

RESPONSE OF BLACK BEARS TO FOREST MANAGEMENT IN THE SOUTHERN APPALACHIAN MOUNTAINS

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Abstract: We evaluated responses of black bears (*Ursus americanus*) to changes in habitat in the Pisgah National Forest in North Carolina, USA. Changes in habitat were due to forest management, which affected bear habitat in complex ways. Harvested stands provided plentiful food resources that decreased with regeneration of the canopy. However, their value was offset by a lack of resources associated with mature overstory. Following canopy closure, early-successional food resources in harvested stands tended to decrease, although some soft mast remained more abundant than in unharvested stands. We used a tested Habitat Suitability Index (HSI) to evaluate effects of harvest management on bear habitat. Values of HSI for harvested stands tended to differ little among young stands and older stands regenerating in pine (*Pinus* spp.) or hardwood, and all had lower HSI values than unharvested stands. Although effects of roads are modeled negatively in the HSI, proximity of harvested stands to logging roads did not bias comparisons to harvested stands. We used time-series analysis to characterize year-to-year changes on HSI maps for our study area from 1981 through 1994, and designated the results as an index of habitat change. We used this index to evaluate use of changed areas by black bears, estimated from 127 home ranges. Adult females used changed areas inversely proportional to the index of change, whereas adult and juvenile males showed no preferences. With respect to year-to-year variation at the peripheries of their home ranges, adult males and adult females selected habitat patches where suitability had increased and rejected patches where suitability had declined. Home ranges of adult males contained proportionally fewer areas of habitat decline than those of females or juvenile males. Adult females used areas where habitat suitability decreased, proportional to the decrease, but did not prefer them to areas of stable or improved suitability. Adult males appeared to avoid areas of decreased suitability altogether. Forest management positively affected some aspects of bear habitat but had an overall negative effect on habitat suitability in the southern Appalachians. Forest management will not improve bear habitat overall in areas where resources are abundant. Where soft mast is limiting, however, trade-offs between overall habitat suitability and improved productivity of soft mast may be warranted.

JOURNAL OF WILDLIFE MANAGEMENT 67(4):692–705

Key words: black bear, forest management, GIS, habitat change, habitat suitability index, home range, management indicator species, North Carolina, Pisgah National Forest, timber harvest, *Ursus americanus*.

Few studies document direct responses of animals to habitat changes, either monitored over time or initiated experimentally. Although these approaches offer the most rigorous insights, costs and logistics associated with experimental manipulation or long-term ecological study can be prohibitive. Additionally, studies generally focus on small, easily studied animals because the spatial and temporal scales at which large, long-lived animals live greatly increase the challenges of assessing both habitat change and responses of animals. Nonetheless, large animals often are the focus of management or conservation efforts (Landres et al. 1988), especially where landscapes are rapidly changing. The lack of rigorously derived information on response of large animals to habitat change is problematic, particularly where management of large animals must be bal-

anced with other, possibly competing, management objectives.

We analyzed how a protected population of black bears inhabiting a national forest in the mountains of western North Carolina responded to changes in their habitat over a 14-year period. Habitat changes during our study were due mostly to timber harvesting (primarily through clear-cutting) and road-building (C. Bolen, U.S. Forest Service [USFS], personal communication), allowing us to assess directly how bears respond to effects of forest management.

Forest management can influence bear habitat through harvesting of trees—which affects food, cover, and denning resources—and by increasing density of roads needed to access stands for harvest, thereby increasing human access into bear habitat. Behavioral responses of bears to these management practices are not clear. Black bears have been shown both to select (Jonkel and Cowan 1971, Lindzey and Meslow 1977, Samson

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and Huot 1998) and to avoid (Young and Beecham 1986, Unsworth et al. 1989, Clark et al. 1994) harvested stands. In the southern Appalachians, growth of vegetation following timber harvesting is rapid and lush, commonly including berry species (blueberries [*Vaccinium* spp.], huckleberries [*Gaylussacia* spp.], and especially blackberries [*Rubus* spp.]) and grapes (*Vitis* spp.) that are important summer and fall foods for bears (Beeman and Pelton 1980). Recently harvested stands can therefore provide important food resources to bears. With the possible exception of huckleberries (Johnson and Landers 1978), however, productivity of berry species tends to decline as harvested stands age (Stransky and Roes 1984, Clark et al. 1994). Effects of timber harvesting on other bear foods and habitat needs are either obvious (e.g., removal of trees that produce hard mast

or provide cavities suitable for denning) or uncertain (e.g., changes in densities of colonial insects). As with harvested stands, bears have been shown both to use (Young and Beacham 1986, Unsworth et al. 1989) and to avoid roads (Hamilton 1978, Quigley 1982, Villarubia 1982, Brody and Pelton 1989). Most hunting mortalities for bears in western North Carolina, however, occur within 1.6 km of a road (Collins 1983).

To assess how forest management practices changed bear habitat over the course of our study, we used a Habitat Suitability Index (HSI) that has been shown to predict strongly the habitat preferences of bears living in our study area (Zimmerman 1992, Powell et al. 1997, Mitchell et al. 2002). The HSI depicts a comprehensive, integrated model of most major habitat components likely to be important to bear fitness (Table 1;

Table 1. Components of a habitat suitability index (HSI) model used to assess the effects of habitat change on black bears in the Pisgah National Forest, North Carolina, USA, 1981–1994.

Index	Sub-index ^a	Habitat component sampled	Estimation method
FY ₁ ^b		Number of fallen logs/ha, an index to abundance of colonial insects	Visual estimate within 3-m radius on ground survey
FY ₂		An index to quality and availability of anthropogenic food	
	FY _{2a}	Anthropogenic food source	Aerial/road survey
	FY _{2b}	Distance to anthropogenic food source	Distance measured to mapped sources using GIS
	FY _{2c}	Distance between anthropogenic food source and escape cover	Distance measured on topographic map
FSp ₁		Distance to perennial water, an index to emerging grasses and forbs associated with moist habitats	Distance measured using GIS
FSp ₂		Percent cover of <i>Smilax</i> spp.	Visual estimate within 3-m radius on ground survey
FSu ₁		Percent cover in berry species ^c	Visual estimate within 3-m radius on ground survey
FSu ₂		Presence of red oak species, an index to productivity of squaw root (<i>Conopholis americana</i>), a parasite of red oaks	Overstory class assigned in CISC ^d database
FF ₁		An index to hard mast productivity	
	FF _{1a}	Forest cover type	Overstory class assigned in CISC database
	FF _{1b}	Age of stand	Age assigned to in CISC database
FF ₂		Number of grape (<i>Vitis</i> spp.) vines/ha	Visual estimate within 3-m radius on ground survey
FF ₃		Distance to nearest road ^e , an index of how roads affect access to fall foods	Measured using GIS
E ₁		Area of conterminous forest not bisected by roads	Measured using GIS
E ₂		Percent closure of understory	Visual estimate within 3-m radius on ground survey
E ₃		Slope of terrain	Calculated from DEM ^f using GIS
E ₄		Distance to nearest road	Measured using GIS
D ₁		Area of conterminous forest not bisected by roads	Measured using GIS
D ₂		Area in <i>Rhododendron</i> sp. or <i>Kalmia</i> sp.	Calculated from aerial photo
D ₃		Slope of terrain	Calculated from DEM using GIS
D ₄		Number of trees ≥90 cm DBH ^g /ha, an index of availability of cavity dens	Visual estimate within 10-m radius on ground survey

^a Variables combined into a single index.

^b The first letter of each index represents association with 1 of 3 life requisite variables in the HSI: Food (F), Escape cover (E), and Denning (D) resources. Subsequent letters indicate season of availability for the component being modeled: year-round (Y), spring (Sp), summer (Su), and fall (F).

^c Includes blueberries (*Vaccinium* spp.), huckleberries (*Gaylussacia* spp.) and blackberries (*Rubus* spp.).

^d Continuous Information of Stand Condition, U.S. Forest Service.

^e Index adjusted for traffic levels according to type of road: temporary, improved dirt, and paved.

^f Digital elevation model, U.S. Geological Survey.

^g Diameter at breast height.

Mitchell et al. 2002). Many of the components modeled in the HSI are affected by forest management (e.g., production of soft and hard mast, understory cover, effects of roads; Table 1); the effect of roads is the only component of the HSI that is explicitly negative with respect to forest management. When all habitat components are combined, however, the HSI does not predict a priori overall positive or negative consequences of forest management. Analyses based on changes in the HSI should more directly assess comprehensive impacts of forest management rather than choosing a single surrogate (e.g., food productivity, forest fragmentation, road density) for habitat suitability.

Garshelis (2000) emphasized the need to associate fecundity, survival, or other demographic surrogates of fitness with habitat characteristics. Obtaining such demographic data for black bears is difficult, however, even over long periods. Alternately, studies suggest that foraging behavior and other resource-selection behaviors are adapted to optimize fitness and therefore are surrogates for fitness (Stephens and Krebs 1986; Krebs and Davies 1991, 1993). Accordingly, we used habitat preferences of bears to indicate their response to changes in habitat. We assessed a behavioral response to habitat change therefore not a demographic one.

Our objectives were to (1) evaluate changes in black bear habitat due to forest management in our study area over a 14-year period, and (2) assess responses of black bears to these changes. To meet our first objective, we evaluated changes in habitat on stand (i.e., a group of trees similar in age structure and species composition) and landscape (i.e., multiple stands) scales. At the stand scale, we compared HSI components affected by timber harvests and the field data used to calculate them between harvested and unharvested forest stands. We expected changes in bear habitat following timber harvest. Prior to closure of the regenerating canopy, these changes would represent trade-offs between an abundance of early-successional foods, a loss of resources associated with mature overstory trees, and some characteristics of timber harvests modeled as explicitly negative by our HSI (e.g., effects of roads; Zimmerman 1992, Powell et al. 1997, Mitchell et al. 2002). We could not predict whether these trade-offs would result in differences in HSI between harvested and unharvested stands. We expected a decrease in food in harvested stands following canopy closure (but prior

to reestablishment of a mature overstory) because productivity of early-successional foods would decline rapidly, whereas productivity of resources associated with a mature overstory could take decades to develop (Goodrum et al. 1971). Thus, we predicted that HSI values for harvested stands with closed canopies would be lower than those for harvested stands with open canopies and for unharvested stands. Because pines offer fewer resources to bears than hardwoods (Hardy 1974, Brody 1984), we also predicted that harvested stands with closed pine canopies would have HSI values lower than those with closed hardwood canopies.

The negative effect of roads on the HSI is weighted by how heavily a road is used by humans (i.e., heavy use of paved roads has a strong effect, light use of gated logging roads has a modest effect; Zimmerman 1992, Powell et al. 1997, Mitchell et al. 2002). Brody and Pelton (1989) suggested that roads used little by humans (e.g., gated logging roads) could be used as travel corridors by bears, thereby having a positive effect on bear habitat (although see Unsworth et al. 1989). It was beyond the scope of this study to test whether effects of roads in the HSI were accurately modeled, but should they be inaccurate, their heavy negative weighting could bias HSI estimates for harvested stands because they were located near logging roads. To examine the potential for this bias, we evaluated whether effects of roads decreased HSI values more for harvested stands than for unharvested stands.

To assess habitat changes on a broad landscape scale, we analyzed spatial and temporal change across maps of HSI generated for each year of our study. We expected changes in HSI values on this scale to correspond with the spatial distribution and juxtaposition of forest management activities (e.g., negative effects of roads and unknown effects of timber harvests) and temporal variation in the intensity of forest management (i.e., extent of roads built and number of stands harvested per year). To assess habitat change on a finer landscape scale, we evaluated changes in HSI within home ranges of bears over the course of our study.

To meet our second objective, we evaluated relationships between an index of habitat change developed from HSI maps and habitat selection by black bears. We predicted that bears would prefer areas where habitat suitability increased over areas where it had decreased, both in their daily activities and in their annual selection and avoidance of habitat on the periphery of their home ranges.

STUDY AREA

We studied black bears living in the Pisgah Bear Sanctuary, located in the southern Appalachian Mountains of western North Carolina, USA, from 1981 through 1994. The Pisgah Bear Sanctuary is the largest (235 km²) of 28 bear sanctuaries established in North Carolina in 1971 and is contained completely within the Pisgah National Forest. Bear management within the sanctuary consisted primarily of protection from hunting; otherwise the forest was managed by the USFS for multiple uses, including timber products and outdoor recreation (e.g., camping, hiking, and hunting for species other than bear).

Topography in the sanctuary ranges from 650 to 1,800 m in elevation and is dominated by the Big Pisgah Ridge, which bisects the sanctuary and along which runs the Blue Ridge Parkway. The region is a temperate rainforest, with annual rainfall approaching 250 cm/year (Powell et al. 1997). The major forest types in the sanctuary are eastern hemlock (*Tsuga canadensis*), cove hardwoods (yellow poplar [*Liriodendron tulipifera*], magnolias [*Magnolia* spp.], and birches [*Betula* spp.]), oak-hickory (*Quercus* spp., *Carya* spp.), pine, and pine-hardwood mix. Little primary forest remains in the sanctuary, and uncut stands averaged 85 ± 25 (SD) years in age. As of 1994, timber was harvested from a total of 133 stands averaging 7.6 ± 3.8 ha and 15 ± 7 years in age. Most stands regenerated naturally after initial site preparation favoring oaks. Conversion of stands from hardwood to pine overstories was uncommon, occurring in 19 of the 133 stands. Timber harvests and road building peaked in the sanctuary in the late 1980s and early 1990s (C. Bolen, USFS, personal communication).

METHODS

Bear Trapping, Telemetry, and Home-range Estimation

Bears were trapped in the sanctuary from May through early summer from 1981 through 1994 (except 1991 and 1992) using modified Aldrich foot snares (Johnson and Pelton 1980) or culvert traps. A first upper premolar was extracted from each bear to estimate age from cementum annuli (Willey 1974). Most captured bears were fitted with motion-sensitive radiocollars (Telonics, Inc., Mesa, Arizona, USA; Lotek, Inc., Newmarket, Ontario, Canada; 3M and Wildlink, both of St. Paul, Minnesota, USA). For our analyses, we considered all bears to be adult at 3.5 years old

except for females known to have produced cubs at age 3, which we classified as adult at 2.5 years.

Each year from April or May until denning (mid-Dec), radiomarked bears were relocated from the ground. Bear locations were estimated by triangulation, generally using a minimum of 3 separate locations obtained within 15 min (Zimmerman and Powell 1995). When possible, each bear was located every 2 hr for 8 consecutive hr. Sampling was repeated every 32 hr to standardize bias from autocorrelation within the 8-hr sampling periods and to minimize that bias between periods (Swihart and Slade 1985; Powell 1987). Observers also estimated the locations of "test" collars at least once during every 8-hr sampling period to determine telemetry error. Zimmerman and Powell (1995) evaluated telemetry error using much of the same data in our study and determined the median error to be 261 m. Ninety-five percent of the estimates were <766 m from the true location, and error did not differ significantly among observers.

We estimated annual home ranges for bears from location data using a fixed-kernel estimator with bandwidth determined by least-squares cross validation (program KERNELHR; Seaman et al. 1998). The kernel estimator depicts use of space by a bear as a utility distribution (i.e., the probability a bear will be found within each cell of a grid that encompasses all location estimates; Worton 1989; Seaman and Powell 1996). We used a minimum of 20 locations for home-range estimates (Noel 1993; Seaman and Powell 1996), and a grid size of 250 m for kernel estimation to match median telemetry error. For analyses, we defined home range for each bear as the area containing 95% of the estimated utility distribution.

Quantifying Habitat

During 1983–1984 and 1993–1994, we collected habitat data (Table 1) used to calculate the HSI at 122 sampling sites systematically located at intersections of major Universal Trans-Mercator (UTM) grid lines within the sanctuary (Powell et al. 1997, Mitchell et al. 2002). All sampling sites fell within unharvested forest stands. Therefore, we also collected habitat data in 46 of the 133 harvested stands in the sanctuary. Harvested stands fell into 3 broad classes according to age and regenerating forest type: stands ≤10 years old, pine stands >10-years-old, and hardwood stands >10 years old. We used means of observed habitat variables in each of the 3 classes of harvested stands to estimate HSI components for all 133

harvested stands in the sanctuary. We selected harvested stands to provide a balanced representation of the 3 classes across the spatial extent of the sanctuary and among different topographic types (e.g., ridge, ridge side, and cove). We collected ground survey data (Table 1) at 5 sub-sites (a center site and 4 sites located 100 m from the center on cardinal headings) located at each UTM grid intersection and in the center of each sampled harvested stand. Data from the 5 sub-sites were averaged to estimate each habitat component for each sampling site. We used analysis of variance (ANOVA; SAS Institute 1990) to evaluate mean HSI for the 3 classes of harvested stands and for unharvested stands to estimate effects of timber harvest and regeneration type on HSI. To evaluate whether road effects modeled in the HSI biased comparisons of harvested to unharvested stands, we used ANOVA to evaluate mean HSI, calculated without the components that model road effects (FF_3 , E_1 , E_4 , and D_1 ; model variables defined in Table 1), for the 3 classes of harvested stands and for unharvested stands.

We used data from harvested and unharvested stands, along with information derived from the USFS Continuous Information of Stand Condition (CISC) database, GIS layers (e.g., digital elevation models for terrain and digital line graphs for roads), aerial photographs, and topographic maps to map HSI components (Table 1) for the sanctuary for each year of our study. We used a GIS (IDRISI; Eastman 1997), to produce final HSI maps for the sanctuary for each year by combining maps for each component in each year (Mitchell et al. 2002). Maps of HSI represented habitat conditions on a scale of zero (poor habitat) to 1 (excellent habitat). We set the grain of final images at 250×250 m to approximate the median error for our telemetry locations of bears (260-m radius).

Changes in Habitat Over Time

To assess changes in HSI on a broad, sanctuary-wide scale, we used the time-series analysis function in IDRISI (Module TSA; Eastman 1997) to evaluate the spatial and temporal changes in HSI throughout the sanctuary from 1981 to 1994. Time-series analysis depicts the extent of spatial changes over a temporal sequence of maps as orthogonal maps of standardized principal components. The first component map represents the "typical" condition over the time series (i.e., aspects of the landscape that changed least over time). Subsequent component maps portray aspects of the landscape that changed most over

time, each component explaining less of the variance within the time series than its predecessor (Eastman 1997). We limited the number of component maps generated by time-series analysis of the HSI to 2: component 1 portraying the typical condition for HSI, and component 2 portraying the strongest changes in HSI during our study.

Time-series analysis evaluates temporal changes in spatially distributed data by correlating maps in the temporal sequence with the 2 component maps. The relative correlations of maps within the time series with component 1 indicate magnitude of change between years. Correlation of a given map within the time series with component 2 indicates the extent to which that period is associated with important spatial changes observed over the entire series. Positive correlation indicates relative contribution to overall patterns of change; negative correlation indicates relative lack of contribution. We analyzed temporal change in HSI graphically by plotting correlations of HSI maps for each year, with the map representing the typical condition against correlations with the map representing major changes. To assess changes in HSI on a finer landscape scale relevant to individual bears, we used ANOVA to evaluate variation in mean HSI of home ranges for all bears we sampled, blocked by sex and age class (i.e., juvenile or adult).

Evaluation of Responses of Bears to Habitat Change

We used the time-series analysis in IDRISI to generate 13 component 2 maps representing major changes between consecutive years from 1981 through 1994. These maps represented year-to-year changes in HSI, differing from the single map we used to represent change across all study years. We used these component 2 values as an index of change in HSI (C) between consecutive years. This index depended not only on annual differences in HSI, but also on the spatial context for those differences. Areas of isolated change were weighed less heavily than those where change was broad, and change in 1 direction for an area was mitigated if near an area with change in the opposite direction. We set resolution of maps of C at 250×250 m to match the resolution of home-range estimates. We used the kernel probabilities estimated for each 250×250 -m cell in the home range of a bear as an index of habitat use. For each bear in each year, we calculated a preference index (P) based on C , using the ratio (Ivlev 1961, Powell et al. 1997):

$$P = \frac{\text{(Use of class } C_i - \text{Availability of class } C_i)}{\text{(Use of class } C_i + \text{Availability of class } C_i)}$$

We then used ANOVA to test whether C predicted habitat preferences of bears.

The cores of home ranges we sampled were generally stable, but the peripheries varied in size and shape between years, primarily in response to annual changes in food productivity (Powell et al. 1997). Thus, some patches at the peripheries of home ranges were added or dropped each year. For each bear with a home-range estimate in 2 consecutive years, we assigned each 250 × 250-m cell of the 2 home ranges to 1 of 2 selection classes: selected (i.e., used in both years or added in the second year) or rejected (i.e., dropped the second year). We also assigned each cell to 1 of 2 change classes based on C : positive (i.e., $C \geq 0$, habitat did not change, or HSI improved) or negative (i.e., $C < 0$, HSI decreased). We used chi-square analysis (SAS Institute 1990) to test whether cells with positive and negative changes were more likely to be selected or rejected by bears from one year to the next. We analyzed data separately for male and female bears by age class (adult and juvenile).

RESULTS

Changes in Habitat

Little changed in the availability or accessibility of anthropogenic food in the Pisgah Bear Sanctuary during our study (Mitchell et al. 2002). The only changes to forest stands were due to forest management: timber was harvested in 111 stands (84% of all harvested stands in the sanctuary) and only logging roads were built (Fig. 1).

Changes in HSI resulting from timber harvesting were complex. Extensive slash left from harvest produced high index values for colonial insects (IF_1) for harvested stands ≤10 years old, but low values for stands >10 years old compared to those in unharvested stands (Table 2). Cover of greenbrier (*Smilax* spp.; FSp_2) was consistently higher in harvested stands of all types than in unharvested stands, but highest in harvested stands ≤10 years old (Table 2). The number of grape vines/ha (FF_2) was also higher in harvested stands of all types than in unharvested stands, but highest in hardwood stands >10 years old. A flush of blackberries following opening of the canopy resulted in a relatively high berry index (FSu_1) in harvested stands ≤10 years old. Blackberries, though present, were sparsely distributed in

unharvested forest where blueberries and huckleberries predominated (Table 2). All berry-producing species were sparse in harvested stands >10 years old, and FSu_1 for these stands was lower than for unharvested stands.

Predictably, the index for hard mast production associated with stand age (FF_{1a}) was very low for harvested stands of all classes compared to unharvested stands. Understory closure (E_2) was very high in harvested stands ≤10 years old, exceeding that found in unharvested stands, but was lower in harvested stands >10 years old than in unharvested stands (Table 2). Harvested stands >10 years old differed strongly in indices for important summer and fall foods (FSu_2 and FF_{1a}) depending on whether they were regenerated in hardwoods or pine (Table 2). Mean HSI was higher for unharvested stands than for all classes of harvested stands, among which no difference existed (Table 3).

By definition (Zimmerman 1992, Powell et al. 1997, Mitchell et al. 2002), HSI was reduced near roads. The winding nature of the logging roads created large areas of negative effect. Because all logging roads built during our study were gated, however, they received relatively light use by humans (e.g., hikers, mountain bikers, hunters on foot). Therefore, the negative effect of these roads on the HSI was less than if they had been paved or ungated (Mitchell et al. 2002). Removing road effects from the HSI altered comparisons between harvested and unharvested stands only somewhat. Mean HSI was still higher for unharvested stands than for all classes of harvested stands. Harvested stands ≤10 years old did not differ from stands >10 years old and regenerating in hardwoods, but both classes differed from harvested stands >10 years old and regenerating in pines (Table 3).

Changes in HSI Over Time

Time-series analysis indicated that much of the sanctuary was unaffected by management activities during our study (Fig. 2A). As the forest aged, HSI increased slightly in areas where no timber harvest or road-building took place (Fig. 2B), but showed relatively strong decreases in localized areas where timber was harvested or roads built (Fig. 2B). The strong correlation (Fig. 3) between the maps of HSI for each year and the map of component 1 (Fig. 2A) indicates that, on a landscape scale, annual changes throughout the sanctuary were small and overall habitat suitability changed only slightly. The plot of correlations between maps of HSI for each year and maps of compo-

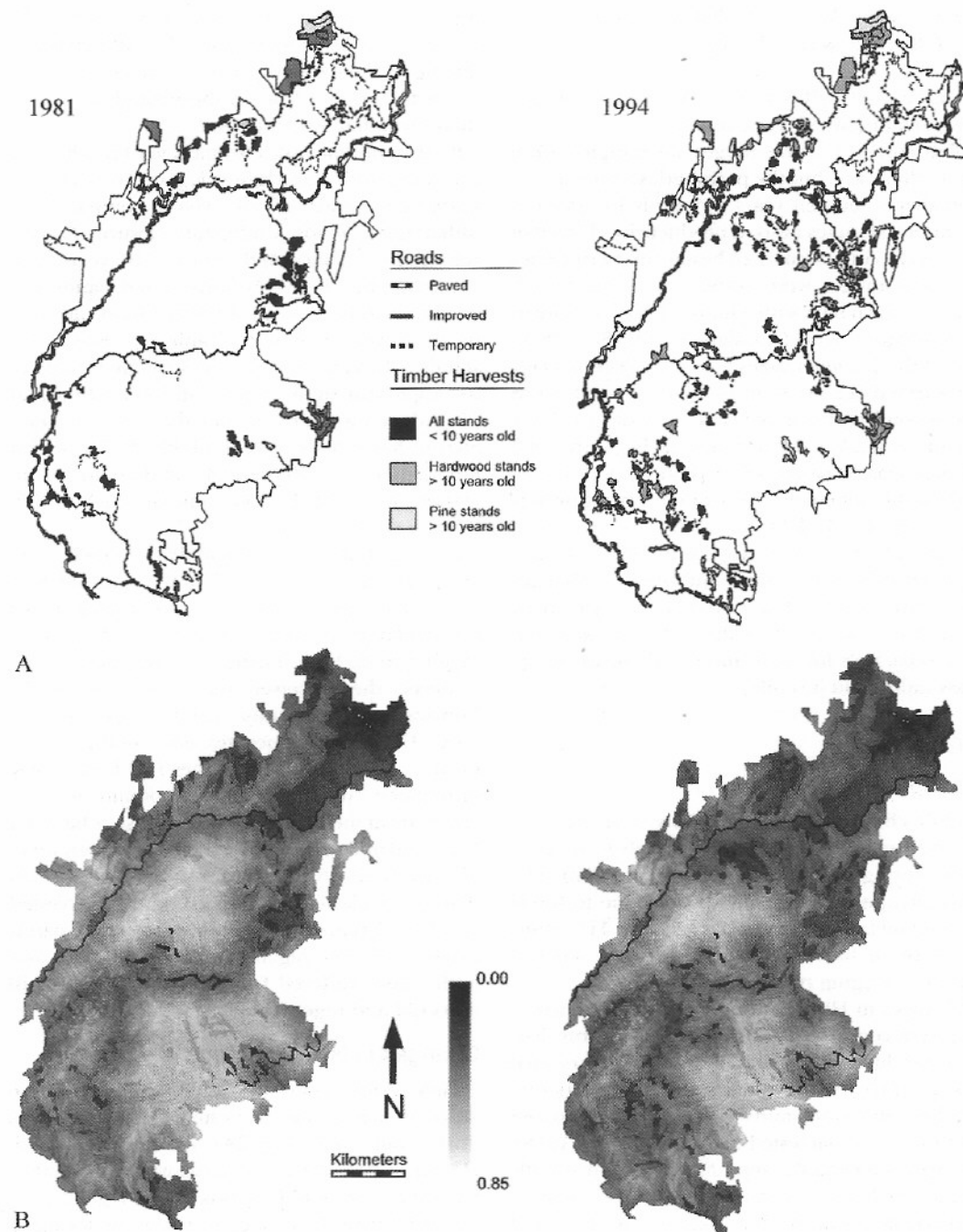


Fig. 1. Maps of (A) roads and timber harvests and (B) of a Habitat Suitability Index (HSI) for black bears for the Pisgah Bear Sanctuary, North Carolina, USA, in 1981 and 1994. Values for the HSI range from zero (black, poor quality) to 1 (white, high quality).

nents 1 and 2 indicates changes in sanctuary-wide habitat suitability began in 1984 and were most intense in the late 1980s to the early 1990s, corresponding to the period of peak forest manage-

ment in the sanctuary (Fig. 3). On a finer scale, mean HSI for 127 home ranges of black bears (38 adult males, 32 juvenile males, 55 adult females, 2 juvenile females; mean number of locations per

Table 2. Mean (SD) habitat measurements and associated index values for components of a black bear Habitat Suitability Index (HSI) for harvested and unharvested stands sampled in the Pisgah Bear Sanctuary, North Carolina, USA, 1981–1994. The 3 classes of harvested stands were based subjectively on differences in HSI components corresponding to canopy closure and to regeneration type. Age of harvested stand = years since harvest. The number of downed logs/ha (FY_1) is an index for abundance of colonial insects. Presence of oak (FSu_2) is an index for the abundance of squaw root based on proportion of red oak in the overstory, U.S. Forest Service Continuous Information of Stand Condition classes. Forest cover type (FFa_{1a}) is an index of hard mast production based on the mix of overstory species.

Habitat feature	HSI component	All harvested stands ≤10 yr old (n = 15)		Harvested stands >10 yr old, regenerating in hardwoods, (n = 17)		Harvested stands >10 yr old, regenerating in pines, (n = 16)		Uncut forest, 85 ± 25 (SD) yr old (n = 122)	
		Observed	Index	Observed	Index	Observed	Index	Observed	Index
No. downed logs/ha	FY_1	154.37 (139.42)	0.23	53.16 (54.43)	0.14	33.74 (42.02)	0.13	62.39 (39.46)	0.15 (0.27)
% cover of <i>Smilax</i>	FSp_2	2.94 (11.16)	0.24	1.87 (3.89)	0.15	1.36 (3.45)	0.11	1.12 (4.23)	0.07 (0.16)
% cover of berries	FSu_1	10.93 (18.03)	0.36	4.13 (13.70)	0.13	4.89 (12.28)	0.16	7.25 (11.11)	0.23 (0.31)
Presence of red oak	FSu_2		0.76		0.65		0.00		0.74 (0.27)
Forest cover type	FFa_{1a}		0.70		0.80		0.01		0.84 (0.24)
Forest age	FF_{1b}	5.00 (2.30)	0.00	17.06 (3.54)	0.01	21.56 (6.04)	0.08	73.51 (18.42)	0.94 (0.18)
No. grape vines/km ²	FF_2	245.21 (662.95)	0.22	744.80 (588.70)	0.82	114.95 (235.14)	0.28	57.18 (157.58)	0.16 (0.33)
% understory	E_2	62.92 (30.10)	0.56	27.01 (22.34)	0.05	28.68 (23.65)	0.06	40.81 (21.94)	0.27 (0.29)

bear was 121.5 ± 72.28) decreased during our study (slope = -0.008 ; $F_{1,123} = 28.86$; $P < 0.01$).

Responses of Black Bears to Habitat Change

Both sex and age class of bears explained a significant proportion of the variability in the preference index for habitat change ($P < 0.01$), so we blocked analyses by both factors. Across all 127 home ranges we analyzed, P varied weakly with C ($r^2 = 0.03$; $F_{4,73} = 4.67$; $P < 0.01$). The preference index estimated from home ranges of adult females showed a strong, positive relationship with C (slope = 0.11 ; $P < 0.01$), whereas the index estimated from the home ranges of juvenile

females ($P = 0.84$) and juvenile and adult males ($P = 0.18$ and $P = 0.17$, respectively) showed no relationship.

We had 40 2-year pairings of home ranges (i.e., home ranges for the same bear in 2 consecutive years) for 36 bears. Adult males ($n = 14$) and adult females ($n = 17$) selected positively changed patches and rejected negatively changed patches (Table 4). Juvenile males ($n = 5$), however, selected patches in which habitat suitability had decreased (Table 4). Although the home ranges of adult males were much larger than those of adult females, patches in which habitat suitability had decreased made up 8% of their home ranges,

Table 3. Comparison of a habitat suitability index (HSI) calculated for 4 classes of forest stands in the Pisgah Bear Sanctuary, Pisgah National Forest, North Carolina, USA, 1981–1994. Classes consisted of unharvested stands 85 ± 25 (SD) years old, harvested stands ≤ 10 years old, harvested stands >10 years old and regenerating in hardwoods, and harvested stands >10 years old and regenerating in pines. To evaluate potential bias associated with negative effects of roads modeled in the HSI (Mitchell et al. 2002), HSI values for the 4 classes calculated without effects of roads also are presented.

	Harvested stands ≤10 yr old		Harvested stands >10 yr old, hardwood		Harvested stands >10 yr old, pine		Unharvested stands		$F_{3,164}$	P
	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD		
HSI	0.38A ^a	0.03	0.36A	0.02	0.28A	0.03	0.47B	0.17	10.75	<0.01
HSI, without road effects	0.62A	0.03	0.64A	0.02	0.56B	0.03	0.75C	0.03	293.55	<0.01

^a Means within a row with the same letter did not differ.

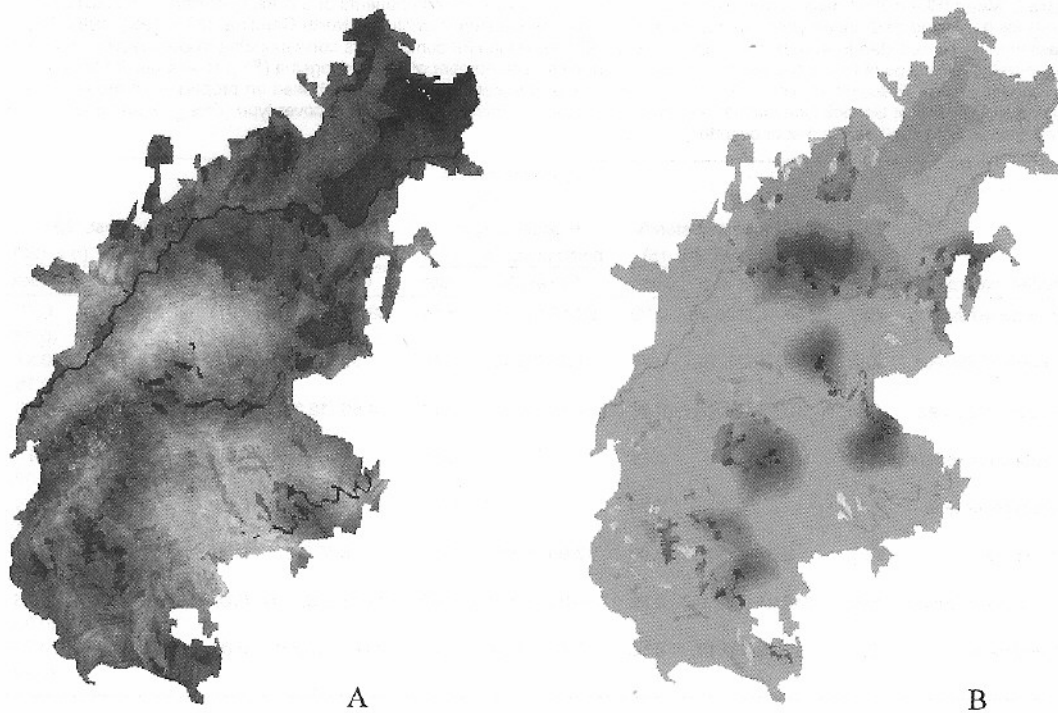


Fig. 2. Time-series analysis of spatial changes in a black bear Habitat Suitability Index (HSI) for the Pisgah Bear Sanctuary, North Carolina, USA, 1981–1994. The maps indicate patterns in spatial variability across HSI maps generated for each year. Map A represents the “typical” condition over the time series (i.e., aspects of the landscape that changed least over time). Values for the HSI range from zero (black, poor quality) to 1 (white, high quality). Map B portrays aspects of the landscape that changed most over time. Values vary from strong negative change (black) to strong positive change (white); the shade of gray covering most of Map B represents slight positive change.

compared to 19% and 21% for adult females and juvenile males, respectively.

DISCUSSION

Changes in Habitat

Our assessment of the effects of forest management on bear habitat assumed that our HSI is a reasonable portrayal of habitat suitability for black bears in the southern Appalachians. The complete HSI model has been tested and shown to strongly predict habitat use by bears (Mitchell et al. 2002). Relationships modeled for each of its components have not been evaluated individually, but are largely based on findings of empirical studies (Zimmerman 1992, Powell et al. 1997, Mitchell et al. 2002). As indices, modeled components of the HSI cannot represent reality with complete accuracy; the potential for biased HSI estimates depends on the extent component models oversimplify or depart from reality. We believe this potential is weak for 3 reasons: (1) the ability of the HSI to predict habi-

tat use by bears would be unlikely if a large number of component models did not approximate biological relationships between bears and their habitat; (2) HSI estimates are not overly sensitive to any of the components (Mitchell et al. 2002), therefore 1 incorrectly modeled component does not have the potential to strongly bias the HSI; and (3) the number of relatively independent components in the HSI make a directional bias in the full model (e.g., consistent underestimation of HSI for a given type of forest stand) unlikely.

As we expected, changes in bear habitat brought about by forest management on a stand scale were complex. Recently harvested stands provided an abundance of food resources to bears. The density of the understory in recently harvested stands also provided excellent escape cover. These habitat improvements were countered by the negative effects of removing overstory, including loss of hard mast production and potential den trees. According to our HSI, this trade-off in resources in the years immediately following timber harvest

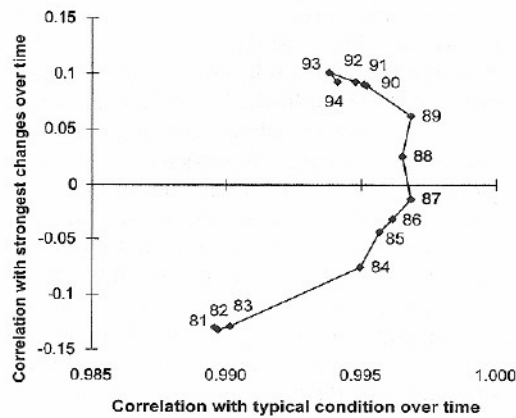


Fig 3. Time-series analysis of temporal changes in a black bear Habitat Suitability Index (HSI) for the Pisgah Bear Sanctuary, North Carolina, USA, 1981–1994. The x-axis depicts the correlation (Pearson's correlation coefficient) of HSI maps generated for each year with the typical condition of HSI over the time series. The y-axis depicts the correlation of HSI maps generated for each year with overall change in HSI over the time series. The relative correlations of annual HSI maps with typical condition indicate magnitude of changes between years. Positive correlation of an annual HSI map with changes over time indicates relative contribution to overall change in HSI from 1981 to 1994; negative correlation indicates relative lack of contribution.

generally was negative, where habitat improvements did not completely offset losses.

As expected, many resources made available by timber harvesting declined as harvested stands aged and early-successional vegetation was shaded out and logging slash decomposed. The high productivity of grapes and greenbrier in these older stands, combined with the reappearance of some hard-mast productivity in hardwood stands, appeared to compensate for these losses because, contrary to our prediction, HSI did not decline significantly following canopy closure. Although

stands regenerating in pine tended to have lower HSI values than those regenerating in hardwoods, this difference was not statistically evident unless the effects of roads were removed from the HSI. This suggests little difference between the 2 types of regenerating stands. The similarity, however, was due to low production of hard mast in the immature hardwood stands (Goodrum et al. 1971); the hard mast index in the HSI for these stands was correspondingly low (Table 2; Mitchell et al. 2002). Production of hard mast, and therefore HSI values, would increase for hardwood stands as they aged but would not for pine stands. We expect that HSI for the 2 stand types would differ for stands older than we sampled.

As harvested stands regenerating in hardwoods age, we expect their HSI values will converge with those for unharvested stands, but we could not demonstrate this with the relatively young (15 ± 7 yr old) harvested stands in our study area. We do not know at what age habitat suitability for a harvested stand becomes comparable to unharvested stands we sampled (85 ± 25 yr old). The HSI component explicitly modeled on age (FF_{1b}), however, indicates some convergence of harvested and unharvested stands at 60 years of age. How other age-related factors (e.g., development of huckleberry and blueberry species, abundance of grape vines) might converge between harvested and unharvested stands is not known. Availability of trees large enough to provide cavities for denning in harvested stands would not be comparable to unharvested stands for decades, unless known cavity trees were retained in harvested stands.

A portion of the negative effect of forest management reflected in our HSI resulted from forest fragmentation and increased exposure to humans caused by roads. Only these components of the HSI explicitly predicted negative effects of forest

Table 4. Year-to-year selection of patches on the periphery of home ranges of black bears living in the Pisgah Bear Sanctuary, North Carolina, USA, 1981–1994. Patches added and dropped between 2 consecutive years from home ranges of 40 were classified based on whether habitat suitability increased (+) or decreased (–) according to an index of habitat change. The likelihood of patches being selected or rejected for a home range between years based on habitat change was assessed for adult females ($n = 17$), and adult ($n = 14$) and juvenile ($n = 5$) males.

Age class and sex of bears	Change in habitat	Observed	Rejected % of total		Selected % of total		χ^2 (df = 1)	P	
			Observed	Expected	Observed	Expected			
Adult female	+	1,368	15.73	1,407.80	5,663	65.13	5,623.20	7.36	< 0.01
	–	373	4.29	333.18	1,291	14.85	1,330.80		
Adult male	+	3,082	22.33	3,158.90	9,628	69.76	9,551.10	31.47	< 0.01
	–	348	2.52	271.15	743	5.38	819.85		
Juvenile male	+	1,092	17.29	980.43	3,931	62.23	4,042.60	77.02	< 0.01
	–	141	2.23	252.57	1,153	18.25	1,041.40		

management because of the proximity of harvested stands to logging roads. The models and relative weighting of road effects in the HSI (Zimmerman 1992, Powell et al. 1997, Mitchell et al. 2002) are consistent with much of the research on effects of roads on bears (Hamilton 1978, Quigley 1982, Villarubia 1982, Brody and Pelton 1989; but see Young and Beacham 1986, Unsworth et al. 1989, and Brody and Pelton's [1989] discussion of abandoned roads) and patterns in hunting mortality of bears in North Carolina (Collins 1983). The ability of the HSI to predict habitat use by black bears and the balanced sensitivity of HSI estimates to components modeling road effects (FE_3 , E_1 , E_4 , and D_1 ; Table 1; Mitchell et al. 2002) suggest that effects of roads are appropriately modeled in the HSI. If this is untrue, however, the strong, negative weighting given to road effects in the HSI had the potential to bias HSI estimates for harvested stands. Removing road effects raised HSI estimates almost equally across all harvested and unharvested stand types. Relative rankings of HSI for harvested and unharvested stands did not change; therefore, road effects in the HSI did not bias estimates for harvested stands. The increased statistical distinction among HSI values for harvested stands once road effects were removed (Table 3) suggests that road effects in the HSI can overwhelm other potentially important differences in habitat. Further research is needed to determine whether this balance between effects of roads and other aspects of bear habitat is biologically appropriate.

Changes in HSI Over Time

On a broad landscape scale, habitat suitability across the sanctuary changed little during our study. As we expected, changes in HSI were associated with the peak period of timber management in the late 1980s and early 1990s (Fig. 3), but timber management did not result in annual distributions of HSI that differed strongly from the average condition over all years (Fig. 3). Although forest management was widespread (Fig. 1), it affected relatively small portions of the sanctuary at any given time, so overall habitat suitability varied little from year to year. On finer landscape scales, however, where timber harvests were clustered or road density was high, changes could be relatively intense (Fig. 2B), and habitat suitability did decline within home ranges of bears during our study.

Responses of Black Bears to Habitat Change

Our assessment of responses of black bears to changes in habitat assumed that habitat selection

is a reasonable indicator of their relationship with habitat. This assumption is valid to the extent that (1) habitat selection is associated with fitness, (2) each individual sampled has equal access to all available habitat conditions, and (3) sampling methodology is sufficient to observe use of habitat across all habitat conditions.

The relationship between selective behavior of animals and fitness is well-documented (Stephens and Krebs 1986, Krebs and Davies 1991, 1993). Strong linkages between black bears and the distribution and productivity of largely vegetative food sources (Amstrup and Beacham 1976, Young and Ruff 1982, Powell et al. 1997) suggest that habitat selection and fitness are closely associated for black bears. This association may not be evident, however, if bears are territorial and individuals have access to different habitat conditions based on social status. Although black bears can be territorial (Rogers 1987, Powell et al. 1997), territoriality has not been observed for bears living in the southern Appalachians (Garshelis and Pelton 1981, Powell 1987, Powell et al. 1997). We have no reason to believe that habitat selection by bears we observed was strongly biased by social status or territorial behavior. Insights into the behavior of animals derived from radiotelemetry have limitations set by the frequency and number of relocations; infrequent or few observations risk missing use of rare but important habitats. Because we collected a large number of relocations (121.5 ± 72.28) across the spectrum of HSI values (Mitchell et al. 2002), we consider it unlikely that unobserved use of uncommon HSI classes biased our findings.

As we predicted, bears responded to habitat changes brought about by forest management, but responses varied among bears depending on sex and maturity. Adult females continued to use areas within their home ranges where habitat changed, but did so inversely proportional to the extent that habitat suitability had declined. Adult males avoided areas of habitat decline more than other bears. In year-to-year selection of patches on home-range peripheries, patches of decline in habitat suitability were less preferred by adults of both sexes than patches where suitability had improved. Juvenile males used habitat where suitability had declined more than did adults of either sex.

These patterns are consistent with sex- and age-specific differences in home-range behavior among black bears. Adult male black bears have larger home ranges than adult females (Amstrup and Beacham 1976, Young and Ruff 1982, Powell

et al. 1997, Mitchell 1997). Adult males, therefore, may be more selective in patch choices than females because their large home ranges present more opportunities to encounter patches of high suitability and relatively poor patches can be avoided altogether. Adult female bears have fewer options in selection of habitat than do wide-ranging adult males and must make use of the habitat available to them in the immediate vicinity. Thus, adult females use patches where habitat has declined within their home ranges, but use them less than patches without decline. Like adult males, females preferred areas where habitat had not declined when selecting patches on the periphery of their home ranges. The pattern we saw for juvenile males may be an artifact of a small sample size ($n = 5$), but is nonetheless plausible. Juvenile males generally have not established permanent home ranges, often range widely, and therefore should be relatively insensitive to habitat change. Further, because adult males prefer areas of high habitat suitability, juvenile males may use relatively poor habitat to avoid large, dangerous males.

By modeling combined effects of forest management practices through our HSI, we did not directly or separately assess use of harvested stands or roads by bears. Because these effects of forest management were the predominant source of habitat change within the sanctuary and had an overall negative impact on the HSI, and we were able to demonstrate that adult bears either avoided areas of decline in HSI or used them less, we inferred that timber harvests and areas near roads were not preferred habitat of bears. This is consistent with studies that have also shown negative effects of timber harvesting (Young and Beecham 1986, Unsworth et al. 1989, Clark et al. 1994) and roads (Hamilton 1978, Quigley 1982, Villarubia 1982, Brody and Pelton 1989) on bear use of habitat, but differs from studies that found positive effects of timber harvesting (Jonkel and Cowan 1971, Lindzey and Meslow 1977, Samson and Huot 1998) and roads (Young and Beacham 1986, Unsworth et al. 1989).

Inconsistencies between findings among these studies and ours may be due in part to varying geographic locations (Arkansas, Clark et al. 1994; Idaho, Young and Beacham 1986, Unsworth et al. 1989; Montana, Jonkel and Cowan 1971; North Carolina, Brody and Pelton 1989; Quebec, Canada, Samson and Huot 1998; Washington, Lindzey and Meslow 1977). Intuitively, effects of forest management on bear habitat will vary depending on the type of forest being managed and local

conditions such as management history, landscape context, and climate. Black bears are adaptable generalists; therefore, the diversity of responses to forest management reported across the varied forest systems and geographic regions they occupy should not be surprising.

Inconsistencies among the studies also may be due to the difficulty of studying large, reclusive animals such as black bears, for which capture success generally is low, monitoring equipment is expensive, logistical constraints limit relocations, and study length often is brief, resulting in relatively few data for habitat analyses. Research on bears can therefore have low analytical power to discern habitat relationships and responses to habitat change. Across the published studies evaluating effects of forest management on black bears that we have cited (Jonkel and Cowan 1971, Lindzey and Meslow 1977, Young and Beecham 1986, Brody and Pelton 1989, Unsworth et al. 1989, Clark et al. 1994, Samson and Huot 1998), mean number of bears tracked was 19.43 ± 13.21 (SD), mean number of locations per bear was 57.09 ± 30.70 , and mean study length was 2.50 ± 2.02 years. By contrast, our study monitored behavior of 127 bears, with 121.5 ± 72.28 locations per bear, over 14 years. Our relatively large sample sizes and long study length imply greater power for evaluating how habitat changes brought about by forest management affect black bear behavior.

MANAGEMENT IMPLICATIONS

Evaluating effects of forest management using an HSI presumes that quality habitat for bears is a management objective or consideration. Although forest management positively affected some aspects of bear habitat in the southern Appalachians, it had a negative effect on overall habitat suitability for bears and on how bears in the Pisgah Bear Sanctuary used habitat. We caution, however, against an overly simplistic interpretation of this finding. We found effects of forest management on bear habitat to be complex and involve trade-offs on both stand and landscape scales. The influence of these effects on bears will be relative to conditions surrounding harvested areas and the resources limiting a bear population. Where habitat resources are abundant and none limit a bear population (e.g., the population is limited by hunting), the resources enhanced by forest management are not likely to positively affect bears. Neither should some decline in overall habitat suitability due to forest management negatively affect such a bear population.

Conversely, where a population is limited by resources enhanced by harvesting timber, using forest management to increase those resources at the cost of overall habitat suitability may be warranted. For example, the early stages of regeneration may provide soft mast and protein to bears where the surrounding forest may provide little (e.g., use by bears of recently harvested stands at the boundaries of a park wherein no timber was harvested; Samson and Huot 1998). Such benefits to bear habitat, however, would last only as long as the canopy remained open and would need to be balanced against the scarcity of other resources (e.g., hard mast, den trees) that would last much longer.

Should a bear population be limited by the less ephemeral resources enhanced by timber harvests, benefits of forest management to bear habitat may be more long term. For example, productivity of fall soft mast is high in harvested stands of all ages and could provide an alternative food source on a landscape where production of hard mast is poor or unreliable. Although results from our study are equivocal on how stands regenerating in hardwoods and pine differed, we suggest that stand conversion from hardwood to pines has the potential to have the greatest long-term negative impact on habitat suitability for bears in the southern Appalachians.

Understanding relationships between black bears and forestry practices is important in the management of Pisgah National Forest, which, along with 6 other National Forests in the eastern United States, has designated the black bear as a management indicator species (MIS; U.S. Forest Service 1994). The MIS concept assumes that responses of a single, monitored species to management practices can be used to indicate the responses of other species that share its habitat associations. The concept has received considerable criticism (Patton 1987, Landres et al. 1988, Niemi et al. 1997) because it has received little critical evaluation, yet it is a widely applied management tool. Ours is the first study of which we are aware to critically assess responses of a designated indicator species to forest management. Our work suggests that bears probably would be poor indicators for most forest management plans. Monitored bears would yield ambiguous indications because their responses to forest management differ according to sex and maturity. Intensive monitoring needed to discern a population-level response from among age- and sex-specific responses is likely to exceed the logistical and financial constraints of most management agencies.

ACKNOWLEDGMENTS

Graduate students G. Warburton, J. Zimmerman, P. Horner, M. Fritz, E. Seaman, J. Noel, A. Kovach, and V. Sorensen helped us collect data, along with the help of over 3 dozen undergraduate interns, technicians, and volunteers and approximately 250 Earthwatch volunteers. Our research received financial and logistical support from B. Bacon and K. Hailpern, J. Busse, Citibank Corp., the Columbus Zoo Conservation Fund, the Geraldine R. Dodge Foundation, Earthwatch/The Center for Field Research, 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. King and D. King, McIntire Stennis funds, the National Geographic Society, the National Park Service, the National Rifle Association, the North Carolina Agricultural Research Service, North Carolina State University, Port Clyde and Stinson Canning Companies, 3M Co., the U.S. Forest Service, Wildlands Research Institute, Wilburt Corp., and Wildlink, Inc. M. Reynolds assisted with preparation of GIS figures. W. Laudenslayer, B. Grand, R. Mirarchi, G. Hepp, S. Ditchkoff, T. White, Jr., and several anonymous reviewers provided valuable comments on early versions of this manuscript. All bears were captured and handled in compliance with requirements of the Institutional Animal Care and Use Committees for North Carolina State University (IACUC# 96-011) and Auburn University (IACUC # 0208-R-2410).

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Received 14 December 2001.

Accepted 1 July 2003.

Associate Editor: White, Jr.

