISCUSSION

To understand how roads affected habitat quality for black bears in the southern Appalachian Mountains, we evaluated habitat selection by bears using a relatively large sample size over a long temporal duration. Although the most reliable method for understanding the effects of roads on habitat quality for animals is to use direct measures of fitness (e.g., survival, reproduction, etc.), collecting such data on large carnivores is difficult. An alternative approach is to use studies of habitat selection, which use indirect measures of fitness. All studies of habitat selection are based on optimal foraging theory, which posits that patch selection, foraging decisions, and time of patch occupancy have been molded by natural selection to maximize fitness (Charnov 1976; Pyke et al. 1977). The proportion of individuals in a population foraging in ways that enhance their fitness will tend to increase over time, therefore, the behaviors manifested in a population should reflect fitness strategies.

Although previous studies on use of roads by black bears hypothesized that paved roads have the largest negative effect on habitat quality because traffic volume is relatively high, we predicted gravel roads would have the largest negative effect on habitat quality for bears in PBS because vehicle collision was a minimal source of mortality for PBS bears relative to poaching. We did not document the frequency of encounters between bears and poachers, but bear poaching did occur in bear sanctuaries in western North Carolina (Beringer et al. 1989; Brody and Pelton 1989; North Carolina Wildlife Resources Commission, in litt.). Moreover, legal bear hunting in western North Carolina was usually done with the aid of hounds (Collins 1983), which were often released into bear sanctuaries (Beringer et al. 1989).

In our study, bears avoided areas near gravel roads more than they avoided areas near paved roads during both summer and fall for 2nd-order selection. These results indicate that PBS bears selected home ranges in places that were away from gravel roads. That 81 of the 296 seasonal home ranges we evaluated contained no gravel roads, yet all 296 contained paved roads, provides further evidence that this might be so. Importantly, our results for 2nd-order selection may have been confounded by slope so it could be that PBS bears selected home ranges in areas near paved roads and avoided areas near gravel roads because the former were relatively steep. Because

TABLE 2.—Model rankings to test whether slope confounded the effects of road type on mean electivity index (preference) for 2nd- and 3rd-order selection, at 4 buffer distances (m), during fall for a population of black bears in Pisgah Bear Sanctuary, North Carolina, during 1981–2001.

Selection order	Buffer	Model[a]	ΔAIC	Model likelihood	AIC weight
2nd	250	Road type, slope	0.00	1.00	0.71
		Road type, slope, sex, age class	1.81	0.40	0.29
	500	Road type × age class, road type, slope	0.00	1.00	0.53
	800	Road type, slope	0.00	1.00	0.34
		Road type, slope, sex, age class, road type × sex	1.18	0.55	0.19
		Road type, slope, sex, age class, road type × age class	1.18	0.55	0.19
	1,600	Road type, slope, sex	0.00	1.00	0.38
		Road type, slope	0.43	0.81	0.31
3rd	250	Age class	0.00	1.00	0.20
		Age class, road type, age class × road type	0.54	0.76	0.15
		Age class, road type	0.85	0.65	0.13
		Age class, slope, age class × slope	1.70	0.43	0.08
	500	Road type	0.00	1.00	0.28
		Road type, sex	0.47	0.79	0.22
		Road type, age class	0.90	0.64	0.18
		Road type, slope	1.91	0.38	0.11
	800	Road type	0.00	1.00	0.36
		Road type, sex	1.37	0.50	0.18
	1,600	Road type, slope	0.00	1.00	0.58

[a] Only models with ΔAIC values < 2.0 are shown. AIC = Akaike's information criterion.

our results for 3rd-order selection were not confounded by slope, we limit the remainder of our discussion to findings based on 3rd-order selection.

When selecting habitats within home ranges, PBS bears avoided areas near gravel roads more than they avoided areas near paved roads. Our results conflicted with those by Quigley (1982), who found bears in the Great Smoky Mountains National Park avoided areas < 200 m from paved roads more than they avoided areas < 200 m from gravel roads during both summer and fall. The discrepancy between our results and those of Quigley (1982) may reflect differences in mortality sources that were most important to bears in Great Smoky Mountains National Park compared to those that were most important to bears in PBS. Vehicle collision may have been a higher mortality risk for bears in Great Smoky Mountains National Park than it was for PBS bears because the latter often used the tops of tunnels to cross the Blue Ridge Parkway (M. J. Reynolds-Hogland, in litt.), which should have decreased their risk of vehicle collision.

Three studies conducted in Harmon Den in western North Carolina found bears crossed highways less than they crossed gravel roads (Beringer et al. 1989; Brody 1984; Brody and Pelton 1989). Because Harmon Den was a bear sanctuary and the primary sources of mortality for bears in Harmon Den should have been similar to those for bears in PBS (i.e., hunting and poaching), our results regarding bear use of paved and gravel roads should have been qualitatively similar to theirs.

TABLE 3.—Relative importance of model variables for mean electivity index (preference) during fall, for 2nd- and 3rd-order selection, for a population of black bears in the Pisgah Bear Sanctuary, North Carolina, 1981–2001. For each variable *j*, Akaike weights (ω) were summed across all models in which *j* occurred.

2nd-order selection			3rd-order selection		
Buffer distance (m)	Model variable	Sum ω_+ (*j*)	Buffer distance (m)	Model variable	Sum ω_+ (*j*)
250	Road type	1.00	250	Age class	0.75
	Slope	1.00		Road type	0.42
	Sex	0.28		Slope	0.27
	Age class	0.28		Sex	0.18
500	Road type	1.00	500	Road type	0.94
	Slope	1.00		Slope	0.31
	Sex	0.11		Sex	0.33
	Age class	0.11		Age class	0.24
800	Road type	1.00	800	Road type	0.99
	Slope	1.00		Sex	0.31
	Sex	0.35		Slope	0.25
	Age class	0.35		Age class	0.25
1,600	Road type	1.00	1,600	Road type	1.00
	Slope	1.00		Slope	1.00
	Sex	0.55		Sex	0.21
	Age class	0.35		Age class	0.21

We speculate that the way hunters used roads outside sanctuaries, coupled with sanctuary size, may help explain why bears in PBS responded to roads differently than did bears in Harmon Den. If paved roads in nonsanctuary areas were used by hunters to gain access to bears, and if bears traveled outside sanctuaries, then the experiences bears had with hunters on paved roads outside the bear sanctuaries may have influenced the way bears responded to paved roads inside sanctuaries. On average, bears in Harmon Den were more likely than bears in PBS to travel in nonsanctuary areas because PBS was much larger (235 km^2) than Harmon Den (57.4 km^2). Therefore, bears in Harmon Den may have had more experiences with hunters on paved roads in nonsanctuary areas. If so, bears in Harmon Den may have avoided paved roads inside the sanctuary because they learned hunters used paved roads outside the sanctuary.

We predicted that bears in PBS would avoid areas near gravel roads more than they would avoid areas near paved roads, but we were surprised to find bears preferred areas near paved roads. It is possible that bears learned to use areas very near paved roads without crossing them (i.e., use tunnels to cross paved roads, use foods near paved roads but not cross paved roads, etc.), thus avoiding negative effects due to vehicle collision.

We predicted bears would avoid gravel roads most during fall when hunting and poaching risk was high, but mean preference for areas near gravel roads during summer did not differ from that during fall (Figs. 2 and 3). Recreational use of the Pisgah Forest (e.g., hiking, biking, horse riding, camping, etc.) was highest during summer and gravel roads provided access to recreational activities throughout PBS. Therefore, bears may have avoided areas near gravel roads during summer to avoid human contact. That bears did not also avoid areas near paved roads during summer is plausible considering the primary recreational activity provided by the Blue Ridge Parkway (the main paved road in PBS) was leisurely motoring. On average, motorists that use Blue Ridge Parkway for sightseeing rarely wander beyond a few meters from their vehicles. Although traffic volume on paved roads was high relative to that on gravel roads, the probability of human contact near paved roads was relatively minimal.

Behavioral differences between sex and age classes.—Habitat selection for areas near gravel roads differed between sex and age classes; however, the most pronounced differences in road use appeared to be between adult females and other bears, not between adult males and juvenile males as we predicted. For example, adult females appeared to avoid areas $\leq$ 800 m from gravel roads in fall, but other bears did not. Most bears hunted in North Carolina were harvested within 800 m of roads (Collins 1983), which indicates hunters are willing, on average, to walk 800 m from roads to pursue bears. If poachers are similar to hunters, with respect to the distance they are willing to walk from roads, then bears in PBS that avoid areas within $\sim$800 m of roads should increase their probability of survival. If gravel roads imposed a mortality risk to PBS bears and if this risk was highest during fall, our results hint at the possibility that adult females were better adapted to areas near gravel roads compared to other bears. A possible explanation could involve the degree to which bears are informed about their environment. Female bears are typically philopatric (Elowe and Dodge 1989; Powell et al. 1997; Schwartz and Franzmann 1992) so they should be intimately familiar with roads, and potential risks associated with roads, in their home ranges compared to males, who travel widely. Even so, it would require time and experience for females to know when mortality risks associated with roads are high, which may help explain why adult females avoided gravel roads in fall whereas juvenile females did not.

Because foods available in fall near gravel roads were at least as equally available as foods available in fall near paved roads (M. J. Reynolds-Hogland, in litt.), we hypothesize 2 reasons to explain why adult females avoided areas near gravel roads during fall. Bears could have been avoiding poachers or they could have been avoiding nonlethal human contact, such as campers, hikers, bikers, and legal hunters. Hunting of all game species except black bear is legal in PBS. Harvest seasons for these game species occur during fall (e.g., deer season runs from mid-September through January) and hunters often use gravel roads to access legal game. Therefore, understanding the causes underlying bear behavior with respect to roads during fall requires linking road use by bears with estimates of bear survival or reproduction, which should be the focus of future research.

Some of the differences in avoidance of roads that we observed between adult females and other bears for 3rd-order selection may have been influenced by habitat selection at a higher scale. Theoretically, habitat selection by wild animals may be hierarchically organized where processes occurring at lower levels may be governed by processes occurring at higher levels (Allen and Starr 1982; King 1997; O'Neill et al. 1986; O'Neill and King 1998). For example, habitat selection within a home range (3rd-order selection) may be constrained by home-range selection (2nd-order selection—Bissonette et al. 1997), which in turn may be affected by broadscale processes such as forest fragmentation, social interactions, and so on. Bears in our study did not appear to be territorial, as evidenced by extensive overlapping of home ranges (Powell et al. 1997). Even so, some of the differences we observed may have been due to social interactions that we were unable to detect. We attempted to account for higher-level processes by evaluating not only 3rd-order selection, but also 2nd-order selection. However, results for 2nd-order selection were confounded by slope.

Hard mast production and risky behavior.—Contrary to our hypothesis, we found a positive relationship between annual productivity of hard mast and preference for areas near roads during fall for adults. For both 2nd- and 3rd-order selection, adult females increased their use of areas near paved roads as hard mast productivity increased, whereas adult males increased their use of areas near gravel roads as hard mast productivity increased. We predicted an inverse relationship if bears demonstrated risk-averse behavior during years when hard mast productivity was high and risky behavior during years when hard mast productivity was low. Our results may help explain previous findings by Noyce and Garshelis (1997), who found bear harvests were increasingly male-biased during years when productivity of foods in fall was high. Assuming bears that use areas near gravel roads are more likely to be poached or hunted, then bear harvests should be male-biased during years when hard mast productivity is high because adult males increase their use of gravel roads during these years.

The spatial extent to which roads affected behavior.—Assuming negative values of preference indicated avoidance, bears avoided areas ≤ 1,600 m from gravel roads when establishing summer and fall home ranges. For 3rd-order selection, adults avoided areas ≤ 800 m from gravel roads during summer and adult females avoided areas ≤ 800 m from gravel roads during fall; however, these negative preference values were close to zero. Therefore, we tentatively conclude that the negative effects of gravel roads on habitat quality occurred over a relatively large spatial extent, which corroborated predictions by Mitchell et al. (2002), Powell et al. (1997), Rudis and Tansey (1995), and Zimmerman (1992), but conflicted with previous findings by Carr and Pelton (1984) and Hellgren et al. (1991).

Our results regarding preference for areas near paved and gravel roads could have been biased by the resolution of our analyses and our field methods. We calculated home ranges using a 250-m grain, which closely matched (but did not exactly match) our telemetry error (261 m). In the field, most of our telemetry locations were collected from the Blue Ridge Parkway, a paved road. Animals that are close to telemetry routes are more likely to be detected (Brody 1984), so our estimates of preference for areas near paved roads could have been biased high relative to our estimates of preference for areas near gravel roads. However, our telemetry route was elevated above most of our study area and we used a relatively large antenna (8-element Yagi), which permitted us to detect radiotransmissions up to 25 km (most bears < 10 km away were detected from at least 1 station) from the Blue Ridge Parkway. The likelihood of detecting bears located near the Blue Ridge Parkway, therefore, should have been similar to the likelihood of detecting bears near gravel roads that were within several miles of the Blue Ridge Parkway. Moreover, estimates of 3rd-order selection for areas near gravel roads were unlikely biased low because area x was considered available only if it occurred within a 95% home range. For area x to be included in an individual's 95% home range implies that we were able to detect the individual's use of area x. If use of area x was detected at least once to include it in a home range, then subsequent use (or nonuse) should have also been detectable.

We minimized bias for 3rd-order selection in 2 additional ways. First, roads beyond our detection radius were not considered to be available. Therefore, estimates of 3rd-order selection for areas near road types, for which roads existed beyond our detection radius, should not have been biased low. Second, we used a kernel density estimator to calculate 95% home ranges. Kernel density estimators do not assume a normal distribution and they provide an unbiased estimate that is not inflated by grid size and placement (Powell et al. 1997). Importantly, areas inside the outermost telemetry locations that were not used by a bear were not included in its home range, which is important because estimates of preference are sensitive to estimates of availability.

Conservation Implications

Regardless of whether PBS bears avoided areas near gravel roads to avoid poachers or whether they were avoiding nonlethal human contact, gravel roads had a negative effect on bear behavior. Our results have conservation implications for managers who use timber harvesting as a tool to increase bear habitat. Although harvesting trees can increase availability of soft mast (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. If bears avoid areas near gravel roads, as our results show, then foods used by bears inside harvested stands may be relatively inaccessible to bears. Therefore, managers must consider not only the trade-offs associated with timber harvesting in terms of increased soft mast and decreased hard mast, but also in terms of how resource accessibility might be limited by gravel roads.

Acknowledgments

We thank R. Powell, J. Yunger, J. Grand, and 2 anonymous reviewers for their comments on this manuscript. We also thank S. Rutzmozer and J. Hogland for geographic information system guidance. Graduate students L. Brongo, J. Sevin, J. Favreau, G. Warburton, P. Horner, M. Fritz, E. Seaman, J. Noel, A. Kovach, V. Sorensen, and T. Langer helped collect data along with visiting scientist F. Antonelli, D. Brown, P. Riley, K. Pacifici, more than 40 undergraduate interns, technicians, and approximately 400 Earthwatch volunteers. Our research received financial or logistical support from the Alabama Cooperative Fish and Wildlife Research Unit at Auburn University, Auburn University's Peaks of Excellence Program, Auburn University's Center for Forest Sustainability, B. Bacon and K. Bacon, J. Busse, Citibank Corp., the Columbus Zoo Conservation Fund, the Geraldine R. Dodge Foundation, Earthwatch–The Center for Field Research, Environmental Protection Agency Star Fellowship Program, Federal Aid in Wildlife Restoration Project W-57 administered through the North Carolina Wildlife Resources Commission, Grand Valley State University, McNairs Scholars Program, International Association for Bear Research and Management, G. and D. King, McIntire Stennis funds, the National Geographic Society, the National Park Service, the National Rifle Association, the North Carolina State University, Port Clyde and Stinson Canning Companies, 3M Co., the United States Department of Agriculture Forest Service, Wildlands Research Institute, Wil-Burt Corp., and Wildlink, Inc. Although the research described in this dissertation has been funded in part by the United States Environmental Protection Agency through grant/cooperative agreement U-91620601 to M. Reynolds, it has not been subjected to the Agency's required peer and policy review and therefore does not necessarily reflect the views of the Agency and no official endorsement should be inferred.

Literature Cited

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pp. 267–281 in Proceedings of the

2nd International Symposium on Information Theory (B. Petrov and F. Cazakil, eds.). Aakademiai Kidao, Budapest, Hungary.

Allen, T. F. H., and T. B. Starr. 1982. Hierarchy: perspectives for ecological complexity. University of Chicago Press, Chicago, Illinois.

Anderson, D. R., K. P. Burnham, and G. C. White. 1994. AIC model selection in overdispersed capture–recapture data. Ecology 75: 1780–1793.

Animal Care and Use Committee. 1998. Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. Journal of Mammalogy 79:1416–1431.

Beecham, J. J. 1980. Population characteristics, denning and growth patterns of black bears in Idaho. Ph.D. dissertation, University of Montana, Missoula.

Beringer, J. J., S. G. Seibert, and M. R. Pelton. 1989. Incidence of road crossing by black bears on Pisgah National Forest, North Carolina. International Conference on Bear Research and Management 8:85–92.

Bissonette, J. A., D. J. Harrison, C. D. Hargis, and T. G. Chapin. 1997. The influence of spatial scale and scale-sensitive properties in habitat selection by American marten. Pp. 368–387 in Wildlife and landscape ecology: effects of pattern and scale (J. A. Bissonette, ed.). Springer-Verlag, New York.

Brody, A. J. 1984. Habitat use by black bears in relation to forest management in Pisgah National Forest, North Carolina. M.S. thesis, University of Tennessee, Knoxville.

Brody, A. J., and M. R. Pelton. 1989. Effects of roads on black bear movements in western North Carolina. Wildlife Society Bulletin 17:5–10.

Brody, A. J., and J. N. Stone. 1987. Timber harvest and black bear population dynamics in a southern Appalachian forest. International Conference on Bear Research and Management 7:243–250.

Bunnell, F. L., and D. E. N. Tait. 1985. Mortality rates of North American bears. Arctic 38:316–323.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference. Springer-Verlag, New York.

Caraco, T., B. W. U. Blanckenhorn, G. M. Gregory, J. A. Newman, G. M. Recer, and S. M. Zwicker. 1990. Risk-sensitivity: ambient temperature affects foraging choice. Animal Behavior 39:338–345.

Carr, P. C., and M. R. Pelton. 1984. Proximity of adult female black bears to limited access roads. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 38:70–77.

Chamberlain, T. C. 1897. The method of multiple working hypotheses. Reprinted in Science (1965) 148:754–759.

Charnov, E. L. 1976. Optimal foraging: attack strategy on a mantid. American Naturalist 110:141–151.

Clark, J. D., E. L. Clapp, K. G. Smith, and B. Ederington. 1994. Black bear habitat use in relation to food availability in the interior highlands of Arkansas. International Conference of Bear Research and Management 9:309–318.

Clark, J. D., J. E. Dunn, and K. G. Smith. 1993. A multivariate model of female black bear habitat use for a geographic information system. Journal of Wildlife Management 57: 519–526.

Collins, J. M. 1983. North Carolina bear kill statistics, in Tri-state bear study. Tennessee Wildlife Resources Agency, Technical Report 83-9:220–227.

Cook, B. 1984. Chemical immobilization of black bears in Great Smokey Mountains National Park. Proceedings of the Eastern Workshop on Black Bear Research and Management 7:79–81.

Costello, C. M., D. E. Jones, R. M. Inman, K. H. Inman, B. C. Thompson, and H. B. Quigley. 2003. Relationship of variable mast production to American black bear reproductive parameters in New Mexico. Ursus 14:1–16.

Eiler, J. H., W. G. Wathen, and M. R. Pelton. 1989. Reproduction in black bears in the southern Appalachian Mountains. Journal of Wildlife Management 53:353–360.

Elowe, K. D., and W. E. Dodge. 1989. Factors affecting black bear reproductive success and cub survival. Journal of Wildlife Management 53:962–968.

Fecske, D. M., R. E. Barry, F. L. Precht, H. B. Quigley, S. L. Bittner, and T. W. Webster. 2002. Habitat use by female black bears in western Maryland. Southeastern Naturalist 1:77–92.

Garner, N. P. 1986. Seasonal movements, habitat selection, and food habits of black bears (*Ursus americanus*) in Shenandoah National Park, Virginia. M.S. thesis, Virginia Polytechnic Institute and State University, Blacksburg.

Garshelis, D. L. 1989. Nuisance bear activity and management in Minnesota. Pp. 169–180 in Bear–people conflicts: proceedings of a symposium on management strategies (M. Bromely, ed.). Northwest Territories Department of Renewable Resources, Yellowknife, Northwest Territories, Canada.

Garshelis, D. L., and M. R. Pelton. 1981. Movements of black bears in the Great Smoky Mountains National Park. Journal of Wildlife Management 45:912–925.

Hamilton, R. J. 1978. Ecology of the black bear in southeastern North Carolina. M.S. thesis, University of Georgia, Athens.

Hellgren E. C., M. R. Vaughan, and D. F. Stauffer. 1991. Macrohabitat use by black bears in a southeastern wetland. Journal of Wildlife Management 55:442–448.

Heyden, M. V., and E. C. Meslow. 1999. Habitat selection by female black bears in the central Cascades of Oregon. Northwest Science 73:283–294.

Ivlev, V. S. 1961. Experimental ecology of the feeding of fishes. Yale University Press, New Haven, Connecticut.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:67–71.

Johnson, K. G., and M. R. Pelton. 1980. Prebaiting and snaring techniques for black bears. Wildlife Society Bulletin 8:46–54.

Kane, D. M. 1989. Factors influencing the vulnerability of black bears to hunters in northern New Hampshire. M.S. thesis, University of New Hampshire, Durham.

Kerley, L. L., J. M. Goodrich, D. G. Miquelle, E. N. Smirnov, H. B. Quigley, and M. G. Hornocker. 2004. Effects of roads and human disturbance on amur tigers. Conservation Biology 16:97–108.

King, A. W. 1997. Hierarchy theory: a guide to system structure for wildlife biologists. Pp. 185–212 in Wildlife and landscape ecology: effects of pattern and scale (J. A. Bissonette, ed.). Springer-Verlag, New York.

Krebs, J. R., and N. B. Davies. 1993. An introduction to behavioural ecology. 3rd ed. Blackwell Science, Oxford, United Kingdom.

Manville, A. M. 1983. Human impact on the black bear in Michigan's Lower Peninsula. International Conference on Bear Research and Management 5:20–33.

Mitchell, M. S., and R. A. Powell. 2003. Response of black bears to forest management in the southern Appalachian Mountains. Journal of Wildlife Management 67:692–705.

Mitchell, M. S., J. W. Zimmerman, and R. A. Powell. 2002. Test of a habitat suitability index for black bears in the southern Appalachians. Wildlife Society Bulletin 30:794–808.

Mumme, R. L., S. J. Schoech, G. E. Woolfenden, and J. W. Fitzpatrick. 1998. Life and death in the fast lane: demographic consequences of road mortality in the Florida scrub jay. Conservation Biology 14:501–512.

NOEL, J. 1993. Food productivity and home range size in black bears. M.S. thesis, North Carolina State University, Raleigh.

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

O'NEILL, R. V., D. L. DEANGELIS, J. B. WAIDE, AND T. F. H. ALLEN. 1986. A hierarchical concept of ecosystems. Princeton University Press, Princeton, New Jersey.

O'NEILL, R. V., AND A. W. KING. 1998. Homage to St. Michael; or why are there so many books on scale. Pp. 3–15 in Ecological systems; theory and applications (D. L. Peterson and V. T. Parker, eds.). Columbia University Press, New York.

PELTON, M. R. 1986. Habitat needs of black bears in the East. Pp. 49–53 in Wilderness and natural areas in the eastern United States: a management challenge (D. L. Kulhavy and R. N. Coner, eds.). Stephen F. Austin State University, Nacogdoches, Texas.

PELTON, M. R. 1989. The impacts of oak mast on black bears in the southern Appalachians. Pp. 7–11 in Proceedings of the Workshop on Southern Appalachian Mast Management (C. E. McGee, ed.). University of Tennessee, Knoxville.

PERRY, R. W., R. E. THILL, D. G. PEITZ, AND P. A. TAPPE. 1999. Effects of different silvicultural systems on initial soft mast production. Wildlife Society Bulletin 27:915–923.

PLATT, J. R. 1964. Strong inference. Science 146:347–352.

POWELL, R. A. 1987. Black bear home range overlap in North Carolina and the concept of home range applied to black bears. International Conference on Bear Research and Management 7:235–242.

POWELL, R. A., AND M. S. MITCHELL. 1998. Topographical constraints and home range quality. Ecography 21:337–347.

POWELL, R. A., J. W. ZIMMERMAN, AND D. E. SEAMAN. 1997. Ecology and behavior North American black bears: home ranges, habitat and social organization. Chapman & Hall, London, United Kingdom.

PYKE, G. H., H. R. PULLIAM, AND E. L. CHARNOV. 1977. Optimal foraging: a selective review of theory and tests. Quarterly Review of Biology 52:137–154.

QUIGLEY, H. B. 1982. Activity patterns, movement ecology, and habitat utilization of black bears in the Great Smoky Mountains National Park, Tennessee. M.S. thesis, University of Tennessee, Knoxville.

REED, R. A., J. JOHNSON-BARNARD, AND W. L. BAKER. 1996. Contribution of roads to forest fragmentation in the Rocky Mountains. Conservation Biology 10:1098–1106.

REYNOLDS-HOGLAND, M. J., M. S. MITCHELL, AND R. A. POWELL. 2006. Spatio-temporal availability of soft mast in clearcuts in the southern Appalachians. Forest Ecology and Management 237: 103–114.

REYNOLDS-HOGLAND, M. J., L. B. PACIFICI, AND M. S. MITCHELL. In press. Linking resources with demography to understand resource limitation for bears. Journal of Applied Ecology.

ROGERS, L. L. 1976. Effects of mast and berry crop failures on survival, growth, and reproductive success of black bears. Transactions of North American Wildlife and Natural Resources Conference 41:432–438.

ROGERS, L. L. 1987. Effects of food supply and kinship on social behavior, movements, and population growth of black bears in northeastern Minnesota. Wildlife Monographs 97:1–72.

RUDIS, V. A., AND J. B. TANSEY. 1995. Regional assessment of remote forests and black bear habitat from forest resource surveys. Journal of Wildlife Management 59:170–180.

SAS INSTITUTE INC. 2000. SAS/STAT user's guide. Version 6. SAS Institute Inc., Cary, North Carolina.

SCHWARTZ, C. C., AND A. W. FRANZMANN. 1991. Interrelationship of black bears to moose and forest succession in the northern coniferous forest. Wildlife Monographs 113:1–58.

SCHWARTZ, C. C., AND A. W. FRANZMANN. 1992. Dispersal and survival of subadult black bears from the Kenai Peninsula, Alaska. Journal of Wildlife Management 56:426–431.

SEAMAN, D. E., B. GRIFFITH, AND R. A. POWELL. 1998. KERNELHR: a program for estimating animal home ranges. Wildlife Society Bulletin 26:95–100.

SEAMAN, D. E., AND R. A. POWELL. 1996. Accuracy of kernel density estimators for home range analyses. Ecology 77:2075–2085.

SMITH, T. R., AND M. R. PELTON. 1990. Home ranges and movements of black bears in a bottomland hardwood forest in Arkansas. International Conference on Bear Research and Management 8:213–218.

SWIHART, R. K., AND N. A. SLADE. 1985. Influence of sampling interval on estimates of home range size. Journal of Wildlife Management 39:118–123.

UNITED NATIONS. 1999. Road development and the environment; methodologies for minimizing environmental damage. United Nations Publication, New York.

UNITED STATES DEPARTMENT OF AGRICULTURE FOREST SERVICE. 2001. Continuous inventory stand condition data for Pisgah National Forest. United States Department of Agriculture Forest Service, Asheville, North Carolina.

UNITED STATES DEPARTMENT OF AGRICULTURE FOREST SERVICE. 2003. Revised forest plan for the Caribou National Forest. United States Department of Agriculture Forest Service, Idaho Falls, Idaho.

UNSWORTH, J. W., J. J. BEECHAM, AND L. R. IRBY. 1989. Female black bear habitat use in west-central Idaho. Journal of Wildlife Management 53:668–672.

VAN HORNE, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893–901.

WARBURTON, G. S. 1995. Study B1—status of black bear in North Carolina. Annual Performance Reports, Federal Aid in Wildlife Restoration. Vol. 47. North Carolina Resources Commission, Raleigh.

WIELGUS, R. B., AND P. R. VERNIER. 2003. Grizzly bear selection of managed and unmanaged forests in the Selkirk Mountains. Canadian Journal of Forest Research 33:822–829.

WILLEY, C. H. 1974. Aging black bears from first premolar tooth sections. Journal of Wildlife Management 39:97–100.

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

YOUNG, D. D., AND J. J. BEECHAM. 1986. Black bear habitat use at Priest Lake, Idaho. International Conference on Bear Research and Management 6:3–80.

YOUNG, B. F., AND R. L. RUFF. 1982. Populations dynamics and movements of black bears in east central Alberta. Journal of Wildlife Management 46:845–860.

ZIMMERMAN, J. W. 1992. A habitat suitability index model for black bears in the southern Appalachian region, evaluated with location error. Ph.D. dissertation, North Carolina State University, Raleigh.

ZIMMERMAN, J. W., AND R. A. POWELL. 1995. Radiotelemetry error: location error method compared with error polygons and confidence ellipses. Canadian Journal of Zoology 73:1123–1133.

Submitted 3 March 2006. Accepted 16 November 2006.

Associate Editor was John A. Yunger.