THE EFFECTS OF FOREST MANAGEMENT ON HABITAT QUALITY FOR BLACK BEARS IN THE SOUTHERN APPALACHIAN MOUNTAINS

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THE EFFECTS OF FOREST MANAGEMENT ON HABITAT QUALITY FOR BLACK BEARS IN THE SOUTHERN APPALACHIAN MOUNTAINS

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THE EFFECTS OF FOREST MANAGEMENT ON HABITAT QUALITY FOR BLACK BEARS IN THE SOUTHERN APPALACHIAN MOUNTAINS

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DISSERTATION ABSTRACT

THE EFFECTS OF FOREST MANAGEMENT ON HABITAT QUALITY FOR BLACK BEARS IN THE SOUTHERN APPALACHIAN MOUNTAINS

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Studies of habitat selection have been used to understand the effects of forest management on habitat quality for black bears (*Ursus americanus*), but results have been incomplete because all behavioral studies have been conducted at only one spatial scale and no study has used direct measures of fitness (e.g., survival, reproduction, etc.). I evaluated how black bears in the Pisgah Bear Sanctuary, in western North Carolina, responded behaviorally and demographically to clearcuts and roads. I linked estimates of hard mast and soft mast with estimates of bear survival, recruitment, and population growth to evaluate resource limitation by bears during 1981-2002. I also linked availability of clearcuts, in which soft mast was high, with estimates of demography. At both the individual and population levels, I linked estimates of habitat preference for roads with estimates of survival. Results of behavioral analyses showed females preferred young clearcuts when selecting resources within home ranges, but not when establishing home ranges. Male and female bears avoided areas near gravel roads, but not paved roads, during both summer and fall for both orders of selection. Results of demographic analyses showed the additive availability of hard mast and soft mast contributed most to population growth. Availability of young clearcuts helped explain recruitment, but not population growth. Avoidance of areas near gravel roads explained individual survival and population survival rate. Based on life history of bears, my results indicate the negative effects of gravel roads on bear survival likely outweighed the positive effects of clearcuts on bear recruitment. Because clearcuts are spatially associated with gravel roads, strategies to increase bear habitat in forested areas by implementing clearcuts must consider not only how clearcuts change availability of bear resources but also how gravel roads associated with clearcuts affect habitat quality. The research approach I used has broad application because it provides a way to distinguish among limiting resources, important resources, and resources that are relatively unimportant for populations of wild animals. By using direct measures of fitness, my approach provides a rigorous method for testing the effects of disturbances on habitat quality for wild animals.

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- Garmin eTrex Legend ® GPS
- Program MARK
- Microsoft
    - Excel ®
    - Word ®
    - Powerpoint ®

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CHAPTER 1

INTRODUCTION

This dissertation presents research performed to evaluate hypotheses about the effects of forest management on habitat quality for black bears (*Ursus americanus*) in the Pisgah Bear Sanctuary (PBS) in western North Carolina. Forest management includes harvesting trees and roads building. 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). Although numerous studies of habitat selection have examined the effects of forest management on habitat quality for black bears (Clark et al 1994; Jonkel and Cowan 1971; Lindzey and Meslow 1977; Mitchell and Powell 2003; Samson and Hout 1998; Unsworth et al 1989; Young and Beecham 1986; Zager et al 1983) findings have been incomplete and possibly biased because all behavioral studies were done at only one spatial scale and no study used direct measures of fitness.

Single scale approaches to studies of habitat selection may yield incomplete inferences (Maurer 1985; Mitchell et al. 2001; O'Neill and King 1998) because ecological processes, such as 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, resource selection within a home range may be constrained by home range selection (Bissonette 1997), which in turn may be affected by broad-scale processes like forest fragmentation, social interactions, etc. Because the cues animals use to establish home ranges may differ from those used to select resources within home ranges, estimates of habitat selection may differ among scales of investigation.

Using studies of habitat selection alone to understand habitat quality for wild animals may yield unreliable inferences because habitat use does not always indicate habitat quality (Garshelis 2000; Hobbs and Hanley 1990; Morrison 2001; Van Horne 1983). Studies of habitat selection assume the time that animals spend in a habitat correlates with the value of the habitat (Emlen 1966; Charnov 1976; McArthur and Pianka 1966), but this relationship may decouple when resources are highly concentrated. Moreover, a habitat or resource that is minimally used by a population may actually be most critical to survival or reproduction (Van Horne 1983). The most robust and reliable way to understand how habitats, resources, and disturbances affect habitat quality for wild animals is to use direct measures of fitness. No study to date has used direct measures of bear fitness to evaluate the effects of forest management on habitat quality for bears.

CLEARCUTS AND BEAR RESOURCES

The first step towards understanding how forest management affects habitat quality for bears is to determine how timber harvesting affects the availability of resources important to bear survival and reproduction. Bears require foods, den sites and escape cover (Powell et al. 1997), of which hard mast (acorns and nuts) and soft mast (fleshy fruits) have been shown to affect bear survival or reproduction (Costello et al. 2003; Eiler et al. 1989; Elowe and Dodge 1989; Pelton 1989; Roger 1977). Although it is known that timber harvesting removes hard mast for 25-50 years, the time required for regenerating hardwoods to reach reproductive age in the Southern Appalachians (Burns & Honkala 1990), it is not understood fully how timber harvesting affects the availability of soft mast in the Southern Appalachians. In Chapter 2, I evaluate the spatio-temporal availability of soft mast in clearcuts (i.e. removal of all trees within a stand), which was the primary harvesting technique used in PBS during 1844-2002.

RESOURCE LIMITATION

Because clearcuts affect the availability of soft mast and hard mast differently, the overall effect of clearcuts on habitat quality for a bear population will depend, in part, on whether hard mast, soft mast, or both limit the population. A resource is limiting if changes in its availability quantifiably affect population growth (Messier 1991). Resource limitation can be examined by augmenting resource availability for an animal population and estimating demographic response (Hart et al. 2006; Hoodless et al. 1999; Hubbs and Boonstra 1997), however, resource augmentation is not always logistically feasible and experimentation has limited spatial and temporal scope (Stephens et al. 2003). An alternative method for examining resource limitation is to link estimates of demographic parameters (e.g., survival, reproduction, population growth etc.) with estimates of resource availability over time (Langvatn et al. 1996; Mduma et al. 1999; Pennycuick 1969).

Because survival and reproduction may not contribute equally to population growth rate (λ), resource availability should be linked with λ for comprehensive understanding of resource limitation. Adult survival, for example, often contributes most to growth rate for populations of slow or K-selected species, whereas reproduction often contributes most to growth rate for populations of fast or r-selected species (MacArthur and Wilson 1967; Partridge and Harvey 1988). Theoretically, a resource may not limit a fast species even if the resource is important to survival. Similarly, a resource may not limit a slow species even if the resource is important to reproduction.

Previous studies on black bears have linked estimates of hard mast or soft mast productivity with bear survival or reproduction (Costello et al. 2003; Eiler et al. 1989; Elowe and Dodge 1989; Pelton 1989; Rogers 1977), but no study has linked food availability with population growth of bears. Moreover, most previous studies lasted ≤ 10 years (mean duration = 6 years), which may have been too short to accurately estimate bear demography (Brongo et al. 2005) or the effects of resources on bear demography (Reynolds and Mitchell, in press). Finally, no study has evaluated the relationships between bear demography and availability of hard mast and soft mast as each resource changed through time due to disturbance and succession. In Chapter 3, I link estimates of survival, recruitment, and population growth of PBS females with estimates of resource availability to evaluate hypotheses about whether hard mast, soft mast, or both limited PBS bears during 1981-2002. I also examine whether availability of young clearcuts, in which soft mast availability was high, influenced bear demography.

BEHAVIORAL RESPONSE OF BEARS TO CLEARCUTS

My demographic analyses assumed that bears used young clearcuts when they were available. If PBS bears did not select young clearcuts, then my demographic results regarding the effects of young clearcuts on bear demography may have been spurious. Several studies of habitat selection have already examined the behavioral response of bears to clearcuts, but the results have been conflicting. Adult female bears have been shown to prefer young clearcuts in some areas (Costello and Sage 1994; Heyden and Meslow 1999; Samson and Hout 1998) and avoid them in other areas (Clark et al. 1994; Mitchell and Powell 2003; Unsworth et al. 1989; Young and Beecham 1986). All of the previous studies evaluated either 2nd order selection (i.e., home range selection; Johnson 1980) or 3rd order selection (i.e., resource selection within home ranges), but none evaluated both orders of selection. I propose conflicting results from previous studies on clearcut use by bears can be resolved, in part, by examining habitat selection at multiple spatial scales. I test this hypothesis in Chapter 4.

ROADS AND HABITAT QUALITY

For black bears, roads may affect bear 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, bear foods may grow along roadsides (Beringer et al. 1989; Brody 1984; Carr and Pelton 1984; Manville 1983; Hellgren et al. 1991), which could affect bear survival and reproduction positively.

Traffic volume has been hypothesized to explain the behavioral responses of bears to roads. Bears have been shown to avoid roads with high traffic volume (e.g., paved roads; Beringer et al. 1989; Brody 1984; Brody and Pelton 1989; Fescke et al. 2002) and prefer roads with relatively low traffic volume (e.g., gravel or gated roads; Beringer et al. 1989; Brody 1984; Brody and Pelton 1987; Hellgren et al. 1991; Young and Beecham 1986). That black bears have also been shown to avoid roads with relatively low traffic volume (Clark et al. 1993; Garner 1986; Heyden and Meslow 1999; Quigley 1982), however, indicates traffic volume alone is insufficient to explain how roads affect habitat quality for bears. The source (or sources) of mortality that have the most impact on a bear population must also 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 or poaching are primary sources of bear mortality, then roads that provide access to hunters and poachers should have the largest negative effect on habitat quality. In Chapter 5, I use information on mortality sources for PBS bears to develop hypotheses regarding the effects of roads on habitat quality. To test my hypotheses, I evaluate habitat selection by PBS bears for areas near paved, gravel, and gated roads at two spatial scales.

ROAD USE AND BEAR SURVIVAL

Although numerous studies have evaluated the behavioral response of black bears to roads (Beringer et al. 1989; Brody 1984; Brody and Pelton 1989; Clark et al. 1993; Hellgren et al. 1991; Heyden and Meslow 1999; Pelton 1986; Unsworth et al. 1989; Young and Beecham 1986), none have tested whether the behaviors affected bear survival. Traditional studies of habitat selection estimate mean preference (based on habitat use and habitat availability; Manly 1983) for an animal population, which may mask differences in habitat preference between individuals with high fitness and individuals with low fitness. Exploiting differences in habitat preference, not homogenizing them, is key to testing whether particular behaviors affect fitness.

Another way to evaluate whether animal behaviors affect fitness is to link estimates of demography with estimates of habitat preference by the population. Previous demographic studies have linked demographic parameters (e.g., survival, fertility, etc.) with explanatory variables such as lichen cover (Skogland 1985), grass production (Mduma et al. 1999), forest fragmentation (Doherty and Grubb 2002), and edge proximity (Moorman et al. 2002), but these studies assumed the explanatory variable was used (or avoided) by the population when it was available. This assumption may not be valid. An increase in a habitat or resource may help explain increased survival for population x, but this correlation is spurious if population x does not use that habitat or resource. By linking estimates of habitat preference with estimates of demography, results should be reliable because habitat use (or avoidance) is not assumed.

In Chapter 6, I link estimates of habitat preference for areas near roads by PBS bears with estimates of survival, at both the individual and population levels. First, I partition the bears into those that were known to have died and those that survived and compare habitat preference for areas near roads between the two survival groups. Second, I link estimates of annual survival rate, which are informed by mortality data, with annual estimates of habitat preference for areas near roads by the population during 1981-2002. To my knowledge, this is the first study to link estimates of habitat preference (i.e., calculated using a ratio of habitat use and habitat availability) with estimates of population demography for any animal population.

HIERARCHY THEORY AND HABITAT QUALITY FOR BEARS

In Chapter 7, I synthesize my demographic and behavioral results within the framework of hierarchy theory to understand the overall effect of clearcuts and roads on habitat quality for PBS bears. Hierarchy theory (Allen and Starr 1982; King 1997; O'Neill et al. 1986) is a framework of system organization whereby ecological processes are understood in terms of both lower-level mechanisms and higher-level constraints. I propose that the temporal scales at which bear survival and reproduction are manifested in a bear population may differ, which may affect the way perturbations (e.g., clearcuts, roads, etc.) affect habitat quality for bears.

RESOURCE THRESHOLDS

Understanding biological thresholds of resource availability is critical to effective management and conservation of wild animal populations, however resource thresholds are difficult to quantify. I propose current methods for interpreting results from modeling population survival (i.e., evaluating model ranking, model weights, slope estimates, and model averaging) can be expanded to determine biological threshold levels of resources.

I demonstrate how interpreting intercepts with respect to odds ratios can yield insights into resource thresholds, assuming logistic regression is used to link estimates of resources with estimates of survival.

BROADER UNDERSTANDING OF HABITAT QUALITY

A broader goal of this research was to improve my understanding of what habitat quality means for black bears in the Southern Appalachians. Previously, a spatially explicit model of habitat quality was developed for black bears that included hypotheses regarding foods, den sites, and escape cover (Zimmerman 1992). The overall habitat model was tested using location data from PBS bears, but the individual components of the model (i.e., foods, den sites, and escape cover) have not been evaluated. To understand whether the habitat model predicted high quality den sites, I evaluate den selection by PBS bears at two spatial scales (Chapter 9). In Chapter 10, I summarize my results regarding bears and roads with respect to Zimmerman's (1992) habitat model. All chapters, except the Introduction (Chapter 1) and the two summary chapters (Chapters 7 and 10) are formatted according to manuscript guidelines for the Journal of Mammalogy with the exception that literature cited for each chapter is presented as a cumulative bibliography at the end of this dissertation.

CHAPTER 2

SPATIO-TEMPORAL AVAILABILITY OF SOFT MAST IN CLEARCUTS IN THE SOUTHERN APPALACHIANS

***Abstract**:* Soft mast is an important resource for many wild populations in the Southern Appalachians, yet the way clear-cutting affects availability of soft mast though time is not fully understood. We tested a theoretical model of temporal availability of soft mast in clearcuts using empirical data on percent cover and berry production of *Gaylussacia*, *Vaccinium*, and *Rubus* spp. plants in 100 stands that were clearcut (0-122 years old) in the southern Appalachian Mountains. We modeled the relationship between soft mast availability and stand age, evaluated the effects of topography and forest type on soft mast, developed statistical models for predicting the spatio-temporal distribution of soft mast, and tested the hypothesis that percent cover of berry plants and berry production provided similar information about soft mast availability. We found temporal dynamics explained berry production better than it predicted percent plant cover, whereas topographic variables influenced percent plant cover more than they influenced berry production. Berry production and percent plant cover were highest in ~2-9 year old stands. Percent plant cover was lowest in 10-69 year old stands and intermediate in 70+ year old stands. Three of our spatio-temporal models performed well during model testing and they were not biased by the training data, indicating the inferences about spatio-temporal availability of soft mast extended beyond our sample data. The methods we used to estimate the distribution of soft mast may be useful for modeling distributions of other resources.

Key words: clearcuts, habitat, timber harvesting, wildlife

Improving habitat quality for some populations of wild animals is often considered an objective of harvesting trees on forested landscapes. Timber harvesting increases availability of soft mast (Clark et al. 1994; Mitchell et al. 2002; Noyce and Coy 1990; Perry et al. 1999; Stransky and Roese 1984), an important component of habitat for many wild animals (Boddy 1991; Castlelberry et al. 2002; Thomas 1984; Thompson and Fritzell 1986; Willson 1986), including black bears (*Ursus americanus*; Elowe & Dodge 1989; Jonkel & Cowan 1971; Rogers 1976). Availability of soft mast in harvested stands and its affect on habitat quality, however, is not static. It changes through time due to succession.

In recently harvested stands, availability of soft mast can be relatively high (Clark et al. 1994; Mitchell et al. 2002; Noyce and Coy 1990; Perry et al. 1999; Stransky and Roese 1984) because conditions favor early successional species, some of which produce soft mast (e.g., *Rubus* spp.; Stransky and Roese 1984). As stands age and forest canopies close, however, availability of soft mast due to early successional species declines (Mitchell et al. 2002; Mitchell and Powell 2003). Eventually, availability of soft mast should increase again as conditions favor later successional species, some of which produce soft mast (e.g., *Vaccinium* and *Gaylussacia* spp. Johnson and Landers 1978).

Knowing the range of stand ages in which soft mast is most available may be key to maintaining levels of soft mast on forested landscapes for wild animals. Equally important is to know the range of stand ages in which soft mast is least available because one way to optimize soft mast availability across a forested landscape is to minimize the proportion of area in stand ages in which soft mast is lowest.

Several studies evaluated temporal dynamics of soft mast availability in harvested stands, but results were incomplete because either the range of stand ages, in which soft mast was measured, was narrow and/or stands were categorized, *a priori*, into arbitrary age classes. In the Ouachita Mountains of Arkansas and Oklahoma, Perry et al. (1999) assessed availability of soft mast in 1-, 3-, 5- and 70+ year old stands and found soft mast was highest in 5-year old shelterwood cuts and in 5-year old clearcuts and lowest in 70+ year old stands. Because soft mast was not measured in 6-69 year old stands, it is unknown whether a range of stand ages between 6-69 years supported levels of soft mast greater than that in 5-year old stands or lower than that in 70+ year old stands. Costello and Sage (1994) compared availability of soft mast in 1-8, 9-16, 17-24, and 24+ year old stands in New York and found summer fruits were highest in 1-8 and 9-16 year old stands and lowest in 24+ year old stands. All stands > 24 years were combined, which may have masked possible changes in soft mast availability that occurred as stands aged beyond 24 years.

In Minnesota, Noyce and Coy (1990) compared soft mast availability in 0-1, 2-4, 5-8, 9-12, 13-16, 30-59, and 60+ year old stands and found soft mast was highest in 5-8 year old stands and lowest in 0-1 and 2-4 year old stands. Importantly, they also found percent cover of berry plants was higher in 60+ year old stands compared to that in 30-59 year old stands, suggesting intermediate aged stands supported relatively low levels of soft mast. The last finding was detectable only because stands > 30 years old were not grouped, *a priori*, into a single category.

Our first objective was to build upon previous research by evaluating how clear-cutting (i.e., removal of all trees within a stand) in the southern Appalachian Mountains affected soft mast availability through time. Currently, little is known about temporal dynamics of soft mast in the southern Appalachian Mountains. Brody and Stone (1987) hypothesized soft mast availability in clearcuts would be very high when clearcuts were young, but then steadily decline until stands were about 70 years old (Fig. 1). To date, this model has not been tested with empirical data. Mitchell and Powell (2003) showed soft mast in western North Carolina was higher in 0- to 10-year-old clearcuts compared to that in 11+ year old stands, but all stands > 10 years old were combined, making it impossible to discern changes in soft mast availability that may have occurred as stands aged beyond 10 years. We wanted to expand their work by analyzing temporal dynamics of soft mast availability in clearcuts without categorizing stands, *a priori*, into specific age groups. By using continuous data, we hoped to uncover patterns in soft mast availability that might be masked by analysis of categorical data.

Factors other than stand age also influence availability of soft mast in harvested stands. Type of harvest technique was important in Texas (Johnson and Landers 1978), New York (Costello and Sage 1994) and Oklahoma (Perry et al. 1999) whereas forest type was a factor in Minnesota (Noyce and Coy 1990) and Arkansas (Clark et al. 1994).

Topography (e.g., aspect, slope, etc.) and spatial location of a stand on the landscape (e.g., ridge top, ridge side, valley) may also affect the availability of soft mast, yet these influences have not been tested in the southern Appalachian Mountains. Therefore, our second objective was to understand how forest type, topography and spatial location on the landscape affected soft mast availability in the southern Appalachian Mountains. Our third objective was to combine temporal and spatial information to develop models for predicting the spatio-temporal distribution of soft mast on Southern Appalachian landscapes.

Finally, estimates of soft mast availability are influenced by how availability is defined. Some studies estimated availability of soft mast in terms of percent cover of berry plants (Mitchell et al. 2002; Mitchell and Powell 2003), but Perry et al. (1999) showed percent cover was not always a reliable measure of potential soft mast production. In their study, poison ivy (*Toxicodendron radicans*) plants were highly available throughout the study area, but they produced few berries. Alternatively, areas could have high berry production but few berry plants. If so, estimates of only plant cover or only berry production may not provide reliable estimates of soft mast availability. Our fourth objective was to evaluate whether percent cover of berry plants and berry production provided similar estimates of soft mast availability in the southern Appalachian Mountains.

MATERIALS AND METHODS

Study area.—We conducted our study in the Pisgah Bear Sanctuary (PBS) in North Carolina (35° 17' N, 82° 47' W) during summers 2001 and 2002. The PBS (235 km^2) was located within the Pisgah National Forest and managed by the United States

Department of Agriculture Forest Service (USDAFS) which harvested ~1000 stands during 1844-2002. Stand ages within PBS ranged from 0 to 158 years old, but most stands (~80 %) represented secondary growth and were 60+ years old in 2001-2002.

Eighty-eight percent of PBS comprised oak and oak-hickory species, including northern red oak (*Quercus rubrus*), southern red oak (*Q. falcata*), white oak (*Q. alba*), chestnut oak (*Q. prinus*) and hickory (*Carya* spp.). Cove hardwoods (*Liriodendron tulipifera*, *Magnolia* spp., *Betula* spp.) and pine-hemlock (*Pinus rigida, P. strobus, P. virginiana, Tsuga canadensis*) constituted approximately 4.5% and 3% of PBS, respectively. Shrub and sub-canopy species (*Rhododendron* spp., *Kalmia* spp. etc) and a mixture of other species (*Corylus* spp., *Liquidambar styraciflua*, etc) constituted the remaining portions of the PBS (Continuous Inventory Stand Condition database, USDA Forest Service 2001). The topography was mountainous with elevations ranging from 650m to 1800m. The region was considered a temperate rainforest, with annual rainfall approaching 250 cm/yr (Powell et al. 1997).

Within PBS, several types of harvest prescriptions were used during 1844-2002, but most stands were clearcut and allowed to naturally regenerate (~90%). Therefore, we measured availability of soft mast in only areas that had been clearcut. Within PBS, the genera producing the majority of berries during summer months were raspberries and blackberries (*Rubus* spp.), huckleberries (*Gaylussacia* spp), and blueberries (*Vaccinium* spp.; Powell et al., 1997) so we measured availability of only these three genera. *Rubus* spp. are commonly considered early successional (Stransky and Roese 1984), whereas *Gaylussacia* and *Vacinnium* spp. are commonly considered late successional (Johnson and Landers 1978).

Measuring soft mast in clearcuts.—We wanted to understand how soft mast availability changed through time as clearcut stands aged from 0 to 40 years old. Before selecting our sample of stands, we first grouped all stands in PBS that were clearcut < 40 years ago into age classes (i.e., 0-5, 6-10, 11-15, etc.) after which we randomly selected 5-10 stands from each group. We categorized stands to minimize bias due to cluster sampling (Ramsey and Schafer 2002); grouping stands prior to selection was the only way we could ensure that our sample represented the full spectrum of stand ages between 0 and 40 years old. Importantly, stands were grouped by age for selection only. For all analyses, stand age was evaluated as a continuous variable.

Within each 0-40 year old stand, we placed 200-m transects with 3-m radius circular plots placed every 50 meters on each transect. To minimize edge effects, all plots were located > 100 meters from the stand edge and all transects were at least 100 meters apart. We sampled at least 2 transects in each stand.

To understand longer term dynamics, we incorporated data from 41+ year old stands (that were clearcut > 41 years ago) that we collected to answer different research questions (Reynolds and Mitchell, unpublished data). Methods for data collection in 41+ year old stands differed slightly from methods used to collect data in 0-40 year old stands in terms of the way stands were selected and the number and placement of plots. Stands that were 41+ years old were systematically selected (stands at the intersection of odd-numbered x and even-numbered y Universal Transverse Mercator coordinates were sampled) and five 3-m radius circular plots were sampled in each stand; one plot at the center of the intersection and one each 100 meters from the center in each of the four cardinal directions (Powell et al. 1997).

Within each 3-m radius cicular plot, we visually estimated percent plant cover of *Gaylussacia*, *Vaccinium*, and *Rubus* spp. and we indexed berry production according to the following scale: 0 = no fruit, 1 = fruits covering between 0 and 33% of the plants, 2 = fruits covering between 34 and 67% of the plants, and, 3 = fruits covering > 67% of the plants (Noyce and Coy 1990). Values of berry production index were unit-less because we did not measure berry production directly (e.g. kg fruit/m^2). We sampled stands during peak fruiting season, between July and August in 2001 and 2002. Flowers and fruit caps were counted as fruit on plants that hadn't yet fruited or where fruit had obviously been eaten.

Within each plot, we documented topographic position (ridge top, ridge side, valley) slope (flat = 0-10 degree slope, moderate = 11-25 degree slope, or steep = >25 degree slope), and aspect (1-90˚ = NE; 91-180˚ = SE; 181-270˚ = SW; 271-360˚ = NW). We recorded "no aspect" for plots that were flat. Finally, we categorized each clearcut as either hardwood (stands in which ≥ 70 % trees were hardwoods; USDA Forest Service stand codes 50-98; Continuous Inventory Stand Condition, 2001), softwood (stands in which ≥ 70 % trees were softwoods; USDA Forest Service codes 2-7, 21-26, and 31-39), or mixed (stands with a mixture of hardwood and softwood species; USDA Forest Service codes 8-20 and 40-49). To minimize observer bias, only 3 observers collected field data and all observers were extensively trained.

Time.—To understand temporal dynamics of soft mast availability, we conducted 2 sets of analyses. First, we included data from only 0-40 year old stands because our sampling methods for these stands differed slightly from sampling methods for 41+ year old stands. We used results from the first analysis to make inferences about clearcut stands that were 0-40 years old. We then combined data from 0-40 year old stands with data from 41+ year old stands for our second analysis and used these results to make inferences about clearcut stands that were 41+ years old.

To determine the range of stand ages in which soft mast was highest and lowest, we modeled mean percent plant cover (C) as a function of stand age for all genera combined. A curvilinear relationship may exist between C and stand age because percent cover of early successional berry plants should be highest in young stands and decrease as stands age, whereas percent cover of later successional berry plants should be lowest in young stands and increase as stands age. Therefore, a simple linear relationship was unlikely to capture the overall dynamics between C and stand age. We modeled the statistical relationship between C and stand age for early successional berry plants by considering two transformations of stand age (stand age^{-1} and stand age$^{-1/2}$), both of which have a decreasing function. We considered both transformations, even though their functions were similar, because slopes differed between the transformations (stand age^{-1} had a smaller slope) and we did not know, *a priori,* which slope best represented the relationship between C and stand age for early successional berry plants. We modeled temporal dynamics of C and stand age for later successional berry plants by transforming stand age (stand age^{2}; Johnson et al. 2004), which had an increasing function. Therefore, we used 70% of the data to develop a suite of models for C of both early and later successional berry plants using stand age, stand age^{-1}, stand age$^{-1/2}$, and stand age^{2} (Proc Reg: SAS Institute 2000). We considered stand age as an explanatory variable because C for later successional berry plants may have been very low and relatively constant for a long time during the early and mid stages of succession. We considered the null model to be that which included the intercept only. We used Akaike's Information Criterion (AIC; Akaike 1973) with an adjustment for small sample sizes to rank the models in terms of their ability to explain the data. We used the remaining 30% of the data to test the model. We used the same method to model berry production index (*P*).

We used results from the above regression analysis to estimate the range of stand ages in which *C* was high, low, and intermediate. To test if *C* was statistically different among the three ranges of stand ages that were estimated using regression analysis, we categorized data on percent cover into the three age groups and compared mean *C* among the groups (Proc GLM: SAS Institute 2000; alpha = .10). For example, if the regression analysis indicated *C* was highest in 0-10 year old stands, intermediate in 11-69 year old stands and lowest in 70+ year old stands (Brody and Stone 1987; Fig. 1), then we categorized percent cover data into 0-10, 11-69, and 70+ age groups and compared mean *C* among the three groups. We used the same method to test for statistical differences in *P* among stand age groups.

For a separate analysis, we partitioned berry species into successional groups and used logistic regression (Proc LOGISTIC: SAS Institute 2000) to model the relationships between *C* and stand age and between *P* and stand age. We considered *Rubus* spp. to be early successional and *Gaylussacia* spp. and *Vaccinium* spp. to be later successional. We considered the intercept only model to be the null model and we ranked models using AIC_c.

Although data on both percent plant cover and berry production contained zeros, we did not adjust for zero inflation because the goal of this research was to understand how clear-cutting affected the temporal availability of soft mast through time. Zeros were important to retain because we wanted to estimate mean soft mast availability as a function of stand age. Had we first modeled the probability of plant cover of berry plants and then modeled the probability of berry production, our results would have reflected the likelihood of berry production given the presence of berry plants, which was not the purpose of this study.

Topography.—To understand how topography affected soft mast availability, we developed a suite of models for *C* using aspect, slope, and topographic position for all genera combined as predictor variables. We used AIC for model selection. Sample size was based on number of plots because topography and spatial location were heterogeneous within stands. To understand how forest type affected soft mast availability, we compared differences in mean *C* and differences in mean *P* among forest types (Proc GLM: SAS Institute 2000). Because the category forest type was homogeneous within a given stand, sample size was based on number of stands (Hurlbert 1984).

Spatio-temporal models.—We developed statistical models for predicting *C* on the landscape using both temporal and topographic parameters. For each sampled stand, we extracted mean values of slope, elevation and aspect (Beers transformation of aspect; Beers et al. 1966) using a Geographic Information System (GIS) at a 30m resolution. We also extracted mean values for curvature of the land, plane of the curvature, profile of the curvature (DEMAT script for ArcView, Behrens 2000), and distance to water (Mitchell et al. 2002). We did not include soil data because soil type did not differ on over 95% of our plots (Hermann 1996).

We regressed each topographic parameter and its square (e.g., elevation and elevation^2; Johnson et al. 2004) as well as stand age and three transformations of stand age (stand age^2, stand age^{-1}, stand age$^{-1/2}$; Proc Reg; SAS Institute 2000) to develop a global model of *C* using 70% of the data. We generated a suite of nested models from the global model, selected the most parsimonious model using AIC and tested the selected model using the remaining 30% of the data (Proc Reg; SAS Institute 2000). We used the same method to develop and test a model for predicting the spatio-temporal distribution of *P*. Because soft mast availability might be best explained by combining measures of *C* and *P* (Clark et al. 1994), we also developed and tested a model for predicting *C* x *P*.

During model testing, we evaluated model bias. If training data (i.e., data used during model development) are unbiased estimators of the population, the amount of variability explained during model development will be similar to the amount of variability explained during model testing (Neter et al. 1996). For each model of *C*, *P*, and *C* x *P*, we compared values of coefficient of determination (r^2) between training and testing models.

Cover in berry plants versus berry production.—To test if *C* and *P* provided similar estimates of soft mast availability, we evaluated three predictions. First, we evaluated the degree to which stand age and topographic variables each explained *C* and *P*. If *C* and *P* provided similar information about soft mast availability, we predicted the effects of stand age and topography on *C* would be similar to the effects of stand age and topography on *P*. Second, we modeled *C* and *P* using berry genus as the predictor variable and used AIC to compare the ability of this model to explain the data relative to the ability of a null model (i.e. an intercept only model). If *C* and *P* provided similar information, we predicted *C* values for each genus would be similar to *P* values. Third, we used least squares regression (Proc Reg; SAS Institute 2000) to examine the variability in *P* explained by *C*. If *C* and *P* provided similar information, we predicted *C* would explain *P* reasonably well.

RESULTS

We collected data in 57 stands that were 0-38 years (no stands in Pisgah Bear Sanctuary were 39 or 40 years old in 2001 or 2002); within which we sampled 579 plots. Percent plant cover of *Gaylussacia*, *Vacinnium,* or *Rubus*, spp. was > 0 in 205 plots (34%). Of the 205 plots, *Gaylussacia* spp. were found in 43% (n = 88), *Vaccinium* spp. were found in 34% (n = 70), and *Rubus* spp. were found in 23% (n = 47). We collected data in 43 stands that were 41-122 years old, within which we sampled 215 plots. Percent plant cover was > 0 in 93 plots (43 %). Of the 93 plots, *Gaylussacia* spp. were in 29% (n = 27), *Vaccinium* spp. were in 61% (n = 57) and *Rubus* spp. were in 10% (n = 9).

Time.—The top ranked model for *P* when all genera were combined for 0-40 year old stands included stand age, stand age^2, stand age$^{1/2}$, and stand age$^{-1/2}$ (Fig. 2). The top ranked model for *C* when all genera were combined for 0-40 year old stands was the null model (i.e., intercept only model; Fig. 3). Results of model testing showed the temporal model of *P* explained 43% variability in predicted *P*. *P* was highest in ~2-9 year old stands (Fig. 2). Data for *C* did not always correlate with data for *P*. For example, several values of *C* for *Gaylussacia* spp. at stand age 23 were high (Fig. 3), but all values of *P* for *Gaylussacia* spp. at stand age 23 were low or zero (Fig. 2).

The top ranked model for *P* when all genera were combined for 0-122 year old stands included stand age, stand age^2, stand age$^{1/2}$, and stand age$^{-1/2}$ (Fig 4). The top ranked model for *C* when all general were combined for 0-122 year old stands was the null model (Fig. 5). Results of model testing showed the temporal model of *P* predicted 28% variability in predicted *P*, indicating the training data did not bias the model. Based on the regression line, *P* was lowest in ~14-49 year old stands (Fig. 4). Based on data, *P* was lowest in ~ 30-68 year old stands (Fig. 4) and berry plants were notably missing in 34-69 year old stands (Fig. 5). Although we sampled 50 plots in 34-69 year old stands, we found berry plants in only 4% of the plots (n = 2).

Based on the relationship between stand age and *P* predicted by our regression analysis (Figs. 2 and 4), soft mast appeared to be highest in ~2-9 year old stands and lowest in ~10-69 year old stands. *P* appeared to increase as stands aged beyond ~ 70 years. When we categorized plots into 2-9, 10-69, and 70+ age groups to test for statistical differences, we found mean *P* in 2-9 year old stands differed from mean *P* in 10-69 and 70+ year old stands ($F_{2, 748} = 63.17$; $r^2 = 0.14$; $P < 0.0001$), but mean *P* in 10-69 year old stands did not differ from mean *P* in 70+ year old stands. Mean *C*, however, differed among all three stand age groups ($F_{2, 748} = 22.75$; $r^2 = 0.06$; $P < 0.0001$). Mean *C* was highest in 2-9 year old stands (mean percent cover = 16.1; SE = 2.42), lowest in 10-69 year old stands (mean percent cover = 4.2; SE = 0.65), and intermediate in 70+ year old stands (mean percent cover = 7.1; SE = 1.13).

When genera were partitioned into successional groups and analyzed using logistic regression, the model of *C* with stand age ranked higher than the null model, but the amount of information that was explained was minimal. The max r^2 value represents the amount of information explained on a scale between 0 and 1. The amount of information explained by stand age for *C* was 0.005. Similarly, the model of *P* that included stand age ranked higher than the null model, but the amount of information explained was minimal (max $r^2 = 0.05$).

Topography.—The top ranked model for *C* in sampled plots included slope, topographic position, and aspect (Table 1). Percent cover in berry plants was highest on flat slopes, in valleys, and in areas with NW aspects. The top ranked model for *P* included only aspect. Production index was highest on NW aspects (Table 1). Of the 100 stands we sampled, 91 were classified as hardwood, 7 were softwood, and 2 were mixed hardwood and softwood. Forest type affected neither *C* ($F_{2, 99} = 0.25$; $P = 0.86$) nor *P* ($F_{2, 99} = 0.68$; $P = 0.56$).

Spatio-temporal models.—The top ranked model for predicting *C* included temporal and topographic parameters. The model that bestsupported the data on *C* in 0-40 year old stands included stand age^{-1}, stand age$^{-1/2}$, slope, slope^2, and distance to water^2 ($F_{5, 36} = 12.09$; $r^2 = 0.66$; $P < 0.0001$; Table 2) and this model performed well during model testing ($F_{1,} 11 = 24.64$; $r^2 = 0.71$; $P = 0.0006$; Table 4). Similarly, the model that fit best the data on *C* in 0-122 year old stands ($F_{6,64} = 9.03$; $r^2 = 0.48$; $p < 0.0001$; Table 2) performed well during model testing ($F_{1, 28} = 22.64$; $r^2 = 0.46$; $p = 0.0001$; Table 4).

The top ranked model for predicting *P* in 0-40 year old stands also included temporal and topographic variables ($F_{6,36} = 10.89$; $r^2 = 0.69$; $P < 0.0001$; Table 3), but this model performed poorly during model testing ($F_{1,11} = 0.97$; $r^2 = 0.08$; $P = 0.35$; Table

4). The model that best fit the data on *P* in 0-122 year old stands ($F_{5,71} = 8.01$; $r^2 = 0.38$; P = 0.0001; Table 3) performed reasonably well during model testing ($F_{1,21} = 9.86$; $r^2 = 0.33$; P = 0.005; Table 4).

Evaluation of model bias showed both spatio-temporal models of *C* were not biased by the training data, but one model of *P* was biased. The variability in *C* explained by the training data for 0-40 year old stands (66%; Table 4) was similar to the variability in predicted *C* (71%; Table 4). Similar results were found for the model of *C* in 0-122 year old stands and the model of *P* in 0-122 year old stands (Table 4). However, the variability in *P* explained by the training data for 0-40 year old stands (69%; Table 4) was not similar to the variability in predicted *P* (9%; Table 4).

The top ranked model for predicting the spatio-temporal distribution of *C* x *P* in 0-40 year old stands included stand age $^{-1}$, stand age$^{-1/2}$, aspect^2, and distance to water^2 ($F_{4,36} = 7.44$; $r^2 = 0.48$; P = 0.0001), but this model performed poorly during model testing ($F_{1,11} = 0.70$; $r^2 = 0.06$; P = 0.42; Table 4). Similarly, the model that best fit the data on *C* x *P* in 0-122 year old stands ($F_{6,64} = 5.64$; $r^2 = 0.37$; P = 0.0001) performed poorly during model testing (Table 4). Both models were biased by the training data (Table 4).

Cover in berry plants versus berry production.— Stand age and topography affected *C* differently than they affected *P*. In 0-122 year old stands, temporal dynamics explained *P* (Fig. 4) but not *C* (null model ranked highest for *C*; Fig. 5), whereas topographic variables influenced *C* more than they influenced *P* (Table 1). Moreover, the top ranked model for both *C* and *P* included berry genera. Based on 95% confidence intervals, *C* and *P* differed among berry genera (Fig. 6). Mean *P* was highest in *Rubus* spp. whereas mean *C* was highest in *Gaylussacia* spp. Results of least squares regression showed mean *C* predicted mean *P* ($F_{1, 99} = 66.78$; $r^2 = 0.41$; $P < 0.0001$).

DISCUSSION

The relationship between clear-cutting and habitat for wild animals is complex. Distilling this complexity requires understanding how clear-cutting affects the availability of resources that are important to populations of wild animals and also understanding how populations respond, demographically and behaviorally, to changes in resource availability through time. The focus of this paper was to understand how clear-cutting in the Southern Appalachians affected the spatio-temporal availability of soft mast.

We found berry production of *Rubus*, *Gaylussacia*, and *Vaccinium* spp. combined was highest in ~2-9 year old clearcut stands (Fig. 2). It appeared that berry production was lowest in ~ 10-69 year old stands and increased as stands aged beyond ~70 years (Figs. 2 and 4), but we found no statistical difference in mean berry production between 10-69 and 70+ year old stands. Based on analysis of continuous data, we did not find a relationship between stand age and percent cover in berry plants. When data on percent cover were grouped into 2-9, 10-69, and 70+ age classes, however, percent cover differed among all three groups. Percent cover in berry plants was highest in 2-9 year old stands, lowest in 10-69 year old stands, and intermediate in 70+ year old stands.

Presence of berry plants did not guarantee berry production. In 0-40 year old stands, percent cover of *Gaylussacia* spp. plants was approximately equally distributed among stand ages, but berry production was not. Of the 57 plots in which *Gaylussacia* spp. were present in 10-38 year old stands, 70% (n = 40) had zero berry production whereas only 20% of the 25 plots in which *Gaylussacia* spp. were present in 2-9 year old stands had zero berry production. Similarly, *Vaccinium* spp. plants were approximately equally distributed among 2-38 year old clearcuts (Fig. 3), but *Vaccinium* spp. in 2-9 year old stands were 3 times more likely to be productive than *Vaccinium* spp. in 10-38 year old stands (Fig. 2). These results indicate that although *Gaylussacia* and *Vaccinium* spp. were present in 2-38 year old stands, they were highly productive in only ~2-9 year old stands. Both percent plant cover (*C*) and berry production index (*P*) of *Rubus* spp. were highest in 1-8 year old stands (Figs. 2 and 3). Therefore, we feel reasonably confident that soft mast availability was highest in 2-9 year old stands.

Beyond stand age 40, availability of soft mast remained relatively low until, at most, stand age 70 (Figs. 4 and 5). Of the 50 plots we sampled that were located in 34-69 year old stands, we found berry plants in only 2 plots (4%; Fig. 5), suggesting the range of stand ages in which soft mast was lowest was ~10-69 years. Our ability to detect soft mast availability in 34-69 year old stands may have been compromised because our sample size of these stands was relatively small (few stands in our study site during 2001-2002 were 34-69 years old). A conservative estimate of the range of stand ages in which soft mast was lowest is ~10-40 year old stands. Future research should test our results by measuring soft mast in other Southern Appalachian forests that contain a larger sample of 34-69 year old clearcut stands.

Our results did not support Brody and Stone's (1987) hypothesis about the temporal dynamics of soft mast availability in Southern Appalachian clearcuts (Fig. 1). They hypothesized soft mast availability would be highest in young stands, after which it would gradually decline and asymptote when stands reach age ~70. Our data showed berry production peaked in ~2-9 year old stands, but then plummeted and remained very low for 30-60 years (Figs. 2 and 4), after which it appeared to increase. Whereas Brody and Stone (1987) hypothesized soft mast availability would be moderate in intermediate aged stands and lowest in stands 70+ years old, we found percent cover in berry plants in 10-69 year old stands was lower than that in 70+ year old stands.

Our results regarding the high availability of soft mast in young stands generally agreed with findings from previous studies in Minnesota (Noyce and Coy 1990), New York (Costello and Sage 1994), Arkansas (Perry et al. 1999) and North Carolina (Mitchell and Powell 2003). In addition, our results regarding the low availability of soft mast in intermediate-aged stands corroborated findings by Noyce and Coy (1994) who found percent cover in berry plants was higher in 60+ year old stands compared to that in 30-59 year old stands.

The temporal dynamics in soft mast availability we found were probably due to changes in canopy closure. In recently harvested stands, the forest canopy is relatively open providing opportunities for early successional plants, such as *Rubus* spp., to flourish. We also found that *Vaccinium* spp. and *Gaylusacia* spp., which are usually considered later successional species (Johnson and Landers 1978), established and produced berries in young stands (Figs. 2-5), which corroborated previous findings by Foote and Jones (1989). That both *Vaccinium* spp. and *Gaylussacia* spp. established and were productive in both young and older stands helps explain why our logistic models of *C* and *P* did not perform well.

After stands aged beyond ~10 years, the sharp decline in soft mast availability probably occurred because forest canopies began to close, making forest conditions less ideal for early successional species. Canopy closure in intermediate aged stands may have been too high for early successional species and too low for later successional species, which would help explain why soft mast availability was relatively low in intermediate aged stands. Older stands (70+ years old) have relatively closed forest canopies with occasional tree gaps, which may help explain why percent cover in berry plants in 70+ year old stands was higher than that in 10-69 year old stands.

We did not test if canopy closure was the mechanism underlying the temporal trends we documented, but results from a previous study supports predictions from this hypothesis. Although rate of forest succession depends on numerous variables including moisture, temperature, duration of solar radiation, soil fertility, site condition, species availability, and herbivory (Donnegan and Rebertus 1999; Gleeson and Tilman 1990; Pickett and McDonnell 1989), forests in the northeast and far upper midwest should have slower successional rates than forests in the Southern Appalachians, on average, because the growing season is shorter in the former. Therefore, forest canopies in the northeast should close slower after clear-cutting compared to rate of canopy closure in the Southern Appalachians. Hence, the range of stand ages in which soft mast availability peaks should be higher in the northeast compared to that in the Southern Appalachians. Soft mast availability in New York was highest in 1-16 year old stands (Costello and Sage 1994), whereas it was highest in 2-9 year old stands in our study.

Our findings yielded two additional insights regarding soft mast availability at a landscape scale. Although mean *P* was highest for *Rubus* spp. (Fig. 5) and *Vaccinium* spp. were found in the most number of plots (129 plots), *Gaylussacia* spp. probably contributed most to total soft mast availability on the Pisgah Bear Sanctuary landscape. Intuitively, the contribution each genus makes to total soft mast should be a function of the number of plots in which the genus was found, *C*, and *P*. *Gaylussacia* spp. were located in 115 plots, within which mean *C* was 30% and mean *P* was 0.65. Alternatively, *Rubus* spp. were located in 56 plots, mean *C* was 17%, and mean *P* was 1.43. Finally, *Vaccinium* spp. were located in 129 plots, mean *C* was 6.5%, and mean *P* was 0.32. Assuming the contribution each genus makes to total soft mast availability is based on the interaction of all three measures of soft mast, *Gaylussacia* spp. contributed most (115 x 0.30 x 0.65 = 22.42), *Rubus* spp. contributed the second most (56 x 0.17 x 1.43 = 13.61), and *Vaccinium* spp. contributed the least (129 x 0.065 x 0.32 = 2.68).

Surprisingly, *Vaccinium* spp. contributed the least to total availability of soft mast on the landscape, even though it was found in more plots than either *Gaylussacia* spp. or *Rubus* spp. Such counterintuitive results provide insights not only about the ecological system in our study site, but also about research techniques that measure resource availability with only presence/absence data. Clearly, presence/absence data alone may lead to biased inferences.

Estimates of *C* and *P* did not always provide similar information about soft mast availability. Topography influenced *C* more than it influenced *P* (Table 1), whereas the relationship between stand age and *P* (Fig. 4) was stronger than the relationship between stand age and *C* (Fig. 5). Moreover, analysis of only *P* suggested *Rubus* spp. contributed most to total soft mast availability, whereas analysis of only *C* suggested *Gaylussacia* spp. contributed most (Fig. 6). In addition, data for *C* did not always correlate with data for *P*, particularly as stands aged beyond 10 years (Figs. 2 and 3). Therefore, we recommend both *C* and *P* are measured for future studies that evaluate soft mast availability.

We were unable to develop an unbiased model for predicting the spatio-temporal distribution of *C* x *P* on forested landscapes in the Southern Appalachians. Our statistical models of *C* x *P* had fairly high r^2 values during model development, but they performed poorly during model testing (Table 4). Our sample size may have been too small to capture both temporal and spatial variability necessary to model *C* x *P*, given *P* was affected by temporal dynamics whereas *C* was affected by topography and spatial location.

Although we were unable to model *C* x *P*, our results highlight the importance of testing models with independent data. Had we developed our models, but then skipped the testing phase, as many researchers do (Romesburg 1981), our results would have represented hypotheses, not conclusions (Platt, 1964; Murphy and Noon 1991). Management strategies based upon untested hypotheses (i.e., models) are likely to be ineffective at best, deleterious at worst (Mitchell and Powell 2002).

We were able to predict the spatio-temporal distribution of *C*. The model for *C* in 0-40 year old stands explained 71% variability in predicted *C* and the model for *C* in 0-122 year old stands explained 46% variability in predicted *C*. Importantly, both models were unbiased, indicating the inferences about the spatio-temporal distribution of *C* extended beyond our sampled data. Therefore, our models can be used to map the spatio-temporal distribution of *C* on forested landscapes in the southern Appalachian Mountains. In addition, the methods we used to estimate the distribution of *C* may be useful for estimating distributions of other resources.

CONSERVATION IMPLICATIONS

Our results regarding the duration of soft mast availability in stands have conservation implications. Although soft mast availability was highest in young stands (2-9 years old), the duration of availability was short (~7 years). Alternatively, soft mast availability was very low in intermediate-aged stands and remained very low for a long time (~30-60 years). Older stands (~70+ years) supported intermediate levels of soft mast for a relatively long period (50+ years). These results indicate that both young stands (2-9 years old) and older stands (70+ years old) should be maintained to sustain availability of soft mast across forested landscapes in the Southern Appalachians. Simultaneously, area of intermediate aged stands, where soft mast availability is lowest, should be minimized. One way to achieve this goal is to harvest or burn intermediate aged stands. Historically, prescribed burns have not been used as a primary forestry tool in the Southern Appalachians, but the US Forest Service has recently begun using prescribed burns to manage oak regeneration in Pisgah National Forest.

In both our study and the study by Noyce and Coy (1994), availability of soft mast was lowest in intermediate aged stands. If older stands (which support intermediate levels of soft mast) are clearcut for the purpose of increasing soft mast availability, the immediate benefits of increased soft mast over a short duration (i.e. when stands are ~2-9 years old) may or may not outweigh the longer term costs of decreased soft mast over a long duration (when stands are ~10-69 years old). Any conservation plan that uses clearcutting to increase soft mast availability, therefore, must carefully consider the tradeoffs associated with short-term benefits and longer-term costs. This tradeoff is more compelling when other management objectives are also considered. For example, managers in the southern Appalachian Mountains are often tasked to maintain simultaneous availabilities of soft mast and hard mast. While clearcuts affect the availability of soft mast positively, at least for ~ 7 years, clearcuts affect the availability of hard mast negatively for 25-50 years, the time required for regenerating hardwoods to reach reproductive age in the Southern Appalachians (Burns and Honkala 1990). How these tradeoffs are evaluated for any system may differ depending on management goals and the stand age distribution of the managed forest, but our results suggest managers can maximize both soft mast and hard mast by, at least, minimizing the proportion of the landscape that provides neither soft mast nor hard mast (i.e. stand ages 10-25 years old).

We found percent cover of soft mast plants was affected by topographic position, slope, and aspect whereas berry production was influenced by aspect. If a management objective is to increase levels of soft mast on forested landscapes in the Southern Appalachians by using clearcutting, then clearcuts should be placed in flat valleys with NW aspects to maximize the probability that berry plants will establish and be productive.

Table 1. Mean values of percent plant cover (*C)* and berry production index (*P*) of *Vaccinium, Rubus*, and *Gaylussacia* spp. (combined) among different levels of topographic position, aspect, and slope. Data were collected within 741 plots in 0-122 year old clearcuts in Pisgah Bear Sanctuary in North Carolina during 2001 and 2002.

	C	95% LCL	95% UCL	*P*	95% LCL	95% UCL	n
Topographic position							
Ridge Top	6.22	3.02	9.40	0.22	0.10	0.34	102
Ridge Side	5.69	4.20	7.14	0.24	0.18	0.30	512
Valley	11.24	7.30	15.18	0.28	0.16	0.38	127
Aspect							
NE	6.00	3.60	8.40	0.22	0.12	0.32	179
NW	16.24	10.90	21.50	0.36	0.24	0.48	114
SE	4.06	2.57	5.55	0.17	0.09	0.25	212
SW	3.09	1.63	4.54	0.19	0.09	0.29	181
Slope							
Flat	10.44	7.06	13.80	0.18	0.10	0.26	163
Moderate	6.29	4.44	8.13	0.26	0.18	0.34	363
Steep	4.57	2.82	6.31	0.25	0.15	0.35	215

Table 2. Predictor variables with slope estimates (and SE) for the top ranked models for predicting the spatio-temporal distribution of percent plant cover (*C*) of *Vaccinium*, *Rubus*, and *Gaylussacia* spp. (combined). Data for models were collected in 0-40 year old clearcuts (n = 57) and in 0-122 year old clearcuts (n = 100) in Pisgah Bear Sanctuary in North Carolina 2001-2002.

Model		Slope	SE	r^2
<u>*C* in 0-40 year old clearcuts</u>				0.66
	Intercept	60.97205	10.27	
	stand age^{-1}	151.37519	47.42	
	stand age$^{-1/2}$	-143.8855	44.43	
	slope	-7.93037	1.38	
	slope^2	0.21155	0.05	
	distance to water^2	0.00006	0.00	
<u>*C* in 0-122 year old clearcuts</u>				0.48
	Intercept	29.36747	13.96	
	stand age	0.11119	0.06	
	stand age^{-1}	155.29195	46.42	
	stand age$^{-1/2}$	-143.9059	42.09	
	slope	-6.74987	1.17	
	slope^2	0.16894	0.03	
	elevation	0.02818	0.01	

Table 3. Predictor variables with slope estimates (and SE) for top ranked models for predicting the spatio-temporal distribution of berry production index (*P*) of *Vaccinium*, *Rubus*, and *Gaylussacia* spp. (combined). Data for models were collected in 0-40 year old clearcuts (n = 57) and in 0-122 year old clearcuts (n = 100) in Pisgah Bear Sanctuary in North Carolina 2001-2002.

Model	Slope	SE	r^2
P in 0-40 year old clearcuts			0.69
Intercept	-11.15722	5.03	
stand age^2	0.00070	0.00	
stand age^{-1}	13.26422	2.39	
stand age$^{-1/2}$	-12.07464	2.16	
aspect^2	0.15303	0.04	
elevation	0.02221	0.01	
elevation^2	-0.00001	0.00	
P in 0-122 year old clearcuts			0.38
Intercept	-0.03430	0.12	
stand age^{-1}	5.38258	1.07	
stand age$^{-1/2}$	-5.39074	1.05	
aspect	-0.60574	0.24	
aspect^2	0.30992	0.11	
distance water	0.00086	0.00	

Table 4. Results of model testing using training data (70% of data) and testing data (30% of data) for spatio-temporal models of percent cover of berry plants (*C*), spatio-temporal models of berry production index (*P*), and spatio-temporal models of *C* x *P*. Berry plants measured included *Vacinnium*, *Rubus*, and *Gaylussacia* spp. (combined) collected in 0-40 year old clearcuts (n = 57) and in 0-122 year old clearcuts (n = 100) in Pisgah Bear Sanctuary in North Carolina 2001-2002.

Model		F	df	r^2	p-value
C in 0-40 year old clearcuts	training data	12.09	5, 36	0.66	<0.0001
	testing data	24.64	1, 11	0.71	0.0006
C in 0-122 year old clearcuts	training data	9.03	6, 64	0.48	<0.0001
	testing data	22.64	1, 28	0.46	0.0001
P in 0-40 year old clearcuts	training data	10.89	6, 36	0.69	<0.0001
	testing data	0.97	1, 11	0.09	0.35
P in 0-122 year old clearcuts	training data	8.01	5, 71	0.38	<0.0001
	testing data	9.86	1, 21	0.33	0.005
C x *P* in 0-40 year old clearcuts	training data	7.44	4, 36	0.48	<0.0002
	testing data	0.7	1, 11	0.06	0.42
C x *P* in 0-122 year old clearcuts	training data	5.64	6, 64	0.37	<0.0001
	testing data	3.54	1, 28	0.12	0.07

Figure Captions

Figure 1. Model of soft mast availability in Southern Appalachian clearcuts, as they age from 0-120 years, taken from Brody and Stone (1987). The y-axis is an index of habitat capability with respect to soft mast availability.

Figure 2. Berry production index (*P*) of *Vaccinium*, *Rubus*, and *Gaylussacia* spp. combined in 579 plots in 0-40 year old clearcuts in Pisgah Bear Sanctuary, North Carolina 2001. Data for each plot are shown by genus, but the regression line predicts mean *P* of all three genera combined and was based on mean *P* per stand (n = 57).

Figure 3. Percent plant cover (*C*) of *Vaccinium*, *Rubus*, and *Gaylussacia* spp. combined in 579 plots in 0-40 year old clearcuts in Pisgah Bear Sanctuary, North Carolina, 2001. Data for each plot are shown by genus. A regression line is not included because stand age was a poor predictor of mean *C* in 0-40 year old clearcuts.

Figure 4. Berry production index (*P*) for *Vaccinium*, *Rubus*, and *Gaylussacia* spp. combined in 794 plots in 0-122 year old clearcuts in Pisgah Bear Sanctuary, North Carolina, 2001-2002. Data for each plot are shown by genus, but the regression line predicts mean *P* of all three genera combined and was based on mean *P* per stand (n = 100).

Figure Captions (continued)

Figure 5. Percent plant cover (*C*) of *Vaccinium*, *Rubus*, and *Gaylussacia* spp. combined in 794 plots in 0-122 year old clearcuts in Pisgah Bear Sanctuary, North Carolina, 2001-2002. Data for each plot are shown by genus. A regression line is not included because stand age was a poor predictor of mean *C* in 0-122 year old clearcuts.

Figure 6. Percent plant cover, with 95% confidence intervals (A), and berry production index, with 95% confidence intervals (B), for *Vaccinium*, *Rubus*, and *Gaylussacia* spp. in 794 plots in 0-122 year old clearcuts in Pisgah Bear Sanctuary, North Carolina, 2001-2002.

Figure 1.

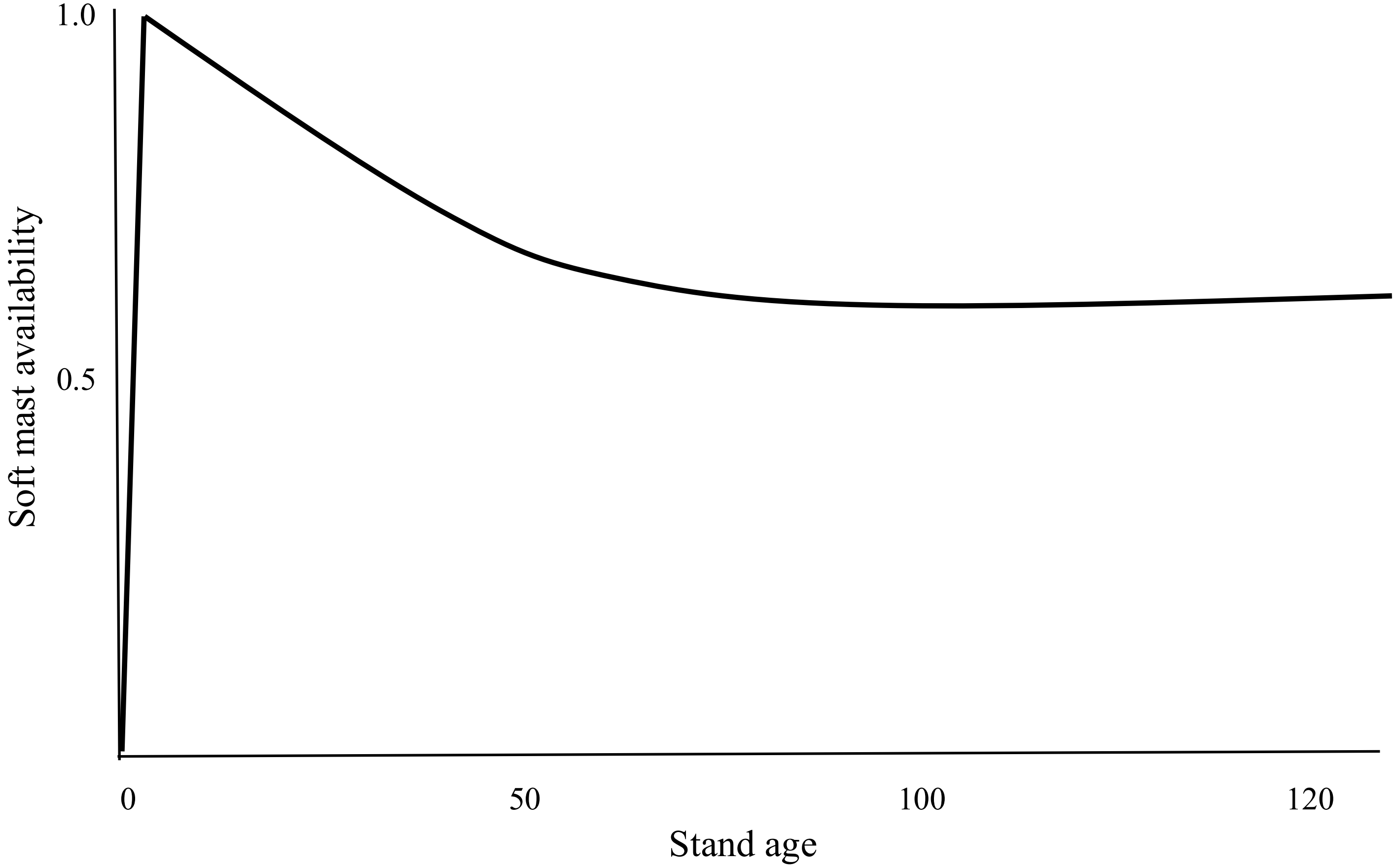
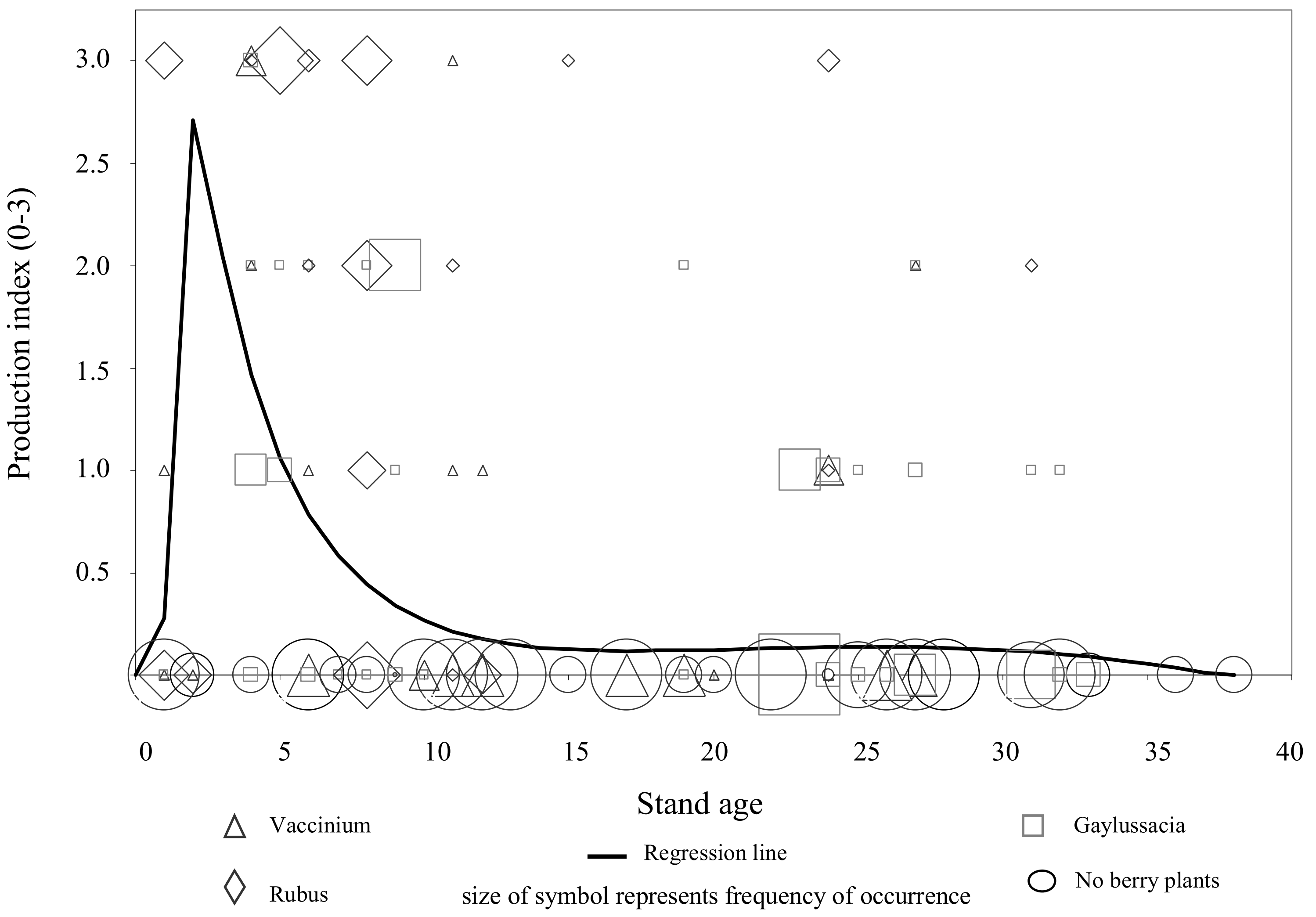
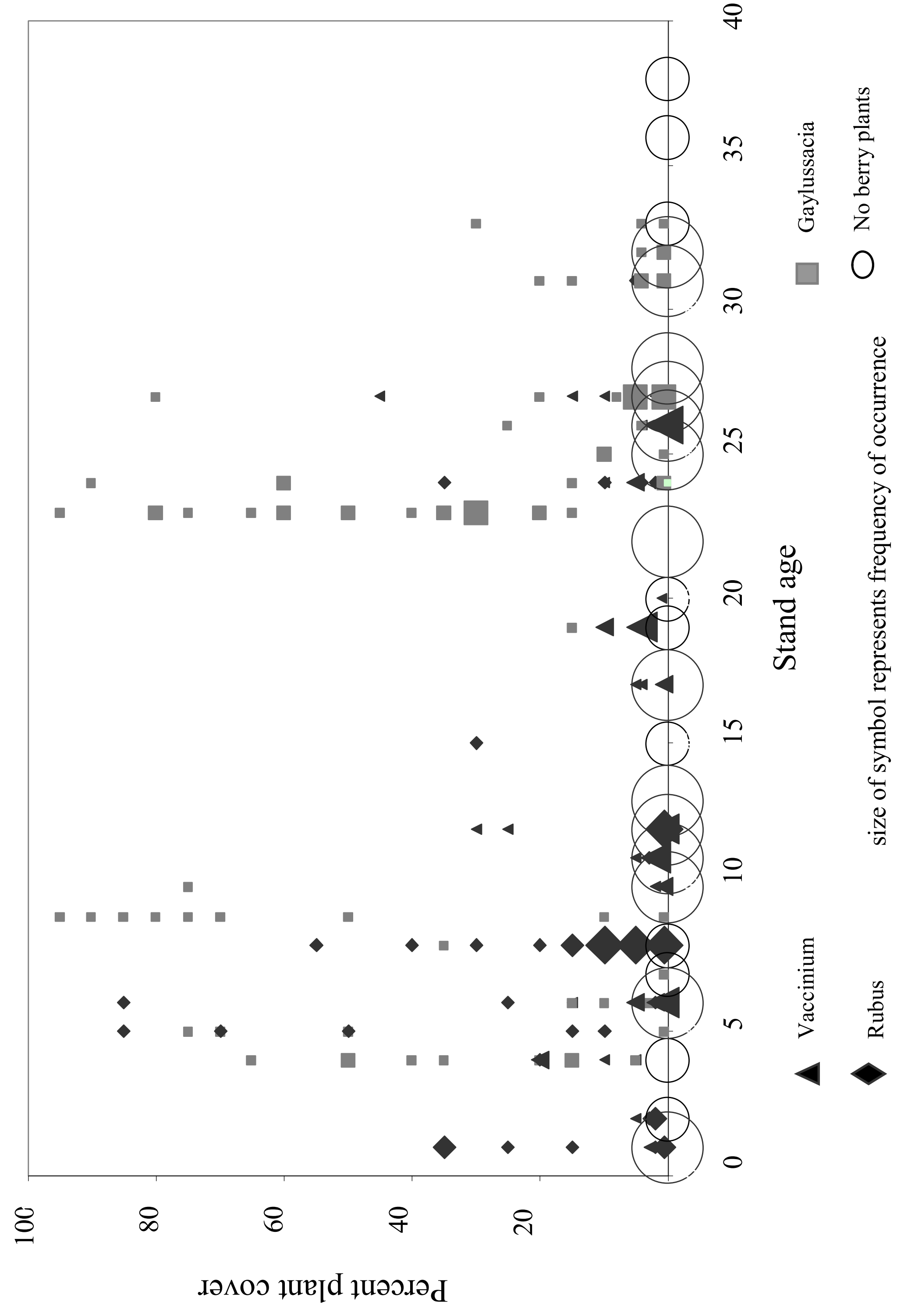


Figure 2.



Production index (0-3)
3.0
2.5
2.0
1.5
1.0
0.5
0
5
10
15
20
25
30
35
40
Stand age
Vaccinium
Rubus
Regression line
size of symbol represents frequency of occurrence
Gaylussacia
No berry plants

Figure 3.



Percent plant cover
100
80
60
40
20
0
5
10
15
20
25
30
35
40
Stand age
Vaccinium
Rubus
Gaylussacia
No berry plants
size of symbol represents frequency of occurrence

Figure 4.

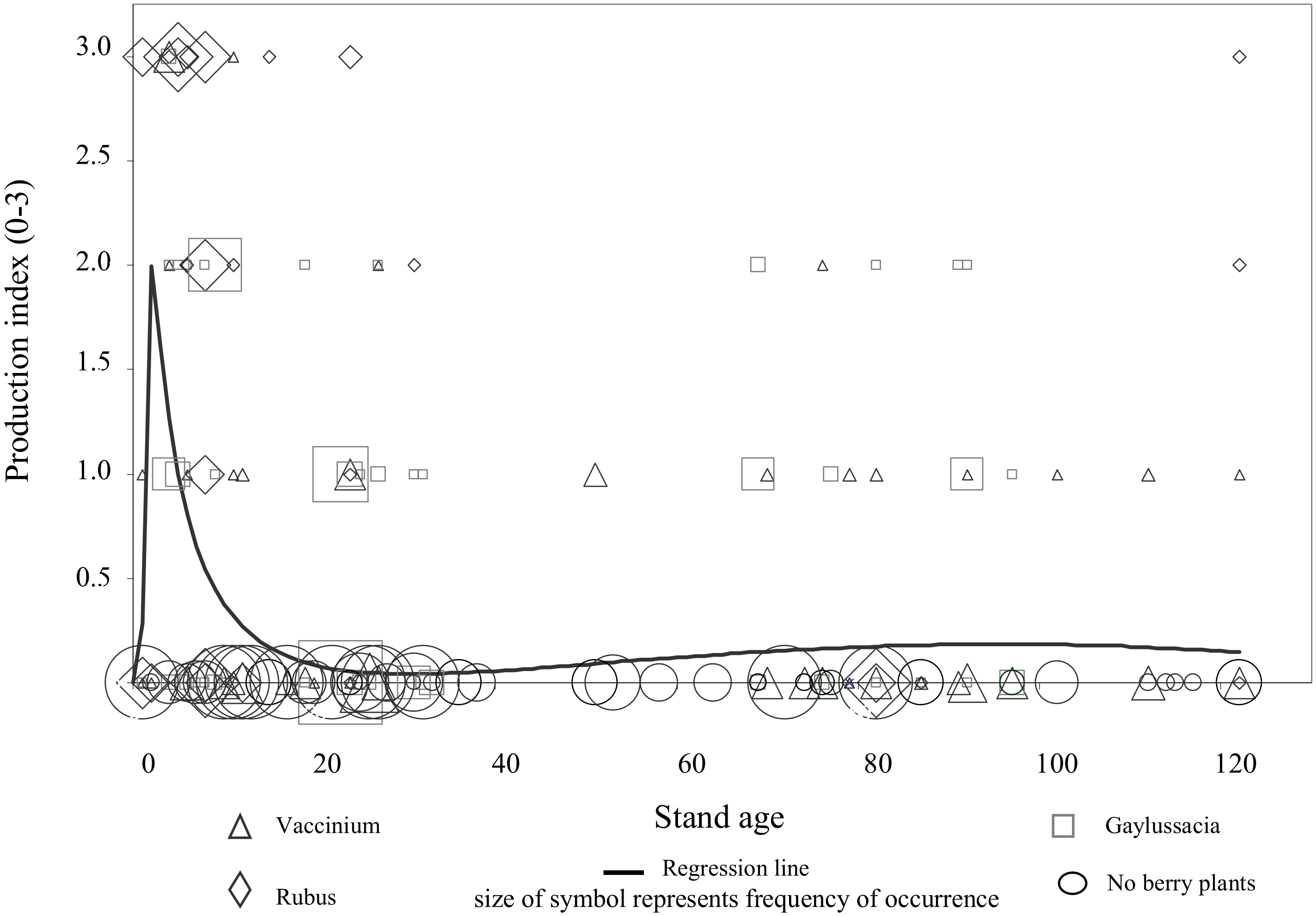

Production index (0-3)
3.0
2.5
2.0
1.5
1.0
0.5
0
20
40
60
80
100
120
Stand age
Vaccinium
Rubus
Regression line
size of symbol represents frequency of occurrence
Gaylussacia
No berry plants

Figure 5.

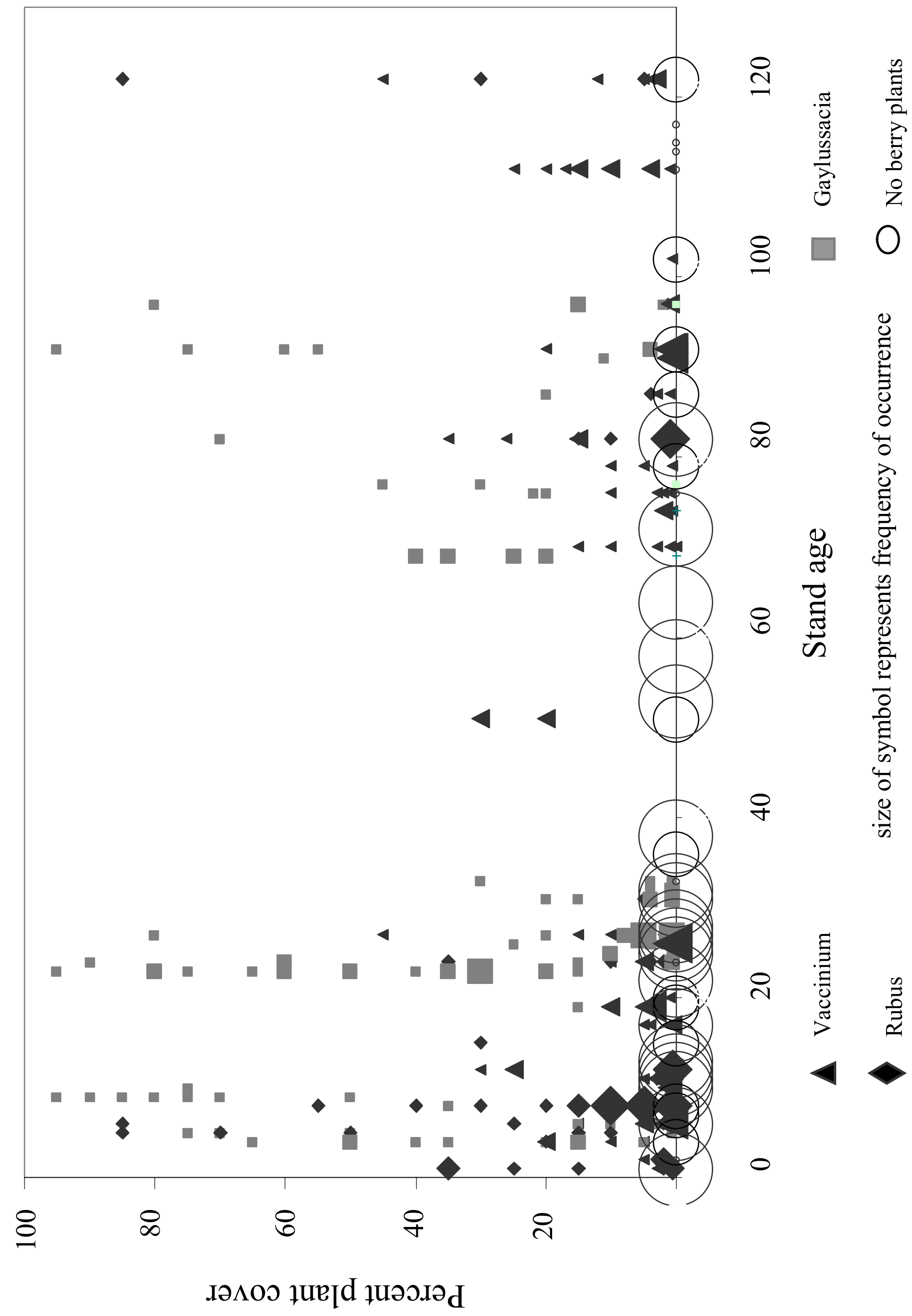
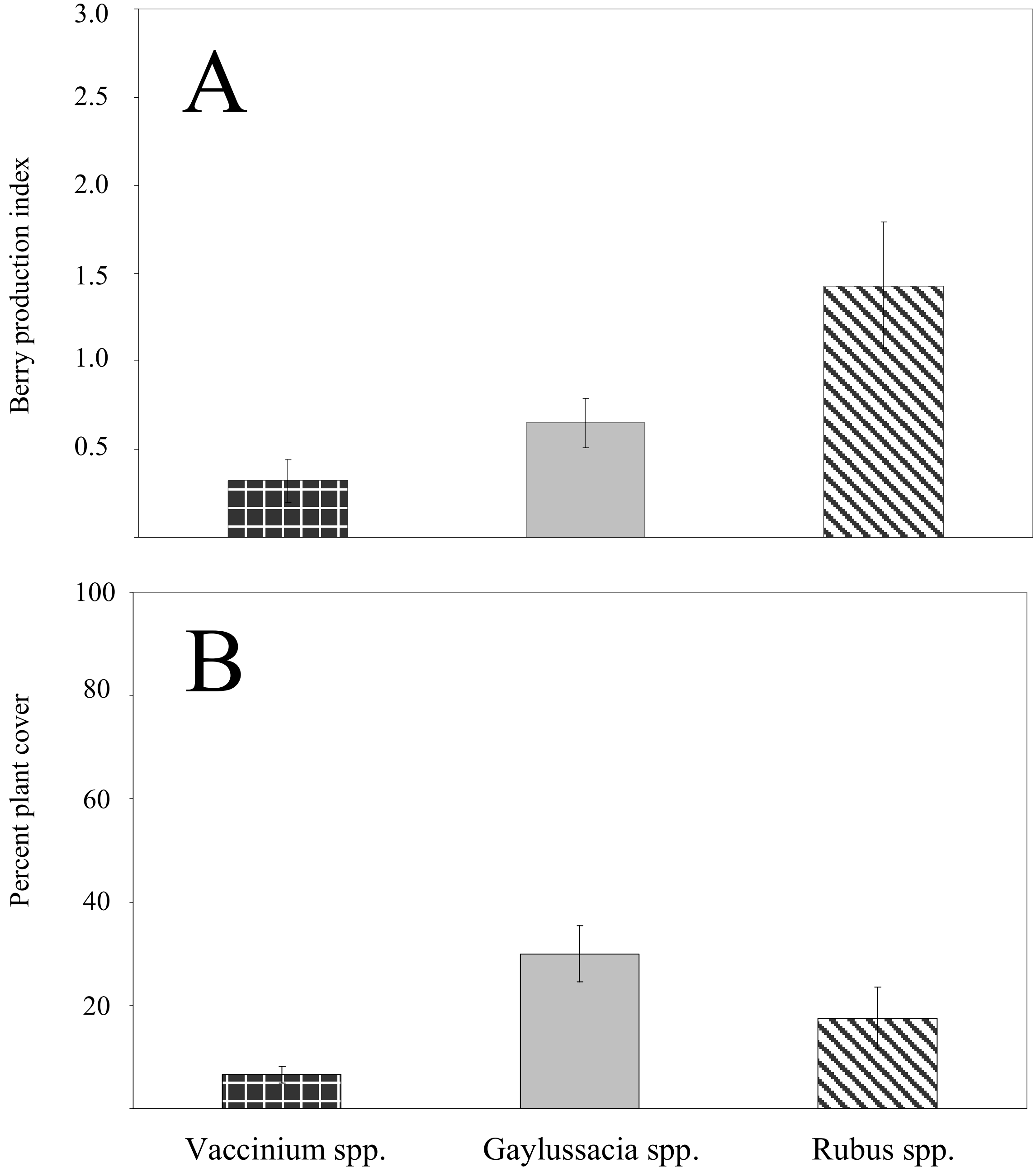

Percent plant cover
100
80
60
40
20
0
20
40
60
80
100
120
Stand age
Vaccinium
Rubus
Gaylussacia
No berry plants
size of symbol represents frequency of occurrence

Figure 6.


A
Berry production index
3.0
2.5
2.0
1.5
1.0
0.5
B
Percent plant cover
100
80
60
40
20
Vaccinium spp.
Gaylussacia spp.
Rubus spp.

CHAPTER 3

LINKING RESOURCES WITH DEMOGRAPHY TO UNDERSTAND RESOURCE LIMITATION FOR BEARS

Abstract: Identifying the resources that limit growth of animal populations is essential for effective wildlife conservation, however resource limitation is difficult to quantify. We linked estimates of resource availability, as they changed due to timber harvesting and succession, with estimates of demography to evaluate competing hypotheses about whether hard mast (acorns and nuts), soft mast (fleshy fruits), or both limited a population of black bears (*Ursus americanus*) in the Pisgah Bear Sanctuary in western North Carolina. Using capture-recapture data from 101 females, we estimated annual survival, recruitment, and population growth rate during 1981-2002. With a GIS, we estimated availabilities of hard mast, soft mast, and young clearcuts (in which soft mast was highly available) and then incorporated estimates of resource availabilities as covariates for each demographic parameter. Using Akaike's Information Criterion for model selection, we found the model with the additive availability of hard mast and soft mast across the landscape predicted recruitment and population growth rate. Availability of hard mast stands was a better predictor of population growth than was hard mast productivity. The null model ranked high for survival, indicating that non-food resources may have affected bear survival. Availability of young clearcuts predicted recruitment, but not population growth. The approach we used has broad application because it provides a way to distinguish among limiting resources, important resources, and resources that are relatively unimportant for populations of wild animals. Such information can be used to help streamline conservation efforts to increase or maintain populations of endangered or game species. Within the framework of adaptive management, linking resources with demography can also be used to evaluate the efficacy of management strategies such as manipulating food resources or implementing artificial nest sites for wild populations.

Key words: clearcuts, habitat quality, lambda, recruitment, resource limitation, survival, *Ursus americanus*

Understanding resource limitation is critical to effective management and conservation of wild populations (Leopold 1933). A resource is limiting if changes in its availability quantifiably affect population growth (Messier 1991). Resource limitation can be examined by augmenting resource availability for an animal population and estimating demographic response (Hart et al. 2006; Hoodless et al. 1999; Hubbs and Boonstra 1997) however, resource augmentation is not always logistically feasible and experimentation has limited spatial and temporal scope (Stephens et al. 2003) An alternative method for examining resource limitation is to link estimates of demographic parameters (e.g., survival, reproduction, population growth etc.) with estimates of resource availability over time (Langvatn et al. 1996; Mduma et al. 1999; Messier 1991; Pennycuick 1969; Skogland 1985;)

Because survival and reproduction may not contribute equally to population growth rate (λ), resource availability should be linked with λ for comprehensive understanding of resource limitation. Adult survival, for example, often contributes most to growth rate for populations of slow or K-selected species, whereas reproduction often contributes most to growth rate for populations of fast or r-selected species (Partridge and Harvey 1988). Theoretically, a resource may not limit a fast species even if the resource is important to survival. Similarly, a resource may not limit a slow species even if the resource is important to reproduction.

Linking estimates of resource availability with individual vital rates (e.g., survival, reproduction, etc.) as well as λ provides a way to help distinguish among limiting resources, important resources, and resources that are relatively unimportant. A limiting resource is one that quantifiably affects λ (Messier 1991). An important resource can be defined as one that affects an individual vital rate but does not affect λ. A resource that is relatively unimportant can be defined as one that has minimal affect on any demographic parameter.

For this research, we linked estimates of resource availability with estimates of survival, reproduction, and λ for a population of black bears in Pisgah Bear Sanctuary (PBS) in western North Carolina, USA during 1981-2002. Previously, Brongo et al. (2005) used capture-recapture data to estimate demography of PBS bears, but they did not examine why vital rates changed through time. Our goal was to expand upon their research by evaluating the effects of resource availability on individual vital rates and on λ.

Black bears require the following resources: foods, den sites, and escape cover. Of these, foods are probably most critical to most bear populations (Powell et al. 1997; Rogers 1987) so we focused on food resources. In the southern Appalachian Mountains, black bears eat herbaceous vegetation, squaw root (*Conopholis americana),* soft mast (fleshy fruit), hard mast (acorns and nuts), insects, and carrion (Beeman and Pelton 1977; Eagle and Pelton 1983). Of these foods, hard mast and soft mast have been shown to affect reproduction or survival of individuals in different bear populations. Hard mast productivity positively correlated with reproduction of individual bears in the southern Appalachian Mountains (Eiler et al. 1989; Pelton 1989) and New Mexico (Costello et al. 2003), whereas berry productivity correlated positively with reproduction of individual bears in Montana (Jonkel and Cowan 1971) and possibly in Arkansas (Clark and Smith 1994). The combined effect of hard mast and soft mast was important to survival and reproduction of individual bears in Minnesota (Rogers 1976, 1987) and Massachusetts (Elowe and Dodge 1989).

No study has linked estimates of hard mast or soft mast productivity with estimates of bear λ. Moreover, all previous studies except Rogers (1987) lasted ≤ 10 years (mean duration = 6 years), which may have been too short to accurately estimate bear demography (Brongo et al. 2005) or the effects of resources on bear demography (Reynolds and Mitchell, in press). Finally, no study has evaluated the relationships between bear demography and availability of hard mast and soft mast as each resource changed through time due to disturbance and succession. The goal of our research was to use long-term data (22 years) to link estimates of hard mast and soft mast with estimates of survival, reproduction, and λ of bears in PBS to evaluate the following hypotheses:

H_1 : Only hard mast limited PBS bears

H_2 : Only soft mast limited PBS bears

H_3 : Both hard mast and soft mast limited PBS bears

H_4 : Neither hard mast nor soft mast limited PBS bears

Information about resource limitation for black bears may be key to effective conservation and management, a common goal of which is to manage population growth by manipulating habitat. For example, timber harvesting is often considered a management tool for maintaining bear habitat in the southern Appalachian Mountains because availability of soft mast can be relatively high in recently harvested stands (Noyce and Coy 1990; Perry et al. 1999; Reynolds et al., submitted$_1$). Harvesting trees by clearcutting (i.e., removal of all trees within a stand), however, eliminates production of hard mast for 25-50 years, the time required for regenerating hardwoods to reach reproductive age in the Southern Appalachians (Burns and Honkala 1990). Because clearcutting affects availability of soft mast and hard mast differently, the overall effect of clearcutting on habitat quality for a bear population will depend, in part, on whether hard mast, soft mast, or both limit the population.

The second goal of this paper was to evaluate the effect of clearcutting on habitat quality for black bears. 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). If clearcutting had a positive effect on habitat quality because it provided increased soft mast, we predicted that both availability of soft mast and availability of young clearcuts would help explain bear reproduction, survival, or population growth and the relationships would be positive. If clearcutting did not have a positive effect on habitat quality because hard mast was removed, we predicted that availability of hard mast would help explain bear reproduction, survival, or population growth but availability of young clearcuts would not.

MATERIALS AND METHODS

Study area.—We conducted our study in the Pisgah Bear Sanctuary (PBS) in North Carolina (35° 17' N, 82° 47' W) during 1981-2002. The PBS encompasses 235 km^2 and is nested within the Pisgah National Forest. From 1960-2002, 184 older stands (50+ years) were harvested, most (77%) were clearcut. Mean proportion of PBS in 50+ year old stands ranged between 77-85% during 1981-2002. Eighty-eight percent of PBS was comprised of oak (*Quercus* spp.) and oak-hickory (*Q*. spp. *Carya* spp.). Cove hardwoods (*Liriodendron tulipifera*, *Magnolia* spp., *Betula* spp.) and pine-hemlock (*Pinus rigida*, *P. strobus, P. virginiana, Tsuga canadensis*) constituted approximately 4.5% and 3.0% of PBS, respectively (Continuous Inventory Stand Condition, USDA Forest Service 2001). The topography is mountainous with elevations ranging from 650m to 1800m. The region is considered a temperate rainforest, with annual rainfall approaching 250 cm/yr (Powell *et al.* 1997).

Trapping bears.—We captured bears in PBS from May through mid-August during 1981-2002 (except 1991 and 1992) using Aldrich foot snares, modified for safety (Johnson and Pelton 1980) or barrel traps. We immobilized captured bears using a combination of approximately 200 mg Ketamine hydrochloride + 100 mg Xylazine hydrochloride/90kg of body mass (Cook 1984) or Telazol administered with a blow dart or jab stick. Immobilized bears were sexed, weighed, measured, tattooed and had two ear tags attached. All procedures complied with requirements of the Institutional Animal Care and Use Committees for Auburn University (IACUC # 0208-R-2410) and North Carolina State University (IACUC # 96-011).

Modeling demographic parameters.—We created encounter histories for each female bear captured during 1981-2002. We used the Pradel model (Pradel 1996) model in Program MARK (White and Burnham 1999) to estimate apparent survival (the probability that the animal is alive and remains on the study area and hence is available for recapture; ϕ) and recapture probability (p). Apparent survival does not account for immigration or emigration, but female black bears rarely disperse (Elowe and Dodge 1989; Powell et al. 1997), so we assumed our study population was closed.

Using methods described by Franklin et al. (2000), and the logit link in Program MARK, we incorporated estimates of annual availability of hard mast and soft mast as covariates to survival. We also included a null model (no covariates) as a base for comparison among the covariate models. We standardized all covariates so effects among covariates would be relative. Values of all covariates were normally distributed so values were standardized to retain normality by subtracting the mean and dividing by the standard deviation.

We added each covariate separately to a base model that held survival constant over all years while allowing recapture probability to vary over all years (Cooch and White 2002). The base model for survival $\{\phi.\ p_t\}$ served as the null model because it included no effects of resource covariates.

We used Akaike's Information Criterion, with an adjustment for small sample bias (AIC_c; Akaike 1973; Anderson et al. 1994), to rank the models in terms of their ability to explain the data. We considered models with ΔAIC_c value < 2.0 to have substantial support (Burnham and Anderson 2002). We evaluated Akaike weights for each model and we evaluated slope estimates for model variables. Model weights provide strength of evidence for model selection, whereas slope estimates reveal whether a relationship between a model variable and the demographic estimate is positive or negative. We used a bootstrap approach to evaluate goodness of fit.

We used annual rates of recruitment (proportion of females added to the breeding population over a specified period of time; f) and realized population growth (λ) that were estimated for PBS bears during years 1981-2002 by Brongo et al. (2005). Because recruitment rate and λ are not bounded between 0 and 1, we did not use the logit link to evaluate the effects of resources on recruitment rate and λ. We developed a suite of models for predicting the log linear relationship between λ and resource covariates (Proc Reg: SAS Institution Inc.), we considered the intercept-only model to be the null model, and then we ranked models using AIC_c. We used a similar method to develop and rank a suite of models for recruitment rate except we modeled the linear relationship between recruitment rate and resource covariates. Because emigration and immigration were so low, recruitment rate represented primarily the number of female cubs per female added to the population that survived to be old enough for capture.

Covariates: annual availability of hard mast and soft mast.—We estimated annual variability in hard mast production using an index estimated annually by the North Carolina Wildlife Resources Commission (NCWRC) for the Pisgah National Forest. NCWRC measured mast production of red oak, white oak, hickory, and beech trees and calculated an index of production for each year (except years 1981, 1982) for each species and for all species combined (Warburton 1995). We used the annual index for all species combined (Fig. 1A).

Most previous studies that evaluated the effect of hard mast on reproduction or survival of individual bears did so by considering only annual variability in hard mast production (Costello et al. 2003; Eiler et al. 1989; Elowe and Dodge 1989; Pelton 1989; Rogers 1976, 1987), but availability of hard mast should also be a function of availability of stands that produce hard mast. We used the following criteria to model the distribution of stands most likely to produce hard mast in PBS: 1) stands had to have at least 70% hardwoods in which hard mast species were dominant (USDA Forest Service stand codes: 51-57, 59, and 60; Continuous Inventory Stand Condition database (CISC), USDA Forest Service, 2001), and, 2) stands had to be between 50-100 years old because most oak and hickory species, which comprised approximately 85% of PBS, are maximally productive in the Southern Appalachians when they are between 50-100 years old (Burns and Honkala 1990). We used a Geographic Information System (GIS; ArcView3.2 and Spatial Analyst 2.0) and the CISC database to calculate the area (hectares) of these stands in PBS for each year 1981-2001 (Fig. 1B). Owing to constraints of the CISC database, we did not map availability of hickory stands separately from availability of different oak stands (e.g., northern red oak, southern red oak, etc.). If bears prefer one mast species over the others, then our estimates of hard mast availability may not reflect what is both available to and preferred by bears.

Hard mast availability should be a function of both hard mast production and availability of stands that produce hard mast. Therefore, we also considered the interaction between hard mast production and availability of hard mast stands as a covariate to each demographic parameter.

We estimated annual availability of berry plants across the PBS landscape, as it changed due to clearcuts and succession, based on field data collected in PBS. Within PBS, several types of harvest prescriptions were used during 1844-2002, but most stands were clearcut (~90%, CISC data base). Therefore, we estimated the temporal availability of soft mast in only clearcuts. The genera producing the majority of berries during summer months in PBS were raspberries and blackberries (*Rubus* spp.), huckleberries (*Gaylussacia* spp), and blueberries (*Vaccinium* spp.; Powell et al. 1997), which were important foods for black bears in the Southern Appalachians (Beeman and Pelton 1977; Eagle and Pelton 1983), so we estimated availability of these genera. We estimated percent plant cover of *Gaylussacia*, *Vaccinium*, and *Rubus* spp. plants in 100 randomly selected stands (0-122 years old). We extracted information on mean slope, elevation, aspect (Beers transformation of aspect; Beers et al. 1966), curvature of the land, plane of the curvature, profile of the curvature (DEMAT script, Behrens 2000), and distance to water for each sampled stand. We modeled percent plant cover of berry species as a function of topographic variables and stand age. Soil type was not considered a predictor variable because it did not differ on over 95% of our plots (Hermann 1996). Seventy percent of the data were randomly selected and used to develop a global model for cover in berry plants (Proc Reg; SAS Institute 2000). We generated a suite of nested models from the global model, selected the best approximating model ($F_{6, 64} = 9.03$; $r^2 = 0.48$; $p <$

0.0001) using AIC_c, and tested the selected model using the remaining 30% of the data ($F_{1,28} = 13.55$; $r^2 = 0.46$; $p < 0.0001$; Reynolds et al., submitted_1). We used the selected model, as well as a GIS, to map the distribution of berry plants in PBS, at a 30-meter resolution, for each year 1981-2001. We estimated annual availability of berry plants in PBS as the sum of berry plant cover within all 30-meter cells. Although values were unit-less, they were useful for comparing availability of berry plants across years (Fig. 1B).

We did not estimate berry production because sufficient data to estimate berry production were lacking for most years 1981-2001. We collected field data on berry production in PBS (Powell et al. 1997), but only for 12 of the 21 years of our study. Based on analysis of the 12 year data set, berry production did not differ statistically among years ($P > 0.65$; Reynolds, unpublished data).

To evaluate the effect of clearcutting on habitat quality, we estimated the distribution of clearcuts most likely to produce soft mast because the change in availability of these stands could have affected survival, recruitment, or λ if soft mast limited Pisgah bears. Based on field data collected on *Gaylussacia*, *Vaccinium*, and *Rubus* spp. within 100 randomly selected clearcuts (ages 0-122 years old) in PBS, both cover in berry plants and berry production were highest in 2-9 year-old clearcuts (Reynolds et al., submitted_1). We used a GIS and the CISC database to calculate the area (hetacres) of 2-9 year-old clearcuts for each year 1981-2001 (Fig. 1C).

If both hard mast and soft mast limited Pisgah bears, their additive or interactive effects may have been important to demography. Therefore, we included the additive and interactive effects between availability of hard mast stands and availability of berry plants as covariates. We also evaluated the additive and interactive effects between availability of hard mast stands and availability of young clearcuts. The interactive effects of hard mast production and soft mast production were not evaluated because sufficient data on berry production were lacking.

RESULTS

Survival.—During 1981-2002, we captured 101 tagged females 194 times. Three models of survival had ΔAIC_c values < 2.0 (Table 1). The top ranked model incorporated availability of berry plants as a covariate. The second ranked model included the additive availability of hard mast stands and availability of berry plants across the landscape. The third ranked model was the null model. As strength of evidence for model selection, the AIC_c weight for the top model was 0.36 and that for the null model was 0.19, indicating the top model was only 1.9 times more likely to be selected over the null, which was not sufficient to differentiate among models (Burnham and Anderson 2002). The slope estimate for the top ranked model was significant (i.e., zero was not in the 95% confidence interval; Table 4). Only the berry component of the second ranked model was significant. We used 500 simulations to test goodness of fit. The estimate of c-hat was 1.3, which when adjusted did not change the rankings of the models.

Recruitment.—Two models of recruitment had ΔAIC_c value < 2.0. The top ranked model incorporated availability of soft mast in clearcuts (Table 2). The second ranked model included the additive availability of hard mast stands and berry plants across the landscape. The null model ranked low and had low model weight. Slope estimates for all components of the top two models were positive (Table 4). As strength of evidence for model selection, the AIC_c weight for the top model was 0.49, indicating it was 2.7 times more likely to be selected over the second ranked model and 24 times more likely to be selected over the null model (AIC_c weight = 0.02). All models with only hard mast covariates ranked relatively low and had low AIC_c weights.

Population growth rate.—Three models of λ had ΔAIC_c value < 2.0 (Table 3). The top ranked model incorporated the additive availability of hard mast stands and availability of berry plants across the landscape, the second ranked model included availability of berry plants across the landscape, and the third ranked model included the interaction between availability of hard mast stands and availability of berry plants across the landscape. As strength of evidence for model selection, the top model (AIC_c weight = 0.41) was 1.32 times more likely to be selected than the second ranked model and 20 times more likely to be selected over the null model. Slope estimates for all components of the top two models were positive and significant (Table 5). The interaction term in the third ranked model was not significant (Table 5). Though we report effect sizes in terms of slope estimates, sufficient causation cannot be established from our study because we did not use controls nor did we replicate our study.

DISCUSSION

Our data supported the hypothesis that both hard mast and soft mast limited Pisgah bears during 1981-2002. The model with the additive availability of hard mast stands and berry plants across the landscape ranked highest for λ. Moreover, this was the only model to rank high for all three demographic parameters. Slope estimates for this model were positive and significant for both λ and recruitment.

That the additive availability of hard mast and soft mast ranked highest for λ indicates that conservation efforts to maintain or increase λ for bears in the Southern

Appalachians should focus on maintaining availability of both hard mast and soft mast. This objective may be achieved by increasing or maintaining acreage of oak stands >50 years old, which can support high levels of hard mast (Burns and Honkala 1990) and intermediate levels of soft mast (Reynolds et al., submitted$_1$).

Other studies that linked food availability with demography of mammals also found variability in foods predicted vital rates, especially at high population densities. Grass production predicted wildebeest survival and reproduction (Mduma et al. 1999), lichen cover predicted reindeer survival and reproduction (Skogland 1985), and climate (a surrogate for food availability) predicted red deer reproduction (Langvatn et al. 1996). We could not determine whether food effects on bear demography were most pronounced when population densities were high because we were unable to accurately estimate population density. Future research should focus on testing whether bears demonstrate density dependence.

Because the top ranked model of λ included the availability of both hard mast and soft mast across the landscape, it was not surprising that the availability of 2-9 year old clearcuts did not predict λ. Although young clearcuts can support relatively high availability of soft mast (Noyce and Coy 1990; Perry et al. 1999; Reynolds et al., submitted$_1$), they provide no hard mast. Interestingly, the additive availability of young clearcuts and hard mast stands across the landscape also did not predict λ, indicating availability of soft mast across the landscape was more important than was the availability of soft mast in only young clearcuts. Our results, based on analysis of resource effects on λ, indicate that the availability of young clearcuts affected habitat quality positively in terms of its contribution to overall availability of soft mast across the landscape, but the availability of young clearcuts alone had little effect on habitat quality.

We could not compare our results regarding the effect of young clearcuts on habitat quality for bears with findings from similar studies because no other study has used measures of survival, recruitment, or λ. All previous studies examined habitat selection to infer the effects of clearcuts on habitat quality for bears. Results have been conflicting: bears have been shown to both select (Costello and Sage 1994; Jonkel and Cowan 1971; Samson and Hout 1998) and avoid (Clark et al. 1994; Mitchell and Powell 2003; Unsworth et al. 1989) young clearcuts. Because habitat use may not be a reliable indicator of habitat quality (Morrison 2001; Van Horne 1983), future studies evaluating the effects of disturbances on bear habitat should use direct measures of fitness. Studies that use habitat use instead should address explicitly the assumed linkage between habitat selection and fitness before inferring effects of habitat change.

Although availability of 2-9 year old clearcuts did not predict λ, it did help explain recruitment. This result is plausible considering female bears must acquire sufficient stores of energy, prior to denning, to successfully reproduce. In addition, females use stores of protein for lactation while they are denned (Tinker et al. 1998). Young clearcuts in PBS can support high levels of *Rubus* spp. (Reynolds et al., submitted$_1$), which provide both energy and protein (Landers et al. 1979). Moreover, young clearcuts may also support other bear foods we didn't measure, such as green briar (*Smilax* spp.) and insects, both of which contain relatively high levels of protein (Landers et al. 1979). Hence, females could acquire some energy and protein stores necessary for successful reproduction by using resources found within 2-9 year-old clearcuts.

Biological thresholds may have existed in PBS that we were unable to detect, which could influence the way 2-9 year-old clearcuts affected habitat quality for bears. During 1981-2001, the proportion of PBS that comprised 2-9 year-old clearcuts was small (mean = 2% SD = 0.05%). If 2-9 year-old clearcuts are more available (e.g., 25% of the landscape), their effect on bear recruitment may be negative.

That availability of 2-9 year old clearcuts predicted recruitment but not λ demonstrates the difference between an important resource and a limiting one. Just because a resource contributes to an individual vital rate does not necessarily mean it limits a population. These results highlight the importance of linking resources with not only individual vital rates, but also λ.

We found models with only hard mast covariates ranked low for recruitment. Our results corroborated findings by Clark and Smith (1994) and Kasbohm et al. (1996), but conflicted with results of Eiler et al. (1989), Costello et al. (2003) and Pelton (1989). Most previous studies (Clark and Smith 1994; Eiler et al. 1989; Kasbohm et al. 1996; Pelton 1989) did not examine the effect of hard mast on bear reproduction relative to the effect of hard mast + soft mast. Had they considered the multiple hypotheses that we evaluated, they may have found that the combined availability of hard mast and soft mast was a better predictor of reproduction compared to the availability of hard mast alone.

Hard mast production did not predict λ or recruitment, which may have occurred if complete crop failures were uncommon in PBS. Beck (1977) and Beck and Olson (1968) examined acorn productivity in the southern Appalachian Mountains from 1962-1973 and found production of white oaks peaked about every four years while production of red oaks peaked about every five years. Hence, complete crop failures were unlikely during their study because large crops of acorns from white oaks compensated for small crops from red oaks and vice versa. If processes occurring during 1981-2002 were similar to those that occurred during 1962-1973, complete crop failures were unlikely.

That availability of hard mast stands predicted λ and recruitment (when combined with availability of soft mast), yet hard mast productivity did not, highlights the importance of estimating resource availability in terms of not only production but also availability across landscapes. Had we estimated only hard mast production, as many researchers do, we would have failed to detect an effect of hard mast on bear λ and recruitment. Importantly, we used availability of hard mast stands to represent hard mast, but other bear resources (e.g., den sites, escape cover, etc.) also may have been available in hard mast stands. The positive relationship that we found between availability of hard mast stands and bear demography, therefore, could indicate the importance of hard mast stands beyond their capacity to provide bear foods.

Unlike results for λ and recruitment, results for survival indicated that the null model had substantial support, suggesting survival may not have varied much during 1981-2002. Alternatively, this result could indicate that variables other than the foods that we considered may have affected survival. Hunting, poaching, and vehicle collision are primary mortality agents for black bears in the southern Appalachian Mountains (Brody and Pelton 1989; Pelton 1986) so these effects on survival may have been greater than those of the foods we considered. Results like those we found for survival, where the null model ranked high, can be key to effective conservation. Knowing where *not* to invest conservation efforts may be just as important as knowing where *to* invest conservation efforts.

Our results provided interesting insights into resource limitation. For a resource to limit λ, positive changes in its availability must affect λ positively (Messier 1991), which typically happens only when a resource is in relatively short supply (Ricklefs 1993). If supply of resource *i* is greater than demand for resource *i*, changes in its availability are unlikely to affect λ. Because changes in availability of hard mast stands and berry plants predicted λ and their slopes were positive, their availabilities in PBS from 1981-2001 were probably in short supply for bears. Alternatively, changes in availability of 2-9 year-old clearcuts did not predict λ, so this resource was probably not in short supply. From 1981-2001, the proportion of PBS that comprised 2-9 year-old clearcuts was small (mean = 2% SD = 0.05%) compared to the proportion of PBS that comprised stands most likely to produce hard mast (mean = 82% SD = 2%). Yet, 2-9 year-old clearcuts were probably not in short supply whereas hard mast stands probably were. Such counterintuitive results not only provide insights about resource limitation of PBS bears, but also demonstrate the folly of assuming a resource that occurs in relatively small amounts is necessarily limiting.

We did not include estimates of annual berry productivity, which may have affected our ability to fit models that included estimates of soft mast. Although berry production in PBS did not differ statistically among the 12 years for which we had berry production data (Reynolds, unpublished data), biological differences in annual berry productivity may have existed that we were unable to detect. If so, and if annual variability in berry production influenced bear demography, then our results regarding the predictability of soft mast were biased low.

CONCLUSION

Linking estimates of resource availability with estimates of animal survival, reproduction, and λ can provide insights into resource limitation for wild animals, including information useful for distinguishing among limiting resources, important resources, and resources that are relatively unimportant. Such information can help streamline conservation efforts to increase endangered populations or maintain game populations.

Although researchers are increasingly using GIS to evaluate habitat use by animals (Gibson et al. 2003; Johnson et al. 2004; Wheatley et al. 2005), habitat use may not have demographic consequences for animal populations (Gill et al. 2001; Sutherland 1998). We used a GIS to estimate temporal and spatial elements of resource availability and then linked estimates of resource availability with estimates of demography. This approach can be folded into existing state and federal programs that monitor wildlife populations and habitat availability. Within the framework of adaptive management, linking resources with demography can be used to evaluate the efficacy of management strategies such as manipulating food resources or implementing artificial nest sites for wild populations.

Conservation is most effective when it is informed by sound science. The approach we used provides a relatively rigorous method for understanding which factors predict animal demography. We evaluated multiple competing hypotheses (Chamberlain 1897), which should provide strong inference (Platt 1964). Our estimates of demographic parameters were informed by recapture probabilities, which can substantially increase precision of parameter estimates (Cooch and White 2002). We used an information theoretic approach (e.g., AIC) to evaluate competing *a priori* hypotheses, including the hypothesis of no effect. For example, we evaluated the effects of foods on bear survival, relative to a null model, and found that non-food resources probably affected bear survival more than did food resources. If the management goal in PBS is to increase bear survival, therefore, our results indicate that managers should focus on examining how non-food resources affect bear survival rather than focusing on increasing bear foods.

For comprehensive understanding, the approach we used should be coupled with information on how individual vital rates contribute to λ. For bears in our study, Brongo (2004) found that adult survival was the vital rate with the greatest potential to contribute to future changes in λ. If the management goal in PBS is to increase λ of bears, Brongo's results indicate that managers should increase bear survival. Strategies to increase bear survival will be more effective when managers know which factors influence vital rates and which factors do not.

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Table 1. Ranking of models of apparent survival, each with different covariates of hard mast and soft mast, for the female population of black bears in Pisgah Bear Sanctuary, North Carolina, during 1981-2002.

Model	ΔAICc	AICc Weight	Model Likelihood	Number parameters
Berry plants	0.00	0.36	1.00	45
Hard mast stands + Berry plants	1.32	0.19	0.52	46
Null	1.34	0.19	0.51	44
Hard mast stands	2.32	0.11	0.31	45
Availability of young clearcuts	3.24	0.07	0.20	45
Hard mast stands*Berry plants	4.22	0.04	0.12	46
Hard mast production	4.77	0.03	0.09	45
Availability of young clearcuts + Hard mast stands	5.99	0.02	0.05	46
Availability of young clearcuts* Hard mast stands	9.21	0.00	0.01	47
Hard mast stands* Hard mast production	9.75	0.00	0.01	47

Table 2. Ranking of models of recruitment, each with different covariates of hard mast and soft mast, for the female population of black bears in Pisgah Bear Sanctuary, North Carolina, during 1981-2002.

Model	ΔAICc	AICc Weight	Model Likelihood	Number parameters
Availability of young clearcuts	0.00	0.49	1.00	45
Hard mast stands + Berry plants	2.00	0.18	0.37	46
Berry plants	2.37	0.15	0.31	45
Hard mast stands*Berry plants	4.83	0.04	0.09	47
Availability of young clearcuts + Hard mast stands	4.83	0.04	0.09	46
Availability of young clearcuts* Hard mast stands	6.37	0.02	0.04	47
Hard mast stands	6.38	0.02	0.04	45
Null	6.60	0.02	0.04	44
Hard mast production	6.74	0.01	0.03	45
Hard mast stands*Hard mast production	12.09	0.00	0.00	47

Table 3. Ranking of models of population growth rate, each with different covariates of hard mast and soft mast, for the female population of black bears in Pisgah Bear Sanctuary, North Carolina, during 1981-2002.

Model	ΔAICc	AICc Weight	Model Likelihood	Number Parameters
Hard mast stands + Berry plants	0.00	0.41	1.00	46
Berry plants	0.50	0.31	0.77	45
Hard mast stands*Berry plants	1.91	0.15	0.38	47
Availability of young clearcuts	3.85	0.06	0.15	45
Null	5.64	0.02	0.06	44
Availability of young clearcuts + Hard mast stands	6.54	0.01	0.03	46
Hard mast stands	7.34	0.01	0.03	45
Availability of young clearcuts* Hard mast stands	7.49	0.01	0.02	47
Hard mast production	8.31	0.01	0.02	45
Hard mast stands* Hard mast production	12.64	0.00	0.00	47

Table 4. Estimates of slope (with 95% confidence intervals) for model variables in top models of apparent survival and recruitment in order of rank, for the female population of black bears in Pisgah Black Bear Sanctuary, North Carolina, during 1981-2002.

Model[a]		Slope[b]	Slope LCL	Slope UCL
Survival				
Berry plants		0.47	0.03	0.90
Hard mast stands + Berry plants				
	Hard mast stands	0.87	-0.11	1.86
	Berry plants	1.35	0.23	2.46
Recruitment				
Availability of young clearcuts		0.09	0.03	0.15
Hard mast stands + Berry plants				
	Hard mast stands	0.10	0.01	0.20
	Berry plants	0.16	0.06	0.26

[a] Only models with Δ AIC$_c$ < 2.0 are shown

[b] Models with additive or interaction terms have more than 1 slope estimate

Table 5. Estimates of slope (with 95% confidence intervals) for model variables in top models of population growth rate in order of rank, for the female population of black bears in Pisgah Black Bear Sanctuary, North Carolina, during 1981-2002.

Model[a]		Slope[b]	Slope LCL	Slope UCL
Hard mast stands + Berry plants				
	Hard mast stands	0.09	0.01	0.17
	Berry plants	0.17	0.07	0.27
Berry plants		0.09	0.03	0.15
Hard mast stands*Berry plants				
	Hard mast stands	0.11	0.03	0.19
	Berry plants	0.18	0.08	0.28
	Interaction term	0.08	-0.07	0.23

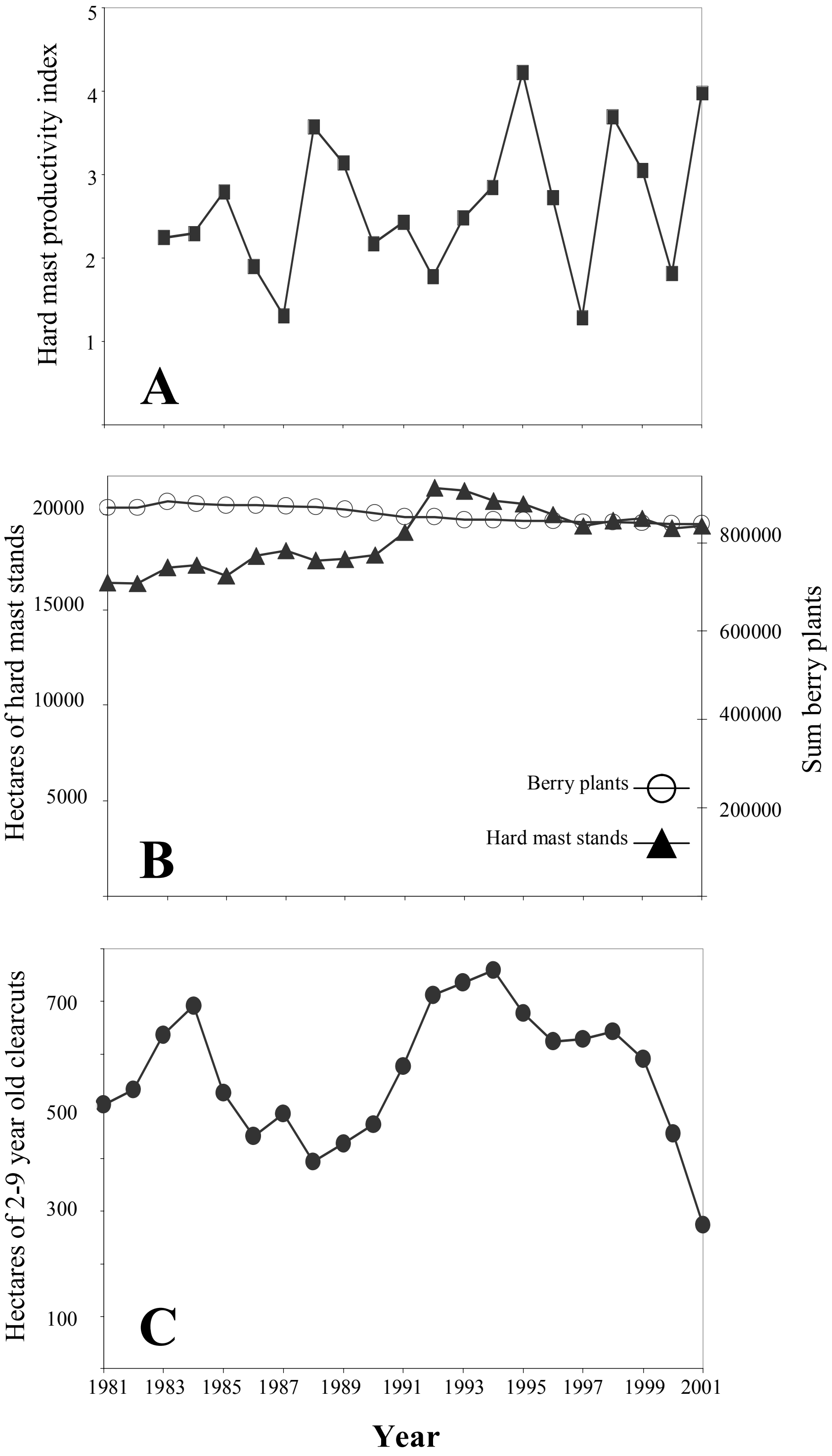
[a] Only models with Δ AIC$_c$ < 2.0 are shown

[b] Models with additive or interaction terms have more than 1 slope estimate

Figure Caption

Figure 1. Availability of hard mast and soft mast in Pisgah Bear Sanctuary, North Carolina USA 1981-2001. A) Index of hard mast production for western North Carolina (data from North Carolina Wildlife Resources Commission). B) Availability of stands most likely to produce hard mast (hectares of stands with ≥70% hard mast producing trees and ≥ 50 years old) and availability of berry plants (sum cover of huckleberry, blueberry, and raspberry plants). C) Availability of stands most likely to produce soft mast (hectares of 2-9 year old clearcuts).

Figure 1.


Hard mast productivity index
5
4
3
2
1
A
Hectares of hard mast stands
20000
15000
10000
5000
Sum berry plants
800000
600000
400000
200000
Berry plants
Hard mast stands
B
Hectares of 2-9 year old clearcuts
700
500
300
100
C
1981
1983
1985
1987
1989
1991
1993
1995
1997
1999
2001
Year

CHAPTER 4

HABITAT SELECTION FOR CLEARCUTS BY BLACK BEARS IS SCALE DEPENDENT

Abstract: Because the way animals perceive resources and habitats can depend on whether they are establishing home ranges or selecting resources within home ranges, estimates of habitat selection can differ among scales of investigation. We evaluated both 2nd and 3rd order selection by black bears (*Ursus americanus*) in Pisgah Bear Sanctuary in western North Carolina and tested whether selection for young clearcuts depended on the order of selection being evaluated. Using 80 summer home ranges for adult females, we found bears preferred young clearcuts when selecting resources within home ranges, but they did not prefer young clearcuts when establishing home ranges. Whereas 3rd order selection was likely driven by availability of bear foods inside young clearcuts, 2nd order selection was probably not. We propose characteristics of young clearcuts other than food availability inside young clearcuts, such as proximity to roads, may drive 2nd order selection by bears. That we also found bears avoided intermediate aged stands (10-69 years old) indicates the negative effects of clearcutting on habitat quality over the longer term. Results based on 3rd order selection corroborated our previous results of demographic analyses, which indicated young clearcuts alone affected habitat quality positively in terms of recruitment but not in terms of population growth.

Key words: black bears, clearcuts, habitat quality, habitat selection, scale

Ecological processes, such as 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 and King 1998; O'Neill et al. 1986). For example, habitat selection within a home range may be constrained by home range selection (Bissonette 1997), which in turn may be affected by broad-scale processes like forest fragmentation, social interactions, etc. Because the cues animals use to establish home ranges may differ from those used to select resources within home ranges, estimates of habitat selection may differ among scales of investigation.

Single scale approaches to studies of habitat selection may yield limited inferences (Maurer 1985; Mitchell et al. 2001; O'Neill and King 1998) and may underlie some of the contradictory results found in the literature. For example, studies of habitat selection have been used to understand the behavioral response of black bears to clearcuts (i.e., removal of all trees within a stand), the results of which have been conflicting. Adult female bears preferred young clearcuts during summer in Quebec (Samson and Hout 1998), New York (Costello and Sage 1994), and Oregon (Heyden and Meslow 1999), whereas adult females avoided young clearcuts during summer in Arkansas (Clark et al. 1994), Idaho (Unsworth et al. 1989; Young and Beecham 1986), and Washington (Lindzey and Meslow 1977).

By considering only the scale of the investigation, most qualitative differences among the previous studies on bear use of clearcuts can be resolved. All three studies that found black bears preferred young clearcuts evaluated 3rd order selection (i.e., resource selection within home ranges; Costello and Sage 1994; Heyden and Meslow 1999; Samson and Hout 1998), whereas three of the four studies that found black bears avoided young clearcuts evaluated only 2nd order selection (i.e., home range selection; Clark et al. 1994; Unsworth et al. 1989; Young and Beecham 1986).

Synthesizing these results, black bears appear to prefer young clearcuts when selecting resources within home ranges yet they avoid young clearcuts when establishing home ranges. A rigorous test of this hypothesis requires evaluating both 2nd and 3rd order selection by one bear population. The goal of this research was to test this hypothesis using long term data on resource selection by black bears in Pisgah Bear Sanctuary (PBS) in western North Carolina.

Previously, Mitchell and Powell (2003) evaluated resource selection by PBS bears during 1981-1994 and found females avoided young clearcuts, but they did not evaluate bear use of clearcuts explicitly. Using a habitat suitability index developed for the PBS (Mitchell et al. 2002; Zimmerman 1992), Mitchell and Powell modeled habitat quality across the PBS, tested whether bears selected areas according to predicted quality, and found, on average, bears avoided areas with low values. That areas with young clearcuts had low values of predicted quality indicated bears avoided young clearcuts. Though appropriate for testing a broad understanding of habitat quality for bears, this approach did not explicitly test whether bears avoided young clearcuts.

Moreover, Mitchell and Powell evaluated only 2nd order selection and they used annual home ranges, which may not be the best choice for testing whether bears avoided young clearcuts. Young clearcuts may be important to bears because they can support relatively high levels of soft mast (i.e. fleshy fruit; Clark et al. 1994; Mitchell et al. 2002; Noyce and Coy 1990; Perry et al. 1999; Reynolds et al. submitted$_1$; Stransky and Roese 1984), a food that has been shown to affect bear survival or reproduction positively (Elowe and Dodge 1989; Jonkel and Cowan 1971; Reynolds et al. submitted$_2$; Rogers 1976, 1987). That most soft mast in PBS is most available during summer (Powell et al. 1997) and bears select foods seasonally (Beeman and Pelton 1977; Eagle and Pelton 1983) suggests summer home ranges should be used to understand the behavioral response of bears to young clearcuts. By using annual home ranges, the potential high use of clearcuts during the summer could be obscured by low use during the rest of the year.

Habitat quality is the capacity of an area to provide resources necessary for survival and reproduction, relative to the capacities of other areas (Van Horne 1983). Understanding how clearcuts affect habitat quality, therefore, requires knowing how clearcuts affect the availability of resources important to bear survival and reproduction and also knowing how bears respond, demographically and behaviorally, to changes in resources due to clearcutting.

Soft mast and hard mast (i.e., acorns and nuts) have each been shown to be important to bear survival or reproduction (Clark and Smith 1994; Costello et al. 2003; Eiler et al. 1989; Elowe and Dodge 1989; Jonkel and Cowan 1971; Pelton 1989, Reynolds et al. submitted$_2$; Rogers 1976), but clearcutting affects availability of soft mast differently than it affects availability of hard mast. Whereas soft mast can be highly available in young clearcuts in the Southern Appalachians (Mitchell et al. 2002, Reynolds et al. submitted$_1$), hard mast is removed for 25-50 years, the time required for regenerating hardwoods to reach reproductive age (Burns and Honkala 1990). Therefore, the overall effect of clearcuts on habitat quality for a bear population will depend, in part, on whether soft mast, hard mast, or both limit the population. A resource is limiting if changes in its availability quantifiably affect population growth rate (λ ; Messier 1991).

Previously, we evaluated how PBS females responded, demographically, to changes in resource availability due to clearcuts (Reynolds et al. submitted$_2$). We linked estimates of resource availability with estimates of survival, fertility, and λ during 1981-2002 and found both hard mast and soft mast across the landscape limited λ. In addition, the availability of young clearcuts, in which soft mast was highly available, helped explain recruitment. During years when availability of young clearcuts was high, recruitment increased. Our results suggested young clearcuts had a positive effect on habitat quality for PBS bears, at least in terms of recruitment. Our demographic approach, however, assumed a resource or habitat that was available was used when it was available. If PBS bears did not use young clearcuts when they were available, our demographic results may have been spurious. Evaluating whether PBS bears avoided young clearcuts will test this assumption of our demographic study.

MATERIALS AND METHODS

Study area.—We conducted our study in the Pisgah Bear Sanctuary (PBS) in North Carolina (35° 17' N, 82° 47' W) during 1981 to 2002. The PBS encompassed 235 km^2 and was nested within the Pisgah National Forest. During 1960-2002, 184 older stands (50+ years) were harvested, most (77%) were clearcut. Mean proportion of PBS in 50+ year old stands ranged between 77 and 85% from 1981 to 2002. Most 50+ year old stands in PBS were clearcut 50+ years ago.

Eighty-eight percent of PBS comprised oak (*Quercus* spp.) and oak-hickory (*Q.* spp. *Carya* spp.). Cove hardwoods (*Liriodendron tulipifera*, *Magnolia* spp., *Betula* spp.) and pine-hemlock (*Pinus rigida*, *P. strobus, P. virginiana, Tsuga canadensis*) constituted approximately 4.5% and 3% of PBS, respectively (Continuous Inventory Stand Condition, USDA 2001). The topography was mountainous with elevations ranging from 650m to 1800m. The region was considered a temperate rainforest, with annual rainfall approaching 250 cm/yr (Powell et al. 1997).

Trapping bears and collecting location data.—We captured bears in PBS from May through mid-August during 1981-2002 (except 1991 and 1992) using modified Aldrich foot snares (Johnson and Pelton 1980) or barrel traps. We immobilized captured bears using a combination of approximately 200 mg Ketamine hydrochloride + 100 mg Xylazine hydrochloride/90kg of body mass (Cook 1984) or Telazol administered with a blow dart or jab stick. We sexed, weighed, measured, tattooed and attached 2 ear tags to each immobilized bear and extracted a premolar to determine age. 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 females > 1 year old were fitted with motion-sensitive radio transmitter collars (Telonics Inc., Mesa, Arizona; Lotek, Newmarket, Ontario; Sirtrak, Havelock North, New Zealand). All procedures comply with requirements of the Institutional Animal Care and Use Committees for Auburn University (IACUC # 0208-R-2410) and North Carolina State University (IACUC # 88-*** to # 00-018).

From May each year until the bears denned (except 1991 and 1992), we located collared bears using telemetry receivers (Telonics Inc., Mesa, Arizona) and a truck-mounted, 8-element yagi antenna. The high elevation of the Blue Ridge Parkway allowed unobstructed line-of-sight with the majority of the study area, reducing the likelihood of signal error due to interference from terrain. Locations were estimated by triangulating compass bearings taken from a minimum of 3 separate locations within 15 minutes (Zimmerman and Powell 1995). Bears were located every 2 hours for 8, 12, or 24 consecutive hours and sampling was repeated every 32 hours to standardize bias from autocorrelation (Swilhart 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 meters. 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 adult female bears. The kernel estimator depicts a bear’s use of space 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 meters was used for kernel estimation to match the resolution of our telemetry data. For analyses, home ranges were defined as the area containing 95% of the estimated utility distribution.

We estimated summer home ranges, defined as the period between July 1 and September 1, because the primary sources of soft mast in PBS, berries of raspberry (*Rubus* spp.), blackberry (*Rubus* spp.), blueberry (*Vaccinium* spp.), and huckleberry (*Gaylussacia* spp.) plants, were most available during this time (Powell et al. 1997). Berries of these genera were important foods for black bears in the Southern Appalachians (Beeman and Pelton 1977; Eagle and Pelton 1983). We included only adult females because our demographic results indicated availability of soft mast influenced bear reproduction, which is most affected by the number of females and the number of cubs each adult female can produce (Schenk and Kovas 1995).

Mapping clearcuts and estimating resource selection.— Availability of soft mast in PBS was highest in 2-9 year old clearcuts, lowest in ~10-69 year old clearcuts, and intermediate in 70+ year old clearcuts (Reynolds et al. submitted[1]). Therefore, we used a Geographic Information System (GIS; ArcView 3.2 and Spatial Analyst 2.0) and the Continuous Inventory Stand Condition database (CISC, USDA Forest Service 2001) to map the distribution of 2-9, 10-69, and 70+ year old clearcuts in PBS for each year 1981-2001, as each distribution changed through time due to timber harvesting and stand aging. For each bear, we mapped its 95% summer home range in a GIS and overlaid the three clearcut maps (i.e., 2-9, 10-69, 70+ year old clearcuts) corresponding to the home range year.

For each summer home range, we indexed preference, *E*, for 2-9, 10-69, and 70+ year old clearcuts using Ivlev's electivity index (1961) modified to make it symmetrical with respect to zero (R. A. Powell, personal communication):

$$E_i = \frac{2 * (\text{Use of resource } i - \text{Availability of resource } i)}{1 + (\text{Use of resource } i + \text{Availability of resource } i)}$$

Where E_i is the index of preference for resource *i*.

We calculated both 2nd order and 3rd order selection (Johnson 1980). For 2nd order selection, availability of resource *i* was considered that which was available within PBS (Mitchell and Powell 2002, 2003; Zimmerman 1992). For 3rd order selection, availability of resource *i* was considered that which was available within each home range. For both orders of selection, use of resource *i* was calculated as the proportion of total kernel density probabilities that were located within resource *i*. Kernel density probabilities were in raster format at a 250 meter grain, whereas each resource *i* was in polygon format. A kernel density probability *j* was considered to be located within resource *i* when at least 50% of raster cell *j* was located within resource *i*. Home ranges that contained no availability of resource *i* were not included in analyses of 3rd order selection because to do so would bias estimates of electivity. Values of electivity index can range from -1 to +1.

We combined all summer home ranges and modeled habitat preference as a function of clearcut group (i.e., 2-9, 10-69, and 70+ year old stands; Proc GLM, SAS Institute 2000) at each order of selection. We used Akaike's Information Criterion, with an adjustment for small sample bias (AIC_c; Akaike 1973; Anderson et al. 1994), to compare the ability of this model to explain the data relative to the ability of the null model (i.e., intercept only model).

RESULTS

During 1981-2002, we captured 101 females in Pisgah Bear Sanctuary (PBS). We collected sufficient telemetry data to calculate 80 summer home ranges for adult females during 16 different years. Year did not explain differences among mean preference for 2-9, 10-69, and 70+ year old clearcuts for either 2nd order selection ($P > 0.96$) or 3rd order selection ($P > 0.99$), so we did not block by year.

For 2nd order selection, the top ranked model included clearcut group. Adult females neither avoided nor preferred 2-9 year old clearcuts (95% CI for mean preference = -0.01, 0.03; Fig 1), but they avoided 10-69 year old clearcuts (95% CI for mean preference = -0.18, -0.12) and preferred 70+ year old clearcuts (95% CI for mean preference = 0.04, 0.08).

For 3rd order selection, the top ranked model included clearcut group. Adult females preferred 2-9 year old clearcuts (95% CI for mean preference = 0.045, 0.085; Fig. 2), avoided 10-69 year old clearcuts (95% CI for mean preference =-0.04, -0.02) and used 70+ year old clearcuts in proportion to availability (95% CI for mean preference =-0.01, 0.01). Our sample size for 3rd order selection was smaller than that for 2nd order selection because although all 80 females had 70+ year old clearcuts in their home ranges, only 36 females had 2-9 year old clearcuts in their home ranges and only 75 females had 10-69 year old clearcuts in their home ranges.

DISCUSSION

Animals should behave in ways that maximize benefits and minimize costs of foraging (Emlen 1966; MacArthur and Pianka 1966). This does not mean, however, that foraging choices must be identical across spatial scales. In our study, the way females in Pisgah Bear Sanctuary (PBS) responded behaviorally to young clearcuts depended on the scale of investigation. For 2nd order selection, females used young clearcuts in proportion to availability (Fig. 1), whereas females preferred young clearcuts for 3rd order selection (Fig. 2). These results indicate the way bears perceive young clearcuts differed depending on whether they were establishing home ranges (2nd order selection) or selecting resources within their home ranges (3rd order selection).

When selecting resources within home ranges, the value of young clearcuts to bears may depend primarily on the foods available within clearcuts, such as soft mast. When selecting home ranges, however, the value of clearcuts may depend less on foods and more on other characteristics of clearcuts. Clark et al. (1994) found female bears avoided regenerating stands during summer when they established home ranges, even though summer foods were highly available therein. They proposed something outside the regenerating stands, rather than the foods inside regenerating stands, affected bear behavior during 2nd order selection.

Minimizing mortality risk, for example, may be more important than maximizing foraging efficiency when bears establish home ranges. If so, bears might establish home ranges in areas away from roads, which can increase risk of mortality due to hunting, poaching, and vehicle collision (Brody and Pelton 1989; Pelton 1986). Young clearcuts are often spatially associated with gravel roads, so bears that avoided young clearcuts when establishing home ranges (Clark et al. 1994; Mitchell and Powell 2003; Unsworth et al. 1989; Young and Beecham 1986) may have done so to avoid roads. That black bears have been shown to avoid gravel roads in forested areas (Garner 1986; Heyden and Meslow 1999; Quigley 1982), and females in PBS avoided areas near gravel roads when establishing home ranges during summer and fall (Reynolds and Mitchell, submitted$_1$), indicates road avoidance can affect 2nd order selection. Explicitly testing how bears respond behaviorally to clearcuts, with respect to roads, could be the focus of future research.

That bears did not prefer young clearcuts when establishing home ranges, yet they preferred young clearcuts when selecting resources within home ranges, could have occurred if the value of clearcuts to bears was relatively low, but bears used clearcuts when higher quality habitats were unavailable. Animals probably cannot select an ideal mix of habitats to compose home ranges because they may not have free and equal access to all habitats due to social interactions, unevenly distributed habitats, etc. Assuming bears have an ideal or despotic free distribution (Fretwell and Lucas 1970), preferred habitats will be settled first by early or dominant individuals, after which animals are forced to settle in poorer and poorer habitats. A bear might prefer to not have clearcuts in its home range, but if clearcut-free areas are taken up by other bears, it will make the best use it can out of whatever habitats are left.

Although our results based on 3rd order selection corroborated most previous studies that evaluated 3rd order selection by bears (Costello and Sage 1994; Heyden and Meslow 1999; Samson and Hout 1998), our results based on 2nd order selection were not similar to findings by previous studies that evaluated 2nd order selection. Previous studies found bears avoided young clearcuts when bears established home ranges (Clark et al. 1994; Mitchell and Powell 2003; Unsworth et al. 1989; Young and Beecham 1986), but we found bears used young clearcuts in proportion to availability. To compare our results with those by Mitchell and Powell (2003), who estimated 2nd order selection by PBS bears, we re-evaluated our data using the preference index they used (i.e., Ivlev's index without the adjustment; use resource *i* – availability resource *i*/use resource *i* + availability resource *i*). We found PBS females avoided young clearcuts when establishing home ranges (Fig. 3), which was consistent with findings from Mitchell and Powell (2003) as well as other studies that analyzed 2nd order selection. We also found bears preferred young clearcuts when selecting resources within home ranges (Fig. 4).

Our results indicated 3rd order selection may have been constrained by 2nd order selection. Even if bears perceived young clearcuts to be valuable, as results of 3rd order selection suggest, their value could not be realized unless young clearcuts were included in home ranges. That 44 of 80 home ranges of PBS females did not include young clearcuts suggests bears may prefer clearcut-free areas when establishing home ranges. If so, 2nd order selection would have imposed constraints on the range of habitat choices available to individuals at smaller scales (Bissonette 1997).

Other studies that evaluated habitat use by wild animals at multiple scales similarly found results differed depending on the scale of observation (Cushman and McGarigal 2004; Kolasa 1989; Mitchell et al. 2000; Parsons et al. 1994). Importantly, discontinuities in data suggest a change in level of organization (O'Neill and King 1998). For example, Bissonette et al. (1997) showed American martens (*Martes americana)* avoided clearcuts when establishing home ranges, but martens did not avoid clearcuts when selecting resources within home ranges. The emergent pattern they found indicated clearcut selection by martens could be hierarchically organized (Allen and Starr 1982; King 1997; O'Neill et al. 1986), whereby ecological processes are understood in terms of both lower-level mechanisms and higher-level constraints. For their study, 3rd order selection was constrained by 2nd order selection. Because higher level constraints have a relatively large effect on the process of interest (e.g., habitat selection by martens), the negative effects of clearcuts on 2nd order selection may have been more important than the positive effects of clearcuts on 3rd order selection. When viewed within the framework of hierarchy theory, our results similarly suggest the positive effects of clearcuts on 3rd order selection by PBS bears may have been less important than the effects of clearcuts on 2nd order selection.

Clearcuts and habitat quality for PBS bears.— The effects of clearcuts on habitat quality for bears is complex, distilling this complexity requires understanding how clearcuts affect the availability of resources important to bear survival and reproduction and also knowing how bears respond, demographically and behaviorally, to changes in resources due to clearcutting. Synthesizing results from our behavioral study on PBS bears with results from our previous demographic research on PBS bears, we conclude that young clearcuts contributed positively to habitat quality, but only in terms of recruitment. Bears preferred young clearcuts when selecting resources within home ranges (3rd order selection) and annual availability of young clearcuts contributed positively to annual recruitment (Reynolds et al. submitted$_2$). That young clearcuts contributed little to population growth and bears did not prefer young clearcuts when establishing home ranges (2nd order selection), however, indicates the overall effect of young clearcuts on habitat quality may have been relatively minimal.

Although results from both our demographic and behavioral analyses indicated that 2-9 year old clearcuts affected habitat quality positively, at least in terms of bear recruitment, these analyses were insufficient to gauge the full effect of clearcuts on habitat quality because they incorporated only the earliest portion of the successional life of a clearcut. Availability of resources inside clearcuts changes through time due to succession. Therefore, the effect of clearcuts on habitat quality will also change through time. Assuming a primary effect of clearcuts on habitat quality for bears is increased availability of soft mast, the positive effect of clearcuts on habitat quality should be relatively short because soft mast is highly available in young clearcuts for only a few years. In PBS, soft mast availability was highest in ~2-9 year old clearcuts and lowest in ~10-69 year old clearcuts (Reynolds et al., submitted$_1$). Bears in PBS avoided 10-69 year old clearcuts for both orders of selection (Figs. 1 and 2), and they preferred 70+ year old clearcuts when establishing home ranges (Fig. 1), which suggests clearcuts had a negative effect on habitat quality for bears over the longer term.

CONCLUSIONS

The effect of young clearcuts on habitat quality for bears is best understood within the context of life history. For black bears, a long lived species with low reproductive potential, adult survival is the vital rate most likely to contribute to future changes in population growth (Brongo 2004; Freedman 2003, Hebblewhite et al., 2003). Therefore, resources, habitats, or disturbances that affect bear survival should have a large effect on habitat quality relative to the effect of resources, habitats, or disturbances that affect only bear recruitment. Availability of young clearcuts helped explain recruitment but not survival of PBS females (Reynolds et al. submitted$_2$), whereas bear use of areas near gravel roads affected survival of PBS females (Reynolds and Mitchell, submitted$_2$). During years when PBS females avoided areas near gravel roads, annual survival increased. Therefore, the negative effect of gravel roads on bear survival may outweigh the positive effect of young clearcuts on bear recruitment.

Clearcuts are spatially associated with gravel roads. Strategies to increase bear habitat in forested areas by implementing clearcuts, therefore, must consider not only how clearcuts change availability of bear resources inside clearcuts but also how gravel roads associated with clearcuts affect habitat quality. Our hypothesis that roads might partly drive 2nd order selection for clearcuts by PBS bears is biologically sensible, based on both demographic and behavioral responses we documented for PBS bears. We stress, however, that this hypothesis is one among several hypotheses (e.g., interspersion of clearcuts on the landscape, area of clearcuts, social interactions, etc.), each of which should be tested to further our understanding of how bears perceive clearcuts when establishing home ranges.

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Figure Captions

Figure 1. 2nd order selection: mean preference (with 95% confidence intervals) for 2-9, 10-69, and 70+ year old clearcuts in summer by adult female bears in Pisgah Bear Sanctuary, USA using Ivlev’s index modified to make it symmetrical with respect to zero.

Figure 2. 3rd order selection: mean preference (with 95% confidence intervals) for 2-9, 10-69, and 70+ year old clearcuts in summer by adult female bears in Pisgah Bear Sanctuary, USA using Ivlev’s index modified to make it symmetrical with respect to zero.

Figure 3. Results based on unmodified Ivlev’s index to compare results with those from Mitchell and Powell (2003). 2nd order selection: mean preference (with 95% confidence intervals) for 2-9, 10-69, and 70+ year old clearcuts in summer by adult female bears in Pisgah Bear Sanctuary, USA.

Figure 4. Results based on unmodified Ivlev’s index to compare results with those from Mitchell and Powell (2003). 3rd order selection: mean preference (with 95% confidence intervals) for 2-9, 10-69, and 70+ year old clearcuts in summer by adult female bears in Pisgah Bear Sanctuary, USA.

Figure 1.

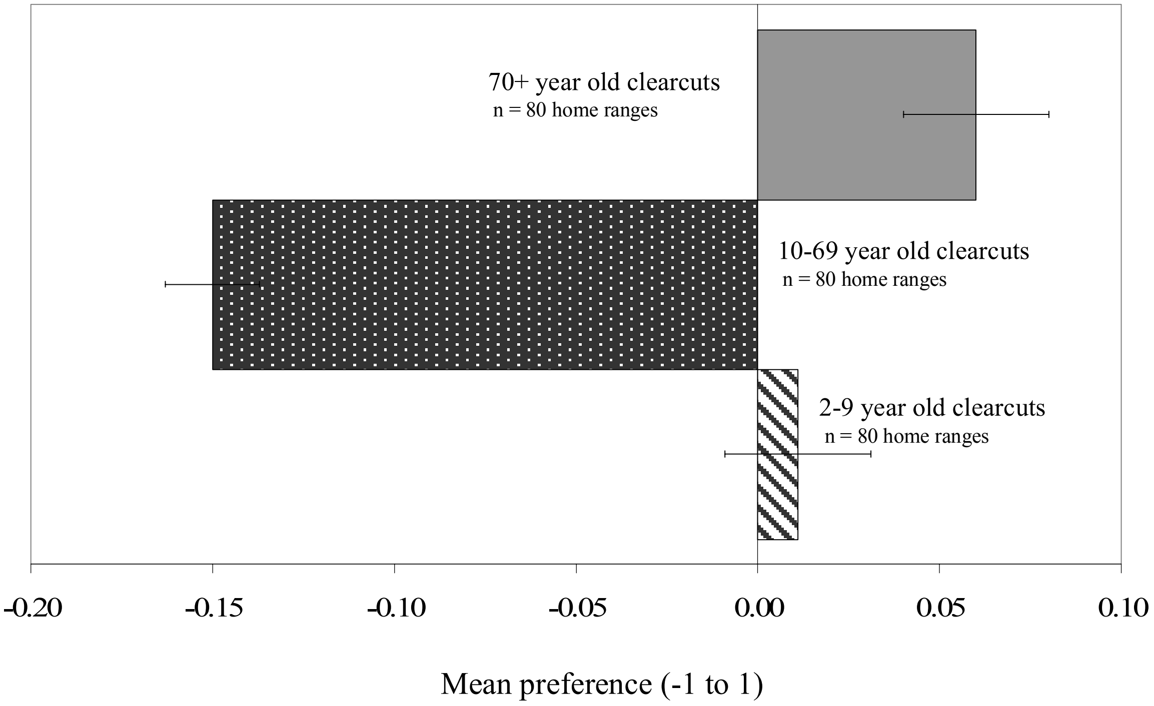

70+ year old clearcuts
n = 80 home ranges
10-69 year old clearcuts
n = 80 home ranges
2-9 year old clearcuts
n = 80 home ranges
-0.20
-0.15
-0.10
-0.05
0.00
0.05
0.10
Mean preference (-1 to 1)

Figure 2.

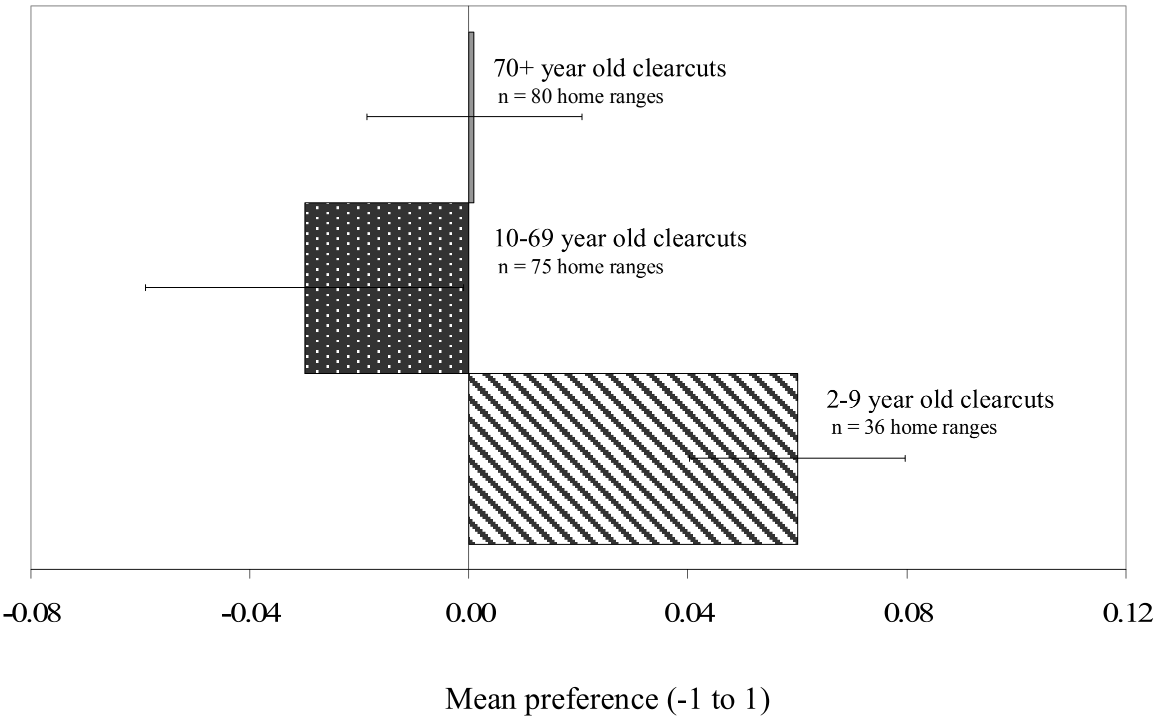

70+ year old clearcuts
n = 80 home ranges
10-69 year old clearcuts
n = 75 home ranges
2-9 year old clearcuts
n = 36 home ranges
-0.08
-0.04
0.00
0.04
0.08
0.12
Mean preference (-1 to 1)

Figure 3.

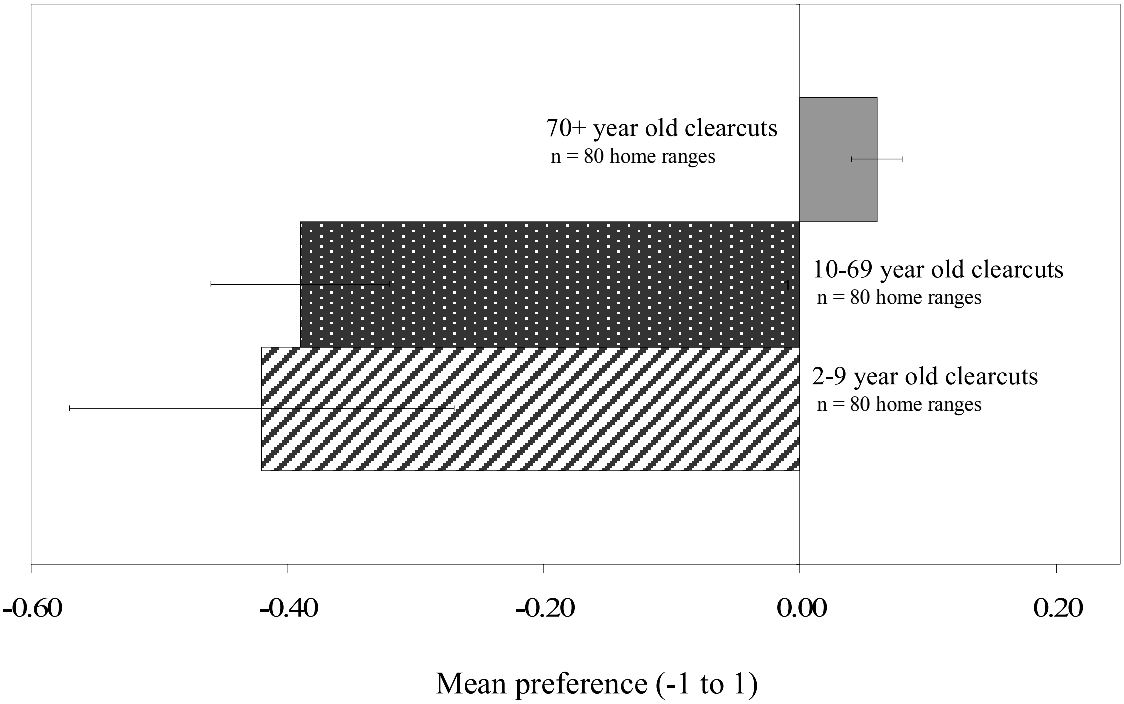
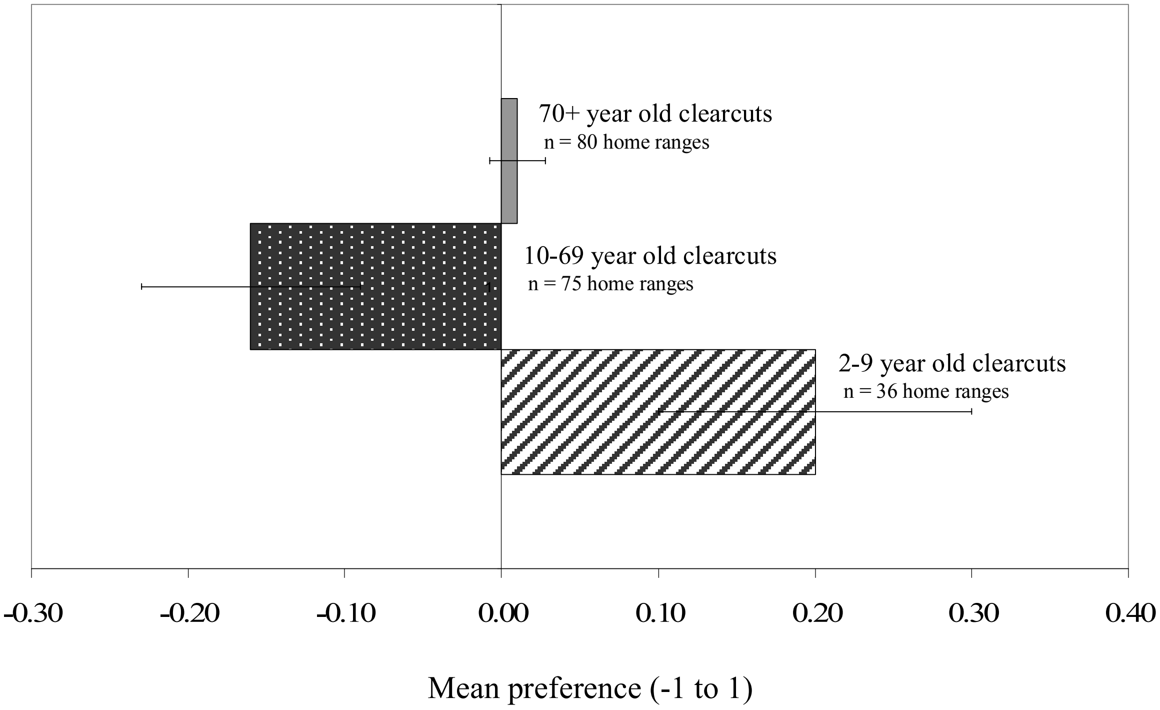

70+ year old clearcuts
n = 80 home ranges
10-69 year old clearcuts
n = 80 home ranges
2-9 year old clearcuts
n = 80 home ranges
-0.60
-0.40
-0.20
0.00
0.20
Mean preference (-1 to 1)

Figure 4.



70+ year old clearcuts
n = 80 home ranges
10-69 year old clearcuts
n = 75 home ranges
2-9 year old clearcuts
n = 36 home ranges
-0.30
-0.20
-0.10
0.00
0.10
0.20
0.30
0.40
Mean preference (-1 to 1)

CHAPTER 5

ROAD EFFECTS ON HABITAT QUALITY FOR BLACK BEARS IN THE SOUTHERN APPALACHIANS: A LONG TERM STUDY

Abstract: We tested the hypothesis that gravel roads, not paved roads, had the largest negative effect on habitat quality for a population of black bears (*Ursus amerianus*) 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 distance at which roads affected bear behavior negatively. Using 178 summer home ranges and 118 fall home ranges for black bears living in the Pisgah Bear Sanctuary in western North Carolina during 1981-2001, we estimated both 2nd and 3rd order selection for areas within 250, 500, 800, and 1600 meters from paved and gravel roads. Bears avoided areas near gravel roads more than they avoided areas near paved roads for both orders of selection during both summer and fall. During fall, adult females avoided areas near gravel roads more than did juvenile females, adult males, and juvenile males. We found a positive relationship between road use by adults and annual variability in hard mast productivity. Overall, bears avoided areas $\leq$ 800 meters of gravel roads. Our results indicate gravel roads had a negative effect on bear behavior. Future research should test our results to determine whether bear avoidance of gravel roads affects bear survival.

Key words: black bears, habitat quality, resource selection, roads, Southern Appalachians, *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. 2000; Reed et al. 1996; Wielgus and Vernier 2003), policy makers (United Nations 1999), and resource managers (USDA 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 black bears, roads may affect bear 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, bear foods 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 paved roads in Maryland (Fescke et al. 2002), North Carolina (Brody 1984, Brody and Pelton 1989, Beringer et al. 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 gravel or gated roads in Michigan (Manville 1983), Idaho (Young and Beecham 1986), North Carolina (Brody 1984; Brody and Pelton 1989; Beringer et al. 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; Heyden and Meslow 1999; Quigley 1982) indicates traffic volume alone is insufficient to explain how roads affect habitat quality for bears. The source (or sources) of mortality that have the most impact on a bear population must also 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 first 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 reported hunted, and 19 were known to be poached or possibly poached (North Carolina Wildlife Resources Commission, unpublished data). 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, personal communication). Because vehicle collision appears to be a small source of mortality for PBS bears relative to poaching, we hypothesized 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 second objective was to determine the spatial extent to which roads affected behavioral response of bears. Carr and Pelton (1984) found bears in the Great Smoky Mountains preferred areas < 200 meters from gravel roads, whereas Quigley (1982) and Clark et al. (1993) found bears avoided areas < 200 meters from roads in the Great Smoky Mountains and bears avoided areas < 240 meters from roads in Arkansas, respectively. Rudis and Tansey (1995) predicted areas < 800 meters 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 meters from non-paved roads. Zimmerman (1992), Powell et al. (1997), and Mitchell et al. (2002) predicted areas < 1600 meters from roads, especially paved roads, would affect habitat quality negatively for bears in western North Carolina. We considered all conclusions and predictions to be *a priori* hypotheses that we tested simultaneously (Chamberlain 1897) for PBS bears, which should yield strong inferences (Platt 1964).

Our third objective was to test if behavioral response of bears to roads differed by sex or age. Although males travel relatively widely (Garshelis and Pelton 1981; Powell et al. 1997; Smith and Pelton 1990; Young and Ruff 1982), making them more vulnerable to hunters (Bunnell and Tait 1985; Garshelis 1989), 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 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).

We also tested the hypothesis that bear use of roads differed by age. If so, the difference should be most pronounced 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 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. 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 final objective was to test if availability of hard mast (acorns and nuts), a fall food important to bear reproduction and population growth (Costello et al. 2003; Eiler et al. 1989; Elowe and Dodge 1989; Pelton 1989; Reynolds et al. submitted$_2$; Rogers 1976, 1987), 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. We defined risk different from that 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, we defined risk as the potential for mortality. To survive winter and ensure reproductive success, bears must acquire sufficient stores of energy during fall (Beecham 1980; Bunnell and Tait 1981; 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 fall foods. We predicted road use by PBS bears would vary inversely with hard mast productivity.

MATERIALS AND METHODS

Study area.—We conducted our study in the Pisgah Bear Sanctuary (PBS) in North Carolina (35° 17' N, 82° 47' W) during years 1981-2001. The PBS (235 km^2) was located within the Pisgah National Forest, where topography was mountainous with elevations ranging from 650m to 1800m. The region was considered a temperate rainforest, with annual rainfall approaching 250 cm/yr (Powell et al. 1997).

Eighty-eight percent of PBS comprised oak and oak-hickory species, including northern red oak (*Quercus rubrus*), southern red oak (*Q. falcata*), white oak (*Q. alba*), chestnut oak (*Q. prinus*) and hickory (*Carya* spp.). Cove hardwoods (*Liriodendron tulipifera*, *Magnolia* spp., *Betula* spp.) and pine-hemlock (*Pinus rigida*, *P. strobus, P. virginiana, Tsuga canadensis*) constituted approximately 4.5% and 3% of PBS, respectively. Sub-canopy and understory species (*Rhododendron spp*., *Kalmia* spp. etc) and a mixture of other species (*Corylus* spp., *Liquidambar styraciflua*, etc) constituted the remaining portions of the PBS (Continuous Inventory Stand Condition database, USDA 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 data base, USDA Forest Service 2001). The Blue Ridge Parkway, which was administered by the U.S. National Park Service, transected the north central portion of PBS, US Highway 276 bounded the western edge of PBS, and State Road 151 (a paved road) ran though a small portion of PBS. Several gravel roads ran through parts of PBS, one of which (Forest road 1206) bisected the Sanctuary. By year 2000, over 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 + 100 mg Xylazine hydrochloride/90kg of body mass (Cook 1984) or Telazol administered with a blow dart or jab stick. We sexed, weighed, measured, tattooed and attached 2 ear tags to each immobilized bear and extracted a first 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 radio transmitter collars (Telonics, Inc. Mesa, Arizona; Sirtrak, Havelock North, New Zealand). Bears were handled in a humane manner and all procedures complied with both ASM guidelines and the requirements of the Institutional Animal Care and Use Committees for Auburn University (IACUC # 0208-R-2410) and North Carolina State University (IACUC # 88-*** to # 00-018).

From May each year until the bears denned (except for years 1991 and 1992), we located collared bears using telemetry receivers (Telonics Inc., Mesa, Arizona; Lotek, Newmarket, Ontario; Sirtrak, Havelock North, New Zealand) and a truck-mounted, 8-element yagi antenna. The high elevation of the Blue Ridge Parkway allowed unobstructed line-of-sight with the majority of the study area, reducing the likelihood of signal error due to interference from terrain. Locations were estimated by triangulating compass bearings taken from a minimum of 3 separate locations within 15 minutes (Zimmerman and Powell 1995). Bears were located every 2 hours for 8, 12 or 24 consecutive hours and sampling was repeated every 32 hours to standardize bias from autocorrelation (Swilhart 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 meters. 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 a bear's use of space 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 meters 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 bear behavior that differed by seasons. Negative effects of roads associated with increased mortality due to hunting and poaching should be most pronounced during fall when non-bear 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 both summer and fall home ranges. We defined the summer season as the period between June 1-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 (GIS; ArcView 3.2 and Spatial Analyst 2.0) to map the distribution of roads in PBS for each year 1981-2001. We partitioned roads into 3 types (paved, gravel, gated; Brody 1984, Powell et al. 1997) and developed a road map for each road type for each year 1981-2001. We included gated roads for completeness. Gated roads were defined as gravel roads which were gated during the entire year, where vehicle access was limited to Forest Service personnel. Information about road type and date of construction were provided by USDA Forest Service at the Pisgah Ranger District, North Carolina.

Using a GIS, we placed 4 vector buffers around each road during each year to test previous results regarding the distance at which roads affected resource selection by bears. We placed 250 meter buffers (Carr and Pelton 1984; Clark et al. 1993; Quigley 1982), 800 meter buffers (Hellgren et al. 1991; Rudis and Tansey 1995), and 1600 meter buffers (Mitchell et al. 2002; Powell et al. 1997; Zimmerman 1992). We included 500 meter buffers as an intermediate distance between 250 and 800 meters.

Estimating resource selection.—For each season during each year, we estimated resource selection for each road type (paved, gravel, and gated) at each buffer distance (250m, 500m, 800m, and 1600m) for each individual bear. We mapped each seasonal 95% kernel home range in a GIS and overlaid the road map corresponding to the home range year. For each home range, we indexed preference for each road type at each buffer distance using Ivlev's electivity index (1961) modified to make it symmetrical with respect to zero (R. A. Powell, pers. comm.):

$$E_i = \frac{2 * (\text{Use of resource } i - \text{Availability of resource } i)}{1 + (\text{Use of resource } i + \text{Availability of resource } i)}$$

Where E_i is the index of preference for resource *i*.

We estimated both 2nd order selection (i.e., home range selection; Johnson 1980) and 3rd order selection (resource selection within home ranges). For 2nd order selection, availability of resource *i* was calculated as the proportion of resource *i* located within PBS (Mitchell and Powell 2002, 2003; Zimmerman 1992), whereas availability of resource *i* for 3rd order selection was calculated as the proportion of resource *i* located within the 95% home range. For both orders of selection, use of resource *i* was calculated as the proportion of total kernel density probabilities that was located within resource *i*. Kernel density probabilities were in raster format at a 250 meter grain, whereas each resource *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 resource *i* when at least 50% of raster cell *j* was located within resource *i*. Home ranges that contained no availability of resource *i* were not included in analyses for 3rd order selection because to do so would bias estimates of electivity. Values of electivity index can range from -1 to +1.

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 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 (BRP), were steep relative to areas near gravel and gated roads (MJR, unpublished data) so any differences in resource selection for road types may be influenced by slope. To test if slope affected resource selection among road types, we used a GIS to estimate mean slope at a 30m resolution within each buffer around each road type for each individual fall home range. 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 (Burhnam and Anderson 2002).

Because slope differed among buffer distances for both paved and gravel roads (MJR unpublished data), we controlled for these differences by testing whether slope confounded the effects of road type by buffer distance. To test our hypotheses, therefore, we ran 2 analyses. The first 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 second 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 index of hard mast production estimated annually by the North Carolina Wildlife Resources Commission (NCWRC) for the Pisgah National Forest. NCWRC measured mast production of southern red oak (*Quercus falcata*), northern red oak (*Q. rubrus*), white oak (*Q. alba*), hickory (*Carya* spp.), and beech (*Fagus* spp.) species and calculated an index of production for most years 1983-2001 for each 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 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 (i.e., ≥ 20 locations per season per bear) to estimate 76 summer home ranges and 48 fall home ranges for 41 adult females, 51 summer home ranges and 35 fall home ranges for 29 adult males, 27 summer home ranges and 18 fall home ranges for 25 juvenile females, and 24 summer home ranges and 17 fall home ranges for 23 juvenile males.

The top-ranked model for 2nd order selection during summer included buffer distance, road type, sex, and age class (Table 1). As strength of evidence for model selection, the AIC weight for the top model was 0.69 and that for the third ranked model (which did not include sex or age class) was 0.09, indicating the top model was at least 7.5 times more likely to be selected over models without sex and age class. The top-ranked model for 2nd order selection during fall included buffer distance, road type, sex, and age class. The AIC weight for the top ranked model was 0.33 and that for the third ranked model (which did not include age class) was 0.32, indicating age class probably contributed little information to 2nd order selection during fall. 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 at least 8.4 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 0.50 and that for the second ranked model was 0.23, indicating the top model was only 2 times more likely to be selected over the second ranked model.

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 (Figs. 1 and 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 meter buffer distance and juvenile females did not avoid gravel roads more than they avoided paved roads at 1600 meter buffer distance. During fall, only adult females avoided areas near gravel roads more than they avoided areas near paved roads at all buffer distances (Fig. 4). Adult males avoided areas within 800-1600 meters of gravel roads more than they avoided areas within 800-1600 meters 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 (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 1600 meters (Table 2) and the summed AIC weight for road type was larger than that for slope at all buffer distances except 1600 meters (Table 3).

Sex and age class.— Both sex and age class helped explain 2nd and 3rd order selection during summer (Table 1). Adult females used areas near gravel roads less than did adult males at all buffer distances during summer (Fig. 1). For 3rd order selection during summer, adult females avoided areas within 250-500 meters of gravel roads more than did adult males (Fig. 3). In addition, adult females used areas within 500 meters of paved roads less than did all other bears (Fig. 3). Though age class did not contribute much information to 2nd order selection during fall (Table 1), adult females avoided areas within 250 meters of gravel roads more than did all other bears and adult females avoided areas within 250, 500, and 1600 meters of gravel roads more than did adult males or 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), adult females avoided areas within 250, 500, and 800 meters of gravel roads more than did adult or juvenile males (Fig. 4). Moreover, only adult females avoided areas near gravel roads more than they avoided areas near paved roads at all buffer distances.

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 meters, 500 meters, and 800 meters of gravel roads more than they avoided areas within 1600 meters of gravel roads for 3rd order selection during summer

(Fig. 3). Overall, bears avoided areas < 1600 meters from gravel roads for 2nd order selection during summer and fall (Figs. 1 and 2). For 3rd order selection during summer, adult females and adult males avoided areas ≤ 800 meters from gravel roads and juvenile females avoided areas ≤ 500 meters from gravel roads (Fig. 3). For 3rd order selection during fall, adult females avoided areas ≤ 800 meters from gravel roads (Fig. 4).

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 fall use of areas within 250, 500, and 800 meters of paved roads as annual hard mast productivity increased (for 250 meter buffer: $P = 0.002$; $r^2 = 0.24$; slope = 0.12). Adult males increased fall use of areas within 250 meters of paved roads ($P = 0.08$; $r^2 = 0.10$; slope = 0.56) and within 250 meters of gravel roads ($P = 0.09$; $r^2 = 0.09$; slope = 0.04) 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 fall use of areas within 250 and 500 meters of paved roads as annual hard mast productivity increased (for 250 meter buffer: $P = 0.007$; $r^2 = 0.19$; slope = 0.049), whereas adult males increased fall use of areas within 250-800 meters of gravel roads as annual hard mast productivity increased (for 250 meter buffer: $P = 0.04$; $r^2 = 0.16$; slope = 0.040).

DISCUSSION

To understand how roads affected habitat quality for black bears in the Southern Appalachians, we evaluated resource selection by bears using a large sample size (n = 296 home ranges) over a long temporal duration (21 years). Whereas previous studies on road use by black bears hypothesized 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 Pisgah Bear Sanctuary (PBS) because vehicle collision was a minimal source of mortality for PBS bears relative to poaching. We did not document the frequency of bear-poacher encounters, 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, unpublished data). 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).

We found PBS bears avoided areas near gravel roads more than they avoided areas near paved roads for 2nd order selection during both summer (Fig. 1) and fall (Fig. 2), suggesting 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. Preference values based on 2nd order selection, however, may have been confounded by slope (Tables 2 and 3). 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.

For 3rd order selection (i.e., resource selection within home ranges), bears avoided areas near gravel roads more than they avoided areas near paved roads in summer (Fig. 3) and adult females avoided areas near gravel roads more than they avoided areas near paved roads in fall (Fig. 4). Unlike 2nd order selection, slope did not confound the effects of road type for 3rd order selection, except possibly at buffer distance 1600 meters (Tables 2 and 3). Because adult females were the only bears that avoided areas near gravel roads more than they avoided areas near paved roads during fall, 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.

In strong contrast to our results, findings from previous studies on road use by black bears concluded paved roads, not gravel roads, had the largest negative effect on habitat quality for bears. Quigley (1982) found bears in the Great Smoky Mountain National Park (GSMNP) avoided areas < 200 meters from paved roads more than they avoided areas < 200 meters from gravel roads. The discrepancy between our results and those of Quigley (1982) may reflect differences in mortality sources that were most important to bears in GSMNP compared to those that were most important to bears in PBS. Vehicle collision may have been a higher mortality risk for GSMNP bears than it was for PBS bears because the latter often used the tops of road tunnels to cross the Blue Ridge Parkway (MJR unpublished data), 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.

We predicted PBS bears 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. Alternatively, it could be that poachers avoided paved roads and, therefore, bears used areas near paved roads to avoid poachers.

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 (Fig. 3) did not differ from that during fall (Fig. 4). 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. Bears may have avoided areas near gravel roads during summer, therefore, 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 (BRP; the main paved road in PBS) was leisurely motoring. On average, motorists that use BRP for sight-seeing rarely wander beyond a few meters from their vehicles. Though 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 class.— Resource selection for areas near gravel roads differed between sex and age classes. Adult females avoided areas near gravel roads more than did adult males when establishing home ranges (Figs. 1 and 2) and when selecting resources within home ranges (Figs. 3 and 4). Our results corroborated results by Quigley (1982) and Young and Beecham (1987) who showed adult females avoided areas near gravel roads more than did adult males. If road avoidance was strictly a learned behavior transmitted from mothers to cubs, then avoidance of roads by juveniles, who had already spent at least a year with their mothers, should have been similar to road avoidance by adult females. We found, however, that adult females avoided areas near gravel roads more than did juvenile males (Figs. 2 and 4) and juvenile females (Fig. 2), which conflicted with findings by Brody and Pelton (1989) who showed road use by black bears in western North Carolina did not differ by sex or age class.

The most pronounced differences in road use were between adult females and other bears, not between adult males and juvenile males as we predicted. For example, adult females avoided areas ≤ 800 meters from gravel roads in fall, but other bears did not (Fig. 4). Most bears hunted in North Carolina were harvested within 800 meters of roads (Collins 1983), which indicates hunters are willing, on average, to walk 800 meters 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 ~800 meters 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 suggest 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 (i.e., zero was in the 95% confidence intervals for juvenile females; Fig. 4).

Because fall foods near gravel roads were at least as equally available as fall foods near paved roads (MJR, unpublished data), 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 non-lethal 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. Teasing apart the causes underlying bear behavior with respect to roads requires understanding whether road use by bears affects fitness, which should be the focus of future research.

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 dominated during years when productivity of fall foods was high. Assuming bears that use areas near gravel roads are more likely to be poached or hunted, then bear harvests should be male dominated 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.— Bears avoided areas ≤ 1600 meters from gravel roads when establishing summer and fall home ranges (Figs. 1 and 2) and adults avoided areas ≤ 800 meters of gravel roads when selecting resources within summer (Fig. 3) and fall (Fig. 4) home ranges. These results indicate the negative effects of gravel roads were relatively far-reaching, which corroborated predictions by Rudis and Tansey (1995), Zimmerman (1992), Powell et al. (1997), and Mitchell et al. (2002), 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 our field methods because most of our telemetry locations were collected from the Blue Ridge Parkway (BRP), 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. Our telemetry route, however, was elevated above most of our study area and we used a relatively large antenna (8 element yagi), which permitted us to detect radio transmissions up to 25 km (most bears < 10 km away were detected from at least 1 station) from the BRP. The likelihood of detecting bears located near the BRP, therefore, should have been similar to the likelihood of detecting bears near gravel roads that were within several miles of the BRP.

CONSERVATION IMPLICATIONS

Regardless of whether PBS bears avoided areas near gravel roads to avoid poachers or whether they were avoiding non-lethal human contact, gravel roads had a negative effect on habitat selection. 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 et al. submitted$_1$), a food important to bear fitness (Elowe and Dodge 1989; Reynolds et al. submitted$_2$; Rogers 1976, 1987), harvested stands are usually spatially associated with gravel roads. If bears avoid areas near gravel roads, as our results show, then bear foods inside harvested stands may be relatively inaccessible to bears. Therefore, managers must consider not only the tradeoffs 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.

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Table 1. Model rankings for mean *E* (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*	Δ AIC	Model likelihood	Model weight
2nd	Summer	Buffer, road type, sex, age	0.00	1.00	0.69
		Buffer, road type, age*sex	2.81	0.24	0.17
		Buffer, road type	4.05	0.13	0.09
		Buffer, road type, age	5.62	0.06	0.04
2nd	Fall	Buffer, road type, age*sex	0.07	1.00	0.33
		Buffer, road type age, sex	0.00	0.99	0.32
		Buffer, road type, sex	0.03	0.97	0.32
		Buffer, road type, age	7.10	0.03	0.01
3rd	Summer	Buffer, road type, age*sex	0.00	1.00	0.76
		Buffer, road type, age	4.32	0.12	0.09
		Buffer, road type, sex ,age	5.23	0.07	0.06
		Buffer, road type	5.25	0.07	0.06
3rd	Fall	Buffer, road type	0.00	1.00	0.50
		Buffer, road type age	1.55	0.46	0.23
		Buffer, road type, sex	2.08	0.35	0.18
		Buffer, road type, sex, age	3.73	0.15	0.08

* Only the top 4 models for each analysis are shown

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

Selection Order	Buffer	Model*	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
	1600	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
	1600	Road type, slope	0.00	1.00	0.58

* Only models with ΔAIC values < 2.0 are shown.

Table 3. Relative importance of model variables for mean *E* (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 (w) were summed across all models in which *j* occurred.

2nd order selection			3rd order selection		
Buffer distance (m)	Model variable	Sum w_+ (*j*)	Buffer distance (m)	Model variable	Sum w_+ (*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
1600	Road type	1.00	1600	Road type	1.00
	Slope	1.00		Slope	1.00
	Sex	0.55		Sex	0.21
	Age class	0.35		Age class	0.21

Figure Captions

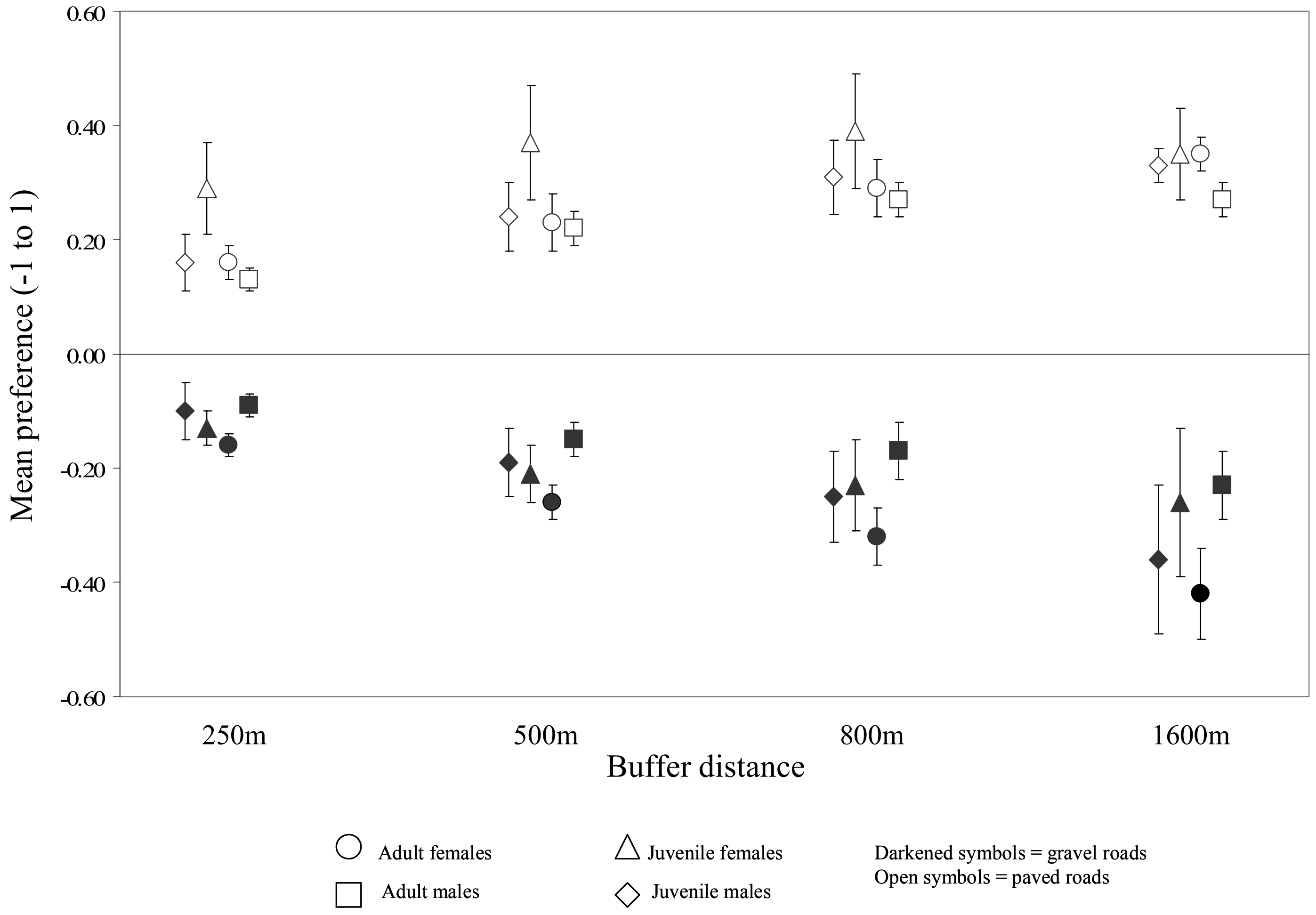
Figure 1. Mean *E* (preference) during summer for 2nd order selection, with 95% confidence intervals, for areas within 250, 500, 800, and 1600 meters of paved and gravel roads by adult female, adult male, juvenile female, and juvenile male bears in Pisgah Bear Sanctuary in western North Carolina during 1981-2001.

Figure 2. Mean *E* (preference) during fall for 2nd order selection, with 95% confidence intervals, for areas within 250, 500, 800, and 1600 meters 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.

Figure 3. Mean *E* (preference) during summer for 3rd order selection, with 95% confidence intervals, for areas within 250, 500, 800, and 1600 meters 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.

Figure 4. Mean *E* (preference) during fall for 3rd order selection, with 95% confidence intervals, for areas within 250, 500, 800, and 1600 meters 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.

Figure 1.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Mean preference (-1 to 1)
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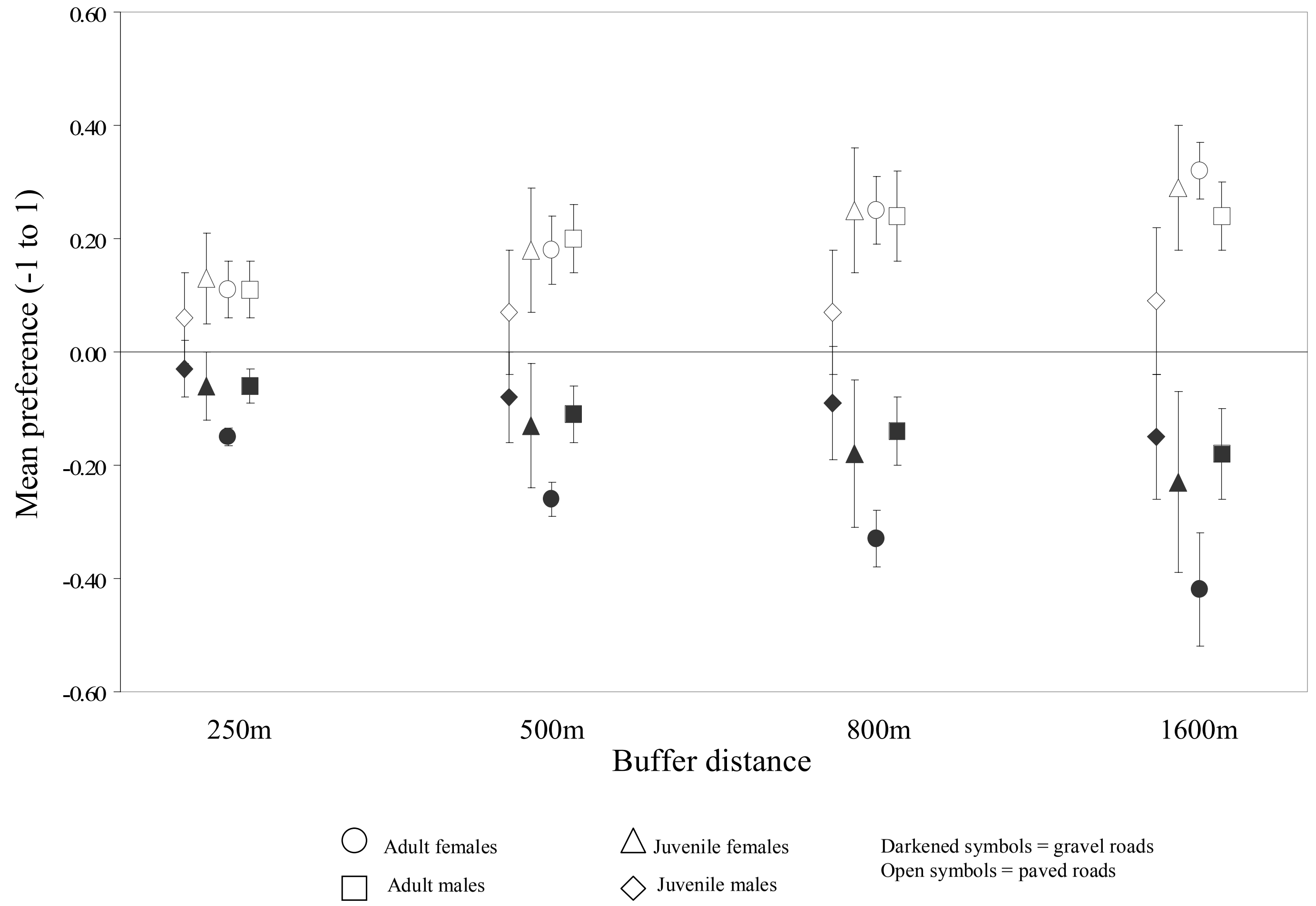
1600m
Buffer distance
Adult females
Adult males
Juvenile females
Juvenile males
Darkened symbols = gravel roads
Open symbols = paved roads

Figure 2.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□ Adult males
△ Juvenile females
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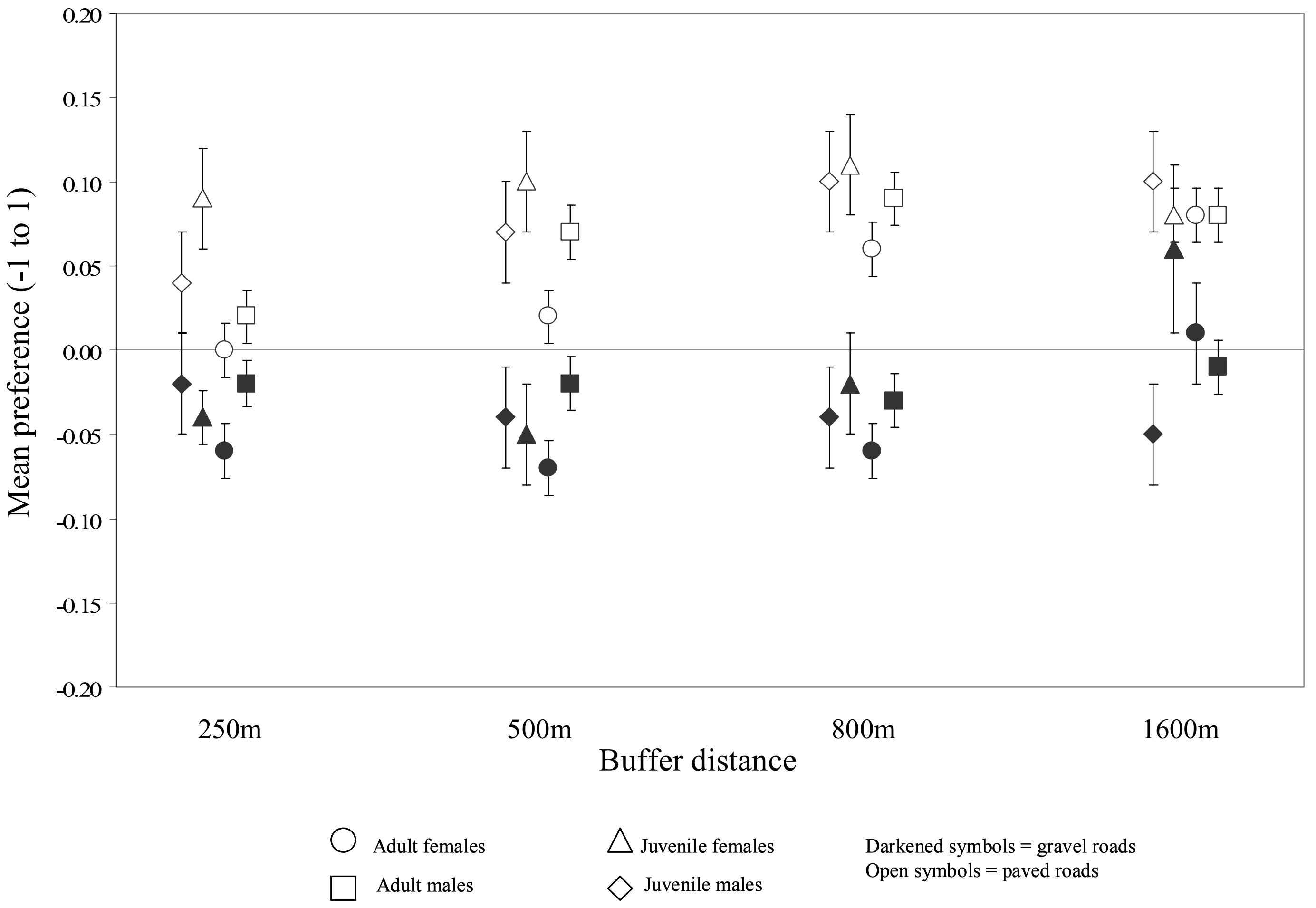
Darkened symbols = gravel roads
Open symbols = paved roads

Figure 3.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Buffer distance
Adult females
Adult males
Juvenile females
Juvenile males
Darkened symbols = gravel roads
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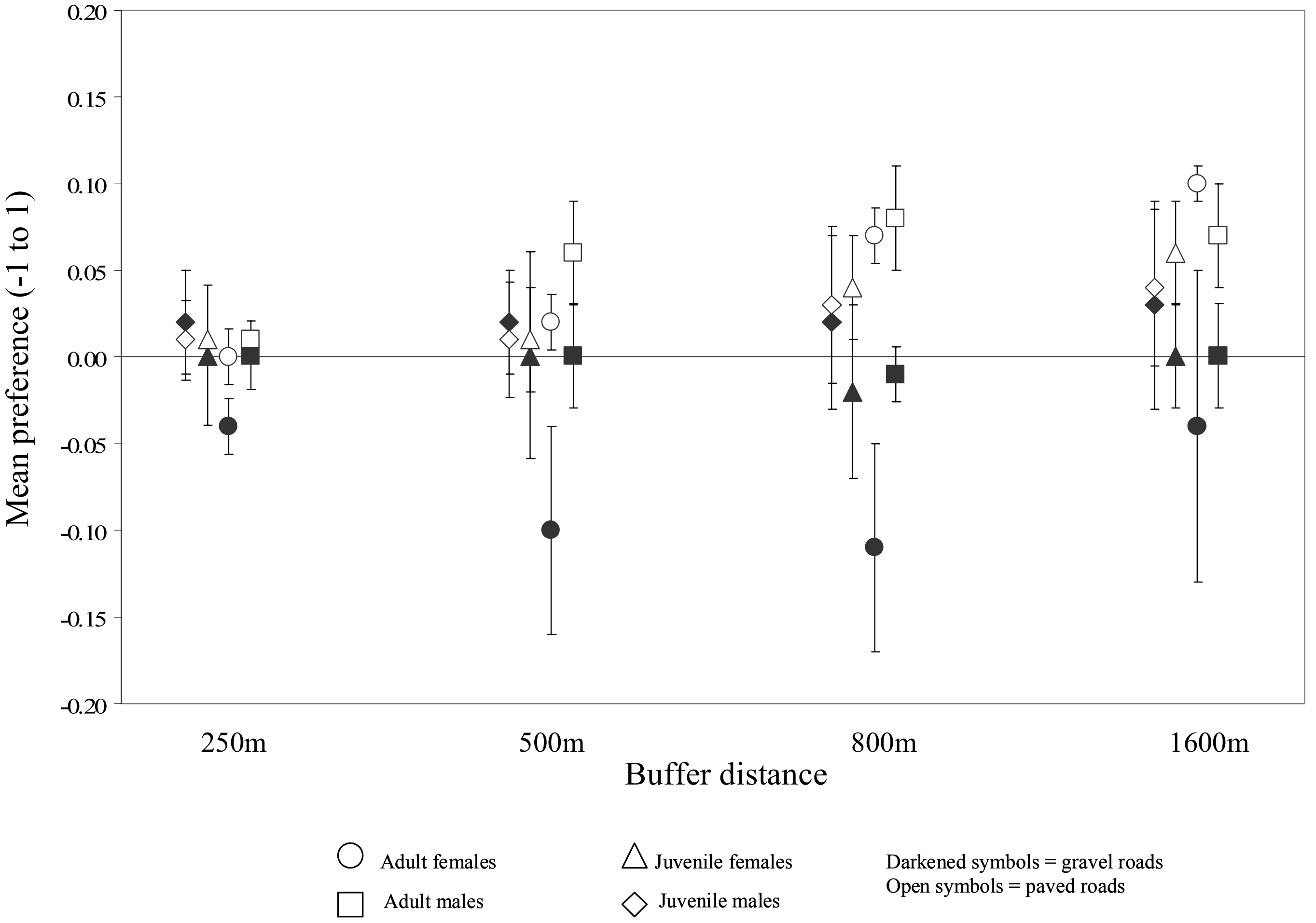
Figure 4.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Buffer distance
Adult females
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Darkened symbols = gravel roads
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CHAPTER 6

HABITAT PREFERENCE FOR ROADS BY BEARS AFFECTS INDIVIDUAL SURVIVAL AND POPULATION SURVIVAL RATE

Abstract: Studies of habitat selection have been central to understanding ecology of wild animals, but inferences from such studies may be biased because habitat use may not be a reliable indicator of habitat quality and differences in behavior may not manifest as differences in fitness. The most reliable and robust way to understand how habitats, resources, and disturbances affect habitat quality is to use direct measures of fitness. We linked estimates of habitat preference for roads by black bears (*Ursus americanus*) with estimates of survival, at both the individual and population levels, to determine whether preference for areas near roads affected bear survival. First, we partitioned bears into those that were known to have been killed and those that survived and then compared habitat preference for areas near paved, gravel, and gated roads between the two survival groups. Second, we used capture-recapture data from 240 bears captured during 1981-2002, and mortality data for bears that were known to have died, to estimate annual survival of bears. We incorporated annual data on habitat preference for areas near paved, gravel, and gated roads as covariates to survival. Whereas previous studies on road use by bears showed bears most avoided paved roads, results from both our approaches showed habitat preference for areas near gravel roads, but not paved roads, affected bear survival negatively. Female bears that were known to have survived avoided areas near gravel roads, whereas females that were known to have died did not. Moreover, annual female survival increased during years when female preference for areas near gravel roads decreased. Our approach can be expanded to include estimates of reproduction and can be generally applied to understand how habitats, resources, and disturbances affect habitat quality for populations of wild animals.

Key words: demography, fitness, habitat quality, roads, Southern Appalachians, survival, *Ursus americanus*

Studies of habitat selection have been central to understanding wildlife ecology (Moorcroft et al. 1999) because they yield inferences about habitat quality, defined as the capacity of an area to provide resources necessary for survival and reproduction relative to the capacities of other areas (Van Horne 1983). Inferences, however, are strong only when methods are scientifically rigorous (Hurlbert 1984; Popper 1962; Platt 1964,) and when assumptions are valid (Ramsey and Schafer 2002). All studies of habitat selection assume optimal foraging theory, which posits animals make choices in ways that optimize the tradeoffs between benefits and costs (Emlen 1966; Charnov 1976; MacAruther and Pianka 1966). Different behaviors are often assumed to reflect differences in fitness (e.g., survival, reproduction, etc.), but this assumption may not be valid (Gould and Lewontin 1979; Pierce and Ollason 1987). Moreover, habitat use may not be a reliable indicator of habitat quality (Garshelis 2000; Morrison 2001;Van Horne 1983). For example, a habitat or resource that is minimally used by a population may actually be most critical to survival or reproduction (Van Horne 1983). The most robust and reliable way to understand how habitats, resources, and disturbances affect habitat quality is to use direct measures of fitness.

Most studies of habitat selection calculate preference indices using a ratio of habitat use and habitat availability (Manly et al. 1993). Traditionally, researchers have estimated mean preference for animal populations, which may mask differences in habitat selection between individuals with high fitness and individuals with low fitness. Exploiting differences in habitat preference, not homogenizing them, is the key to testing whether particular behaviors affect fitness. Numerous studies have evaluated habitat or resource selection by animals with respect to fitness surrogates (e.g., energy gain, foraging time; Belovsky 1978; Helfman and Winkelman 1991; Kacelnik 1984; Suarez and Gass 2002) but we found only 2 studies on habitat or resource selection that used direct measures of animal survival or reproduction (Morris and Davidson 2000; Ritchie 1990).

Another way to evaluate whether animal behaviors affect survival or reproduction is to link estimates of habitat preference by the population with estimates of population demography. Previous demographic studies have linked demographic parameters (e.g., survival, fertility, etc.) with explanatory variables such as lichen cover (Skogland 1985), grass production (Mduma et al. 1999), forest fragmentation (Doherty and Grubb 2002), and edge proximity (Moorman et al. 2002), but these studies assumed the explanatory variable was used (or avoided) by the population when it was available. This assumption may not be valid. An increase in a habitat or resource may help explain increased survival for population *x*, but this correlation is spurious if population *x* does not use that habitat or resource. By linking estimates of habitat preference with estimates of demography, results should be reliable because habitat use (or avoidance) is not assumed.

For this research, we linked estimates of habitat preference with estimates of survival, at both the individual and population levels, to test hypotheses about the effects of paved and gravel roads on habitat quality for a population of black bears in the Pisgah Bear Sanctuary (PBS) in western North Carolina. Roads may affect habitat quality for black bears 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 habitat quality positively by providing travel corridors (Brody and Pelton 1989; Manville 1983; Hellgren et al. 1991; Young and Beecham 1986) or food availability along roadsides (Beringer et al. 1989; Brody 1984; Carr and Pelton 1984; Manville 1983, Hellgren et al. 1991), which could affect bear survival and reproduction positively.

Traffic volume has been hypothesized to explain the behavioral responses of bears to road types. Bears have been shown to avoid areas near roads with high traffic volume (e.g., paved roads; Beringer et al. 1989; Brody 1984; Brody and Pelton 1989; Fescke et al. 2002) and prefer areas near roads with relatively low traffic volume (e.g., gravel or gated roads; Beringer et al. 1989; Brody 1984, Brody and Pelton 1987; Hellgren et al. 1991; Young and Beecham 1986). That black bears have also been shown to avoid roads with relatively low traffic volume (Clark et al. 1993; Garner 1986; Heyden and Meslow 1999; Quigley 1982), however, indicates traffic volume alone is insufficient to explain how roads affect habitat quality for bears.

The way roads affect habitat quality for bears should depend, in part, on the mortality source (or sources) that have the most impact on a bear population (Reynolds and Mitchell, submitted$_1$). For example, if vehicle collision is a primary mortality source for a bear population, then roads with high traffic volume (e.g., paved roads) should have the largest negative effect on habitat quality. Alternatively, if hunting is the primary source of bear mortality, then roads that provide hunter access should have the largest negative effect on habitat quality. If poaching is the 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 primary mortality sources for bears in our study were hunting and poaching. Of the 240 bears in PBS that we tagged during 1981-2001, 5 were reported killed by vehicle collisions, 43 were reported as legal harvests, and 19 were known to be poached or possibly poached (North Carolina Wildlife Resources Commission, unpublished data). 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, personal communication).

Previously, we found that adult females in PBS avoided areas near gravel roads, but not areas near paved roads, during fall (Reynolds and Mitchell submitted$_1$). We hypothesized 2 reasons to explain our findings. Bears could have been avoiding poachers, who likely use gravel roads to access bears because doing so minimizes risk of detection by enforcement officers. Alternatively, bears could have been avoiding non-lethal 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 many of 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. Determining whether bears avoided gravel roads to avoid lethal or non-lethal human contact requires understanding whether road use by bears affects bear survival.

Our first objective was to partition our study animals into bears that were known to have been killed and those that survived and compare habitat preference for areas near paved and gravel roads between the two groups. If use of areas near gravel roads by bears affected bear survival negatively, we predicted preference for areas near gravel roads by bears that were killed would be greater than that by bears not killed. Alternatively, if use of areas near paved roads by bears affected bear survival negatively, we predicted preference for areas near paved roads by bears that were killed would be greater than that by bears not killed. If preference for roads did not differ between killed and bears not killed, this would suggest roads, and the behavioral response of bears to roads, did not affect bear survival.

Our second objective was to link estimates of annual survival of PBS bears with estimates of habitat preference for areas near gravel and paved roads. If bear use of areas near gravel roads imposed a mortality risk to PBS bears, we predicted preference for areas near gravel roads would help explain annual survival and habitat preference would have an inverse relationship with annual survival. If bear use of areas near paved roads imposed a mortality risk to PBS bears, we predicted preference for areas near paved roads would help explain survival and habitat preference would have an inverse relationship with annual survival. If bear response to gravel and paved roads had no effect on bear survival, this would suggest roads, and bear response to roads, had little effect on habitat quality for PBS bears.

MATERIALS AND METHODS

Study area.—We conducted our study in the Pisgah Bear Sanctuary (PBS) in North Carolina (35° 17' N, 82° 47' W) during years 1981-2002. The PBS (235 km^2) was located within the Pisgah National Forest, where topography was mountainous with elevations ranging from 650m to 1800m. The region was considered a temperate rainforest, with annual rainfall approaching 250 cm/yr (Powell et al. 1997).

Roads in PBS included 48.5 km of paved roads, 65.7 km of gravel roads, and 200.3 km of gated roads (Continuous Inventory Stand Condition data base, USDA Forest Service 2001). The Blue Ridge Parkway, administered by the National Park Service, transected the north central portion of PBS, U.S. Highway 276 bounded the western edge of PBS, and State Road 151 (a paved road) ran though a small portion of PBS. Several gravel roads ran through parts of PBS, one of which (Forest road 1206) bisected the Sanctuary. By year 2000, over 80 gated roads ran throughout PBS.

Although bears were legally protected from hunting in all 28 bear sanctuaries in North Carolina, including PBS, bears were killed in and adjacent to bear sanctuaries (Beringer et al. 1989, Brody and Pelton 1989). Other hunting (e.g., deer, turkey, small game) was legal in PBS.

Trapping bears and collecting location data.—We captured bears in PBS from May through mid-August during 1981-2002 (except 1991 and 1992) using Aldrich foot snares modified for safety (Johnson and Pelton 1980) or barrel traps. We immobilized captured bears using a combination of approximately 200 mg Ketamine hydrochloride + 100 mg Xylazine hydrochloride/90kg of body mass (Cook 1984) or Telazol administered with a blow dart or jab stick. We sexed, tattooed, and attached two ear tags to each immobilized bear and extracted a first premolar to determine age. 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 radio transmitter collars (Telonics, Inc. Mesa, Arizona; Sirtrak, Havelock North, New Zealand). All procedures complied with requirements of the Institutional Animal Care and Use Committees for Auburn University (IACUC # 0208-R-2410) and North Carolina State University (IACUC # 88-*** to # 00-018).

From May each year until the bears denned (except 1991 and 1992), we located collared bears using telemetry receivers (Telonics Inc., Mesa, Arizona; Lotek, Newmarket, Ontario; Sirtrak, Havelock North, New Zealand) and a truck-mounted, 8-element yagi antenna. The high elevation of the Blue Ridge Parkway allowed unobstructed line-of-sight with the majority of the study area, reducing the likelihood of signal error due to interference from terrain. Locations were estimated by triangulating compass bearings taken from a minimum of 3 separate locations within 15 minutes (Zimmerman and Powell 1995). Bears were located every 2 hours for 8, 12, or 24 consecutive hours and sampling was repeated every 32 hours to standardize bias from autocorrelation (Swilhart 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 meters. 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 a bear's use of space 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 (Seaman and Powell 1996), and a grid size of 250 meters was used for kernel estimation to match the resolution of our telemetry data. For analyses, home ranges were defined as the area containing 95% of the estimated utility distribution.

We estimated home ranges during fall only because the primary effect of roads on bear habitat in western North Carolina is increased risk of mortality due to hunting and poaching (Brody and Pelton 1989), which should be most pronounced during fall when hunting outside the sanctuary is legal. We defined the fall season as the period between September 1 and the time when bears entered their dens. We did not pool telemetry locations across years to estimate fall home ranges.

Mapping roads.—We mapped the distribution of roads in PBS for each year using a Geographic Information System (GIS; ArcView 3.2 and Spatial Analyst 2.0). We partitioned roads into 3 types (paved, gravel, gated; Brody 1984, Powell et al. 1997) and developed a road map for each road type for each year 1981-2001. Although we were interested in testing the effects of paved and gravel roads, we included gated roads for completeness. Gated roads were defined as gravel roads which were gated during the entire year, where vehicle access was limited to forestry personnel. Information about road type and date of construction were provided by USDA Forest Service at the Pisgah Ranger District, North Carolina.

Based on the literature, the way bears use areas near roads can depend on how close bears are to roads. Carr and Pelton (1984) found bears in the Great Smoky Mountains preferred areas < 200 meters from gravel roads, whereas Quigley (1982) and Clark et al. (1993) found bears avoided areas < 200 meters from roads in the Great Smoky Mountains and bears avoided areas < 240 meters from roads in Arkansas, respectively. Rudis and Tansey (1995) predicted areas < 800 meters 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 meters from non-paved roads. Zimmerman (1992), Powell et al. (1997), and Mitchell et al. (2002) predicted areas < 1600 meters from roads, especially paved roads, would affect habitat quality negatively for bears in western North Carolina. Using a GIS, we placed 4 vector buffers (i.e., 250 meters, 500 meters, 800 meters, and 1600 meters) around each road during each year to test previous results regarding the distance at which roads affected resource selection by bears. We included 500 meter buffers as an intermediate distance between 250 and 800 meters.

Estimating habitat preference.—We estimated habitat preference for each road type (paved, gravel, and gated) at each buffer distance (250m, 500m, 800m, and 1600m) for each individual bear for each fall during years 1981-2001. We mapped each 95%

kernel home range in a GIS and overlaid the road map corresponding to the home range year. For each home range, we indexed preference, *E*, for each road type at each buffer distance using Ivlev's electivity index (1961) modified to make it symmetrical with respect to zero (Powell, personal communication):

$$E_i = \frac{2 * (\text{Use of habitat } i - \text{Availability of habitat } i)}{1 + (\text{Use of habitat } i + \text{Availability of habitat } i)}$$

where E_i is the index of preference for habitat *i*.

We estimated 3rd order selection (Johnson 1980) because we wanted to evaluate bear response to roads within home ranges. Availability of habitat *i* was calculated as the proportion of habitat *i* located within the 95% home range. 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 meter 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 availability of habitat *i* were not included in analyses for 3rd order selection because to do so would bias estimates of electivity. Values of electivity index can range from -1 to +1.

Habitat preference between survival groups.—We classified PBS bears into survival groups using mortality information from the North Carolina Wildlife Resources Commission (NCWRC) and field observations. During 1981-2002, we had mortality information for 79 bears that we tagged, most of which were killed by hunters (33 males, 10 females), poached (2 males, 6 females), or possibly poached (3 males, 8 females).

The remaining 17 mortalities were due to predation by other bears (3 males, 2 females), collisions with automobiles (4 males, 1 female), unknown causes (1 male, 2 females), euthanasia (2 males), or reaction to drugs (1 male, 1 female).

To evaluate behaviors based on survival at the individual level, our sample size of killed bears was limited to those bears that were not only tagged and killed, but also those that were collared and for which we had sufficient telemetry data (20+ locations) during the falls in which the bears were killed. Mean preference did not differ among hunted, poached, or possibly poached bears for males or females, so we combined these bears into one killed group by gender to increase sample size. To test if bear response to roads affected individual survival, we modeled habitat preference for areas near roads by sex using survival group (i.e., killed versus not killed), road type, and buffer distance as predictor variables (Proc GLM; SAS Institute 2000). We considered the intercept-only model to be the null model. We controlled for sex because female bears in PBS used areas near roads differently than did males (Reynolds and Mitchell, submitted$_1$). We used Akaike's Information Criterion (AIC; Akaike 1973; Anderson et al. 1994) with an adjustment for small sample bias to rank models in terms of their ability to explain the data.

Modeling population survival rate.—We created encounter histories for each bear captured during 1981-2002 and used logistic regression and the joint capture-recapture and tag mortality parameterization (Barker 1997) in Program MARK (White and Burnham 1999) to estimate apparent survival (the probability that the animal is alive and remains on the study area and hence is available for recapture, ϕ) and recapture probability (*p*) for the male population and for the female population. We combined capture-recapture data with mortality data to increase the precision of survival estimates (Barker 1997). We partitioned survival estimates by sex because we wanted to link estimates of survival probability with estimates of resource selection, which differed by sex.

Using methods to incorporate covariates into estimates of demographic parameters described by Franklin et al. (2000), we incorporated estimates of habitat preference for areas near paved, gravel, and gated roads as covariates to survival. For each fall, we estimated mean preference for each buffer distance for each road type by sex. We standardized all covariates, by subtracting the mean and dividing by the standard deviation, so effects among covariates would be relative. We then added each covariate separately to a base model that held survival constant over all years (Cooch and White 2002). We considered the base model to be the null model because it included no effects of covariates. To our knowledge, this is the first study to link estimates of habitat preference (i.e., calculated using a ratio of habitat use and habitat availability) with estimates of population demography for any animal population.

Based on our definition of survival, we used a time lag when we incorporated covariates of habitat selection. Survival was defined as the probability of surviving from year t to year t +1, so any effect of road use on survival at time t should be measurable at time $t + 1$. This explains why we used capture-recapture data collected during years 1981-2002 to estimate survival, whereas we used habitat selection for years 1981-2001.

To understand if bear use of roads affected bear survival, we used AIC with an adjustment for small sample bias to rank the models in terms of their ability to explain the data. Models with ΔAIC_c value < 2.0 have substantial support when models are nested (Burnham and Anderson 2002). When these conditions do not exist, as with our data, Burnham and Anderson (2002) recommend using a higher cutoff value so we considered models with ΔAICc values < 4.0 to have substantial support. We evaluated Akaike weights and slope estimates for each model. Model weights provide strength of evidence for model selection, whereas slope estimates reveal the magnitude of the relationship between a model variable and the demographic estimate. We did not test goodness of fit because no means of testing model fit currently exist for models developed using Barker's parameterization (Cooch and White 2002).

RESULTS

During 1981-2002, we captured 101 female bears 194 times and 139 male bears 199 times in Pisgah Bear Sanctuary (PBS). We collected sufficient location data to estimate 66 fall home ranges for females (45 adults and 21 juveniles) and 52 fall home ranges for males (32 adults and 20 juveniles).

Habitat preference by survival groups.—We estimated 9 fall home ranges for hunted females, 10 for poached females, 7 for females that were possibly poached, and 38 for females that were never reported dead. The top ranked model for habitat preference for areas near roads by females included road type, survival group, and buffer distance. Females that were not killed avoided areas within 500 meters (95% CI for mean preference = -0.11, -0.03), within 800 meters (95% CI for mean preference = -0.14, -0.06), and within 1600 meters (95% CI for mean preference = -0.14, -0.06) of gravel roads, but killed females did not (95% CIs for mean preference contained zero or mean preference was positive; Table 1). Females that were not killed preferred areas within

500 and 800 meters of paved roads but females that were killed did not (Table 1). Killed females and females that were not killed neither preferred nor avoided areas near gated roads.

We estimated 18 fall home ranges for hunted males, 3 for possibly poached males, and 25 for males that were not killed. The top ranked model for habitat preference for areas near roads by males was the null model.

Population survival rate.—We used 240 capture histories and mortality information on 79 bears to estimate annual survival. To estimate covariates of habitat preference, we used 118 fall home ranges. For the female population of PBS bears, five models had Δ AIC$_c$ values < 4.0, suggesting all had substantial support. The top ranked models included preference for areas within 250 and 800 meters of paved roads and preference for areas within 500, 800, and 1600 meters of gravel roads (Table 2). The null model and all models including covariates of gated roads had Δ AIC$_c$ values > 4.0, indicating these models had little support. As strength of evidence for model selection, the AIC$_c$ weight for the top model was 0.49 and that for the second ranked model was 0.15, suggesting the top model was only 3.2 times more likely to be selected over the second ranked model, which was not sufficient to differentiate among models (Burnham and Anderson 2002).

Of the top models for female survival (i.e., models with Δ AIC$_c$ values < 4.0), slope estimates for models with covariates of paved roads differed qualitatively from slope estimates for models with covariates of gravel roads. Both models that incorporated preference for areas near paved roads had positive slope estimates, whereas all three models that incorporated preference for areas near gravel roads had negative slope estimates (Table 3). For models with covariates of gravel roads, slope estimates increased as buffer distance decreased (Table 3). Zero was not included in the 95% confidence interval for any slope estimate for the top five models.

For the male population of PBS bears, the null model ranked highest (Table 4). Although all models had Δ AIC_c values < 4.0, all models had zero within the 95% confidence interval for slope estimates (Table 5).

DISCUSSION

Inferences from studies of habitat selection that do not use direct measures of fitness may be biased, thereby biasing our understanding of what habitat quality means for wild animals. 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). By linking estimates of habitat preference with estimates of animal survival or reproduction, inferences about the way resources, habitats, and disturbances affect habitat quality should be relatively reliable.

For our study, we linked estimates of habitat preference for roads by black bears with measures of bear survival to understand how roads affected habitat quality for bears. Although numerous studies have evaluated behavioral response of black bears to roads (Beringer et al. 1989; Brody 1984; Brody and Pelton 1989; Clark et al. 1993; Hellgren et al. 1991; Heyden and Meslow 1999; Pelton 1986; Unsworth et al. 1989; Young and Beecham 1986), none have tested whether the behaviors affected bear survival.

Using measures of survival at the individual level, we found bear preference for areas near gravel roads affected habitat quality negatively for females in Pisgah Bear Sanctuary (PBS). Females that were not killed avoided areas within 500-1600 meters of gravel roads (95% CIs for mean preference did not include zero), but killed females did not (95% CIs for mean preference included zero or mean preference was positive). Moreover, females that were not killed avoided areas within 1600 meters of gravel roads more than did killed females (Table 1). Age class (i.e., adults versus juveniles) did not confound our findings because the proportion of killed females that were adult (73%) was similar to the proportion of females not killed that were adult (71%).

Our demographic results regarding gravel roads and the female population (Table 2) corroborated our findings based on individual measures of survival (Table 1). Annual variability in preference for areas near gravel roads helped explain survival probability (Table 2) and the relationship was negative (Table 3). Survival probability decreased during years when female preference for areas near gravel roads increased. The magnitude of the relationship between survival of the female population and avoidance of gravel roads varied with distance to gravel roads. As distance to gravel roads increased, slope estimates decreased (Table 3), indicating the negative effects of gravel roads on bear survival diminished the further bears were from gravel roads.

In strong contrast, we found paved roads did not affect habitat quality negatively for PBS females. Preference for areas within 250-800 meters of paved roads differed between killed females and females not killed (Table 1), but not the way they should have if paved roads exacted a negative selective pressure on bear survival. Killed females avoided areas near paved roads more than did females that were not killed. Similarly, our demographic results regarding paved roads and the female population (Table 2) showed preference for areas within 250 and 800 meters of paved roads helped explain survival probability, but the relationships were positive (Table 3). Survival probability increased as female preference for areas near paved roads increased. If paved roads exerted a negative pressure on bear survival, survival should have varied inversely with preference.

We graphed the relationships between survival probability and mean preference for areas within 500, 800, and 1600 meters of gravel roads (Fig. 1). Preference within all three buffer distances had an inverse relationship with survival probability, but preference for areas within 800 meters may have had the strongest relationship with survival probability because it had the steepest slope. This helped explain why the model that incorporated preference for areas within 800 meters of gravel roads ranked higher than all other models with covariates of gravel roads (Table 2) even though slope was highest for preference within 500 meters of gravel roads (Table 3). Interpretation of the y-axes showed survival probability was 0.67 when females used areas within 500 and 800 meters of gravel roads randomly (i.e. when mean preference = 0, which means females neither preferred nor avoided these areas). Survival probability was higher (0.77) when females used areas within 1600 meters of gravel roads randomly. The negative effect of random behavior on survival, with respect to preference for areas near gravel roads, was more pronounced when females were closer to gravel roads.

Overall, our results showed females avoided areas near gravel roads and the behavioral response to gravel roads had survival consequences. Two reasons might explain our findings. One, bears may have avoided areas near gravel roads to avoid poachers. Although bears were legally protected in PBS, poaching occurred in bear sanctuaries in North Carolina (Beringer et al. 1989; Brody and Pelton 1989). Moreover, legal bear hunting in North Carolina was usually done with the aid of hounds (Collins 1983), which were often released into bear sanctuaries (Beringer et al. 1989). In addition, some hunters used illegal bait piles to lure bears out of sanctuaries so they could be hunted along sanctuary perimeters (Beringer et al. 1989). Poachers in PBS likely use gravel roads to access bears because doing so lowers their risk of detection by enforcement officers or other drivers who may report them to enforcement officers. Therefore, bears who avoid areas near gravel roads may decrease their risk of mortality due to poaching.

Alternatively, our results could indicate that bears avoided gravel roads inside PBS because this behavior, when practiced while traveling outside the PBS, decreases mortality risk due to hunting. Most of the female home ranges we used in our analysis were contained completely within PBS. Even so, some females may have used areas outside PBS. That 10 females we tagged in PBS during 1981-2002 were reported legally hunted (NCWR, unpublished data) indicates some PBS females probably traveled outside PBS. Fifty percent and 73% of black bears that were legally harvested in North Carolina were killed within 800 meters and 1600 meters of roads that provide four-wheel-drive access, respectively (Collins 1983). Assuming the behavioral response of bears to roads outside the PBS was similar to that inside the PBS, morality risk should be relatively low for bears who avoid areas within 800 meters and within 1600 meters of gravel roads.

Our finding that paved roads had a positive effect on habitat quality for PBS females was surprising, but plausible. Assuming the primary mortality risk associated with paved roads was vehicle collision, bears could have learned to use areas very near paved roads without crossing them, thus avoiding any negative effect on survival. For example, bears in PBS often use the tops of road tunnels to cross the Blue Ridge Parkway (MJR, unpublished data). Importantly, our results regarding the positive effect of paved roads on habitat quality could be misleading if estimates of preference for paved roads reflected primarily avoidance of gravel roads. Though not mutually exclusive, most areas near paved roads represented areas away from gravel roads. As such, preference for areas near paved roads may not have reflected a positive effect of paved roads as much as they reflected a negative effect of gravel roads.

Alternatively, our results could indicate that bears are relatively likely to use areas where human disturbance is predictable (Linnell et al. 2000). In PBS, the primary paved road is the Blue Ridge Parkway (BRP), which provides leisurely motoring opportunities for tourists. On average, motorists who are sight-seeing along the BRP rarely wander more than a few meters from their vehicles. Therefore, human use of paved roads in PBS is predictably high and human use of areas near paved roads is predictably low. Alternatively, gravel roads in PBS are used not only as scenic byways but also for accessing hiking and biking trails, camp sites, and hunting or poaching sites. A motorist driving along a gravel road in PBS might stop at a trailhead, a camp site, a hunting site, or it might not stop at all. Therefore, human use of gravel roads, and areas near gravel roads, is relatively unpredictable.

Gated roads did not affect habitat quality negatively for PBS females. We found no differences in preference for areas near gated roads between survival groups (Table 1) and models that included covariates of gated roads ranked very low (Table 2). In forests managed by the USDA Forest Service, such as Pisgah National Forest in which PBS is located, access roads are built to reach forest stands for timber harvesting. After trees are harvested, many access roads are gated. Results from this study indicate gating roads was an effective strategy for minimizing potential negative effects of roads on habitat quality.

Unlike female survival, male survival was relatively unaffected by road use. The null model ranked highest for analyses based on the individual level and for analyses based on the population level (Table 4). Although all models of survival had substantial support, slope estimates for covariates of all models included zero within the 95% confidence interval (Table 5).

Demographic results for males could have been biased because we estimated apparent survival, which did not account for immigration or emigration. We assumed that our population was closed, which should have been valid for females who are typically philopatric (Elowe and Dodge 1989; Powell et al. 1997; Schwartz and Franzmann 1992). This assumption may not have been valid for males, which typically travel widely when dispersing (Garshelis and Pelton 1981; Rogers 1987).

We could not compare our results with those from previous studies on black bears, because none have linked estimates of road use with estimates of survival. A recent study on grizzly bears (*Ursus arctos*) in Canada modeled the spatial distribution of human-caused bear mortalities and found harvested bears were killed close to water, roads, and edge features (Nielsen et al. 2004). Though they did not evaluate habitat selection by grizzly bears by considering habitat use relative to habitat availability, their results indicate grizzly bears that avoid areas near roads should have a fitness advantage.

CONCLUSION

By linking estimates of habitat preference for roads with estimates of bear survival, we found that female bears avoided areas near gravel roads and the behavioral response of bears to roads had survival consequences. Bears that were known to have survived avoided areas near gravel roads whereas bears that were known to have died did not. At the population level, annual female survival increased during years when females avoided areas near gravel roads. These results indicate that gravel roads had a negative effect on habitat quality for black bears in PBS. To our knowledge, this is the first study to link estimates of habitat preference (i.e., calculated using a ratio of habitat use and habitat availability) with estimates of population demography for any animal population.

The approach we used provides a relatively rigorous method for understanding how habitats and disturbances affect habitat quality for wild animals. We evaluated multiple competing hypotheses (Chamberlain 1897), which should provide strong inference (Platt 1964). Our estimates of survival were informed by recapture probabilities as well as mortality data, both of which can substantially increase precision of parameter estimates (Barker 1997; Cooch and White 2002). We used an information theoretic approach (e.g., AIC) to evaluate competing *a priori* hypotheses, including the hypothesis of no effect. Our study on black bears included only estimates of survival because we *a priori* hypothesized roads would affect bear survival, but our methods can be expanded to include estimates of other fitness measures (e.g., fertility, population growth rate, etc.) for other studies.

Information about how roads, and other disturbances, affect habitat quality for bears may be key to effective conservation and management, a common goal of which is to manage population growth by manipulating habitat. For example, timber harvesting is often considered a management tool for maintaining bear habitat in the southern Appalachian Mountains because availability of soft mast, a food important to bear fitness (Elowe & Dodge 1989; Reynolds et al. submitted$_2$; Rogers 1976, 1987) can be relatively high in recently harvested stands (Noyce and Coy 1990; Perry et al. 1999; Reynolds et al.

submitted$_1$). Harvested stands, however, are usually spatially associated with gravel roads. If bears avoid areas near gravel roads, as our data suggest, then bear foods in harvested stands may be relatively inaccessible to bears. Strategies to increase bear habitat by using timber harvesting, therefore, must consider not only how bear foods will be affected but also how roads will affect food accessibility.

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Table 1. Mean preference (with 95% confidence intervals) for areas near roads during fall for females bears that were killed and female bears that were not killed in Pisgah Bear Sanctuary, North Carolina 1981-2001.

Road Type	Buffer	Killed Preference	Not Killed Preference
Paved	250 m	-0.04 (-0.08, 0.00)	0.02 (-0.02, 0.06)
	500 m	-0.02 (-0.06, 0.02)	0.05 (0.01, 0.09)
	800 m	0.03 (-0.01, 0.07)	0.08 (0.04, 0.12)
	1600 m	0.08 (0.04, 0.12)	0.09 (0.05, 0.13)
	n	26	38
Gravel	250 m	-0.01 (-0.03, 0.05)	-0.04 (-0.08, 0.00)
	500 m	-0.05 (-0.11, 0.01)	-0.07 (-0.11, -0.03)
	800 m	-0.04 (-0.10, 0.02)	-0.10 (-0.14, -0.06)
	1600 m	0.09 (0.07, 0.11)	-0.10 (-0.14, -0.06)
	n	15	26
Gated	250 m	0.00 (-0.04, 0.04)	0.00 (-0.04, 0.04)
	500 m	0.00 (-0.04, 0.04)	0.03 (-0.01, 0.07)
	800 m	0.02 (-0.04, 0.08)	0.04 (0.00, 0.08)
	1600 m	0.02 (-0.04, 0.08)	0.01 (-0.03, 0.05)
	n	16	36

Table 2. Ranking of models of apparent survival, each with different covariates of preference for areas near roads, for female black bears in Pisgah Bear Sanctuary, North Carolina, during 1981-2002.

Model	AICc	Δ AICc	AICc Weight	Model Likelihood	Deviance
Preference within 800m paved roads	563.31	0.00	0.49	1.00	276.41
Preference within 800m gravel roads	565.70	2.39	0.15	0.30	278.80
Preference within 250m paved roads	565.93	2.63	0.13	0.27	279.04
Preference within 1600m gravel roads	565.97	2.66	0.13	0.26	279.07
Preference within 500m gravel roads	567.03	3.72	0.08	0.16	280.13
Null	572.28	8.97	0.01	0.01	288.28
Preference within 250m gravel roads	572.48	9.17	0.00	0.01	285.58
Preference within 500m gated roads	572.73	9.42	0.00	0.01	285.83
Preference within 1600m paved roads	573.20	9.89	0.00	0.01	286.30
Preference within 250m gated roads	573.60	10.29	0.00	0.01	286.70
Preference within 1600m gated roads	574.16	10.86	0.00	0.00	287.26
Preference within 500m paved roads	574.65	11.34	0.00	0.00	287.75
Preference within 800m gated roads	575.16	11.86	0.00	0.00	288.27

Table 3. Estimates of slope (with 95% confidence intervals) for top 5 models of apparent survival, in order of rank, for female black bears in Pisgah Black Bear Sanctuary, North Carolina, during 1981-2002.

Model[a]	Slope	SE	Slope LCL	Slope UCL
Preference within 800m paved roads	0.92	0.28	0.37	1.48
Preference within 800m gravel roads	-0.81	0.27	-1.36	-0.27
Preference within 250m paved roads	1.03	0.38	0.28	1.78
Preference within 1600m gravel roads	-0.71	0.24	-1.18	-0.24
Preference within 500m gravel roads	-1.02	0.46	-1.93	-0.11

[a] Only models with Δ $AIC_c < 4.0$ are shown

Table 4. Ranking of models of apparent survival, each with different covariates of preference for areas near roads, for male black bears in Pisgah Bear Sanctuary, North Carolina, during 1981-2002.

Model	AICc	Δ AICc	AICc Weight	Model Likelihood	Deviance
Null	630.36	0.00	0.19	1.00	245.72
Preference within 1600m gravel roads	631.33	0.97	0.12	0.62	243.98
Preference within 800m gravel roads	631.60	1.24	0.10	0.54	244.25
Preference within 500m gravel roads	631.98	1.62	0.09	0.44	244.62
Preference within 1600m gated roads	632.19	1.83	0.08	0.40	244.84
Preference within 250m gravel roads	632.49	2.13	0.07	0.34	245.13
Preference within 800m gated roads	632.74	2.39	0.06	0.30	245.39
Preference within 250m gated roads	632.83	2.48	0.06	0.29	245.48
Preference within 800m paved roads	632.91	2.55	0.05	0.28	245.55
Preference within 250m paved roads	632.95	2.59	0.05	0.27	245.60
Preference within 1600m paved roads	632.98	2.63	0.05	0.27	245.63
Preference within 500m paved roads	633.39	3.04	0.04	0.22	246.04
Preference within 500m gated roads	633.41	3.05	0.04	0.22	246.06

Table 5. Estimates of slope (with 95% confidence intervals) for models of apparent survival, in order of rank, for male black bears in Pisgah Black Bear Sanctuary, North Carolina, during 1981-2002.

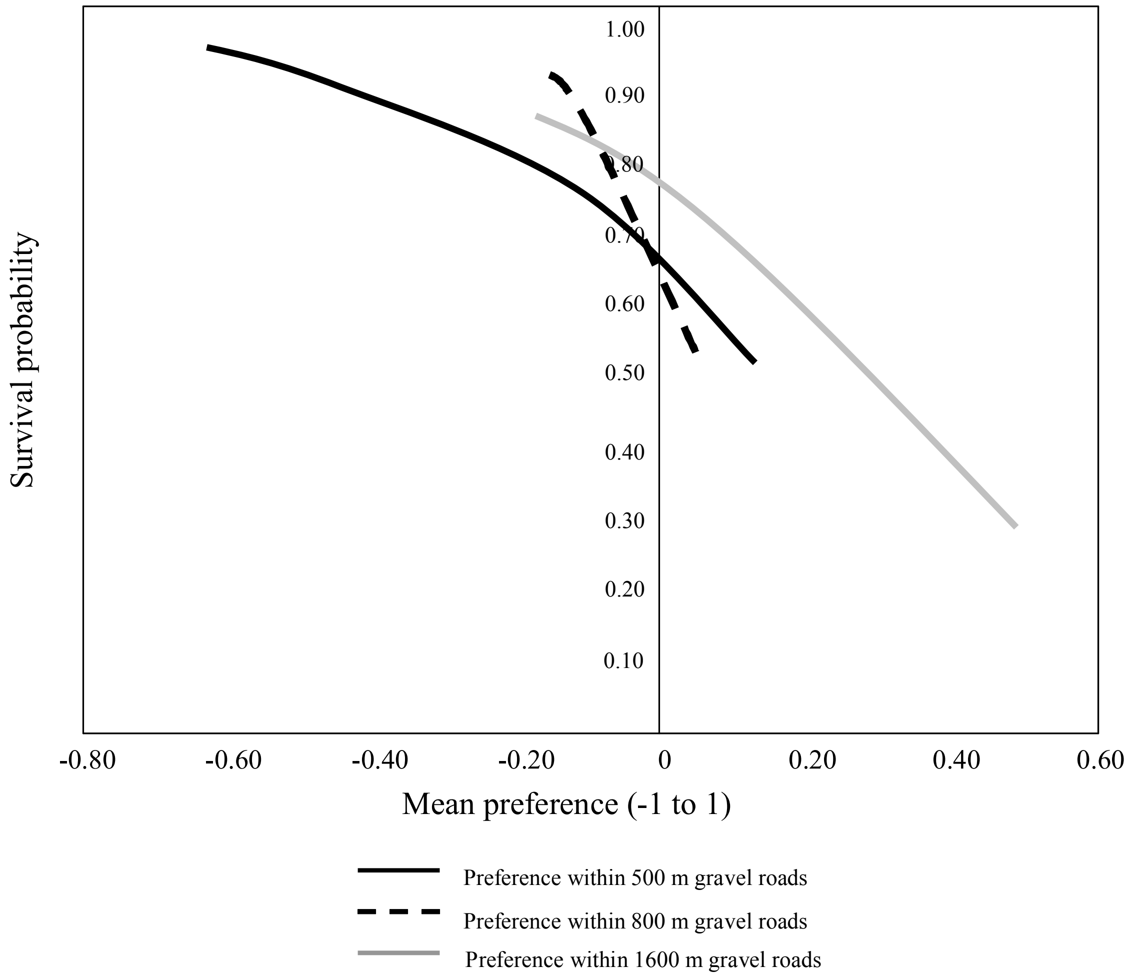
Model[a]	Slope	SE	Slope LCL	Slope UCL
Null	NA	NA	NA	NA
Preference within 1600m gravel roads	0.30	0.23	-0.15	0.76
Preference within 800m gravel roads	0.31	0.26	-0.20	0.82
Preference within 500m gravel roads	0.26	0.25	-0.23	0.75
Preference within 1600m gated roads	0.24	0.21	-0.17	0.65
Preference within 250m gravel roads	0.18	0.24	-0.29	0.65
Preference within 800m gated roads	0.13	0.22	-0.31	0.57
Preference within 250m gated roads	-0.18	0.23	-0.63	0.27
Preference within 800m paved roads	-0.10	0.26	-0.61	0.4
Preference within 250m paved roads	0.08	0.24	-0.38	0.55
Preference within 1600m paved roads	-0.07	0.25	-0.57	0.42
Preference within 500m paved roads	-0.06	0.24	-0.54	0.42
Preference within 500m gated roads	-0.05	0.23	-0.51	0.41

[a] All models had Δ AIC$_c < 4.0$

Figure Caption

Figure 1. Relationship between survival probability and mean preference (unstandardized) for areas within 500, 800, and 1600 meters of gravel roads for the female population of black bears in Pisgah Bear Sanctuary, North Carolina, during 1981-2002.

Figure 1.


Survival probability
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
-0.80
-0.60
-0.40
-0.20
0
0.20
0.40
0.60
Mean preference (-1 to 1)
Preference within 500 m gravel roads
Preference within 800 m gravel roads
Preference within 1600 m gravel roads

CHAPTER 7

SYNTHESIZING DEMOGRAPHIC AND BEHAVIORAL RESULTS WITHIN THE FRAMEWORK OF HIERARCHY THEORY

To understand the overall effect of forest management on habitat quality for PBS bears, we invoked hierarchy theory (Allen and Starr 1982; King 1997; O'Neill et al. 1986) to synthesize our demographic and behavioral results. Hierarchy theory is a framework of system organization whereby ecological processes are understood in terms of both lower-level mechanisms and higher-level constraints. The framework comprises a triadic structure such that the focal level (L) includes the ecological process of interest, the L-1 level includes lower-level mechanisms, defined by faster process rates and stronger interactions than those seen at L, and the L+1 level includes the higher-level constraints, defined by slower process rates and interactions that constrain those seen at L (Fig. 1). Each level, and each holon (i.e., strongly interacting processes: Allen and Starr 1982) within levels, is demarcated by differences in rate structure.

Hierarchy theory provides a framework for objectively defining levels of explanation (O'Neill and King 1998). It is important to note that traditional notions of biological hierarchy (i.e., community, population, individual, organs, tissues, cells, etc.)

may not be relevant to a study and could actually be inappropriate for understanding ecological systems with hierarchical levels defined by rate structures (King 1997).

DEFINING HIERARCHICAL ORGANIZATION FOR BLACK BEARS

For our study, we defined habitat quality in terms of survival and reproduction. Because female black bears rarely disperse (Elowe and Dodge 1989; Powell et al. 1997), our estimates of recruitment in Chapter 3 represented primarily fertility, defined in this chapter as the number of female cubs per female added to the population that survived to be old enough for capture (Pradel 1996). Survival and fertility are each probably hierarchically organized, but the temporal resolution at which each vital rate is manifested for bears likely differs.

Survival hierarchy.—To understand how clearcuts and roads affect habitat quality for bears in our study area by understanding the effect on bear survival, one can visualize a realistic hierarchy for bear survival as follows:

Phylogeny	L + 1
Annual survival rate	L
Daily survival	L-1
Daily energy intake	L-2
Daily avoidance of mortality factors	L-2
Foraging efficiency	L-3

If we take annual survival to be the focal level (L), then it is constrained by phylogeny (L+1), which occurs slowly over evolutionary time. Bear survival is a day by day, minute by minute process, however, so annual survival is explained by daily survival, which is intimately linked with daily energy intake and daily avoidance of mortality factors (e.g., predators, hunters, and automobile collisions). Hence, daily energy intake and daily avoidance of mortality factors can be visualized to occur at the L-2 level, and, foraging efficiency at the L-3 level.

Fertility hierarchy.—Alternatively, annual fertility for bears in our study area may be hierarchically organized as follows:

Phylogeny	L +1
Annual fertility rate	L
Energy intake	L-1
Foraging efficiency	L-2

Annual fertility rate is constrained by phylogeny (L+1). Unlike bear survival, bear fertility is not a day by day occurrence. If females do not acquire sufficient stores of energy during the year, they will abort their fetuses. Therefore, daily energy intake affects annual fertility, but only as a cumulative effect. Therefore, unlike the day-by-day processes that best explain annual survival for bears, annual fertility is most strongly linked with average energy intake over a year. Average energy intake is explained by foraging efficiency.

COMBINING DEMOGRAPHIC AND BEHAVIORAL RESULTS

Results from our demographic analyses on PBS bears showed availability of 2-9 year old clearcuts affected annual fertility positively but had relatively little effect on annual survival or population growth (Chapter 3). The null model ranked high for survival (Chapter 3), indicating something other than foods may have affected bear survival. Habitat preference for areas near gravel roads affected annual survival of PBS females negatively (Chapter 6). During years when females avoided areas near gravel roads, annual survival increased.

Results from our behavioral analyses on PBS bears showed adult females preferred 2-9 year old clearcuts for 3rd order selection (i.e., resource selection within home ranges; Johnson 1980) but not for 2nd order selection (i.e., home range selection) during summer (Chapter 4). All bears avoided areas near gravel roads for 2nd order selection during both summer and fall (Chatper 5) and adult females avoided areas near gravel roads for 3rd order selection during both summer and fall (Chapter 5).

We also found that availability of 2-9 year old clearcuts in home ranges of reproductively successful females was more clustered compared to that in home ranges of reproductively unsuccessful females (MJR, unpublished data). Foraging effort is minimized and energy accumulation can be maximized when foods are relatively clustered (Stephens and Krebs 1986) so the spatial pattern of 2-9 year old clearcuts (in which soft mast was highly available) may affect bear fitness. Our results indicated that the spatial arrangement of young clearcuts may have been important to bear reproduction, but our sample size was small (n = 10) so conclusions should be viewed with caution.

We also partitioned the female population into survival groups (i.e., bears that survived and bears that died) and compared habitat preference for areas near paved, gravel, and gated roads (Chapter 6), as well as habitat preference for 2-9 year old clearcuts, between the two survival groups (MJR, unpublished data). We found females that were known to have survived avoided areas near gravel roads in fall but females that died did not (Chapter 6). Conversely, preference for 2-9 year old clearcuts during summer did not differ between the two survival groups (MJR, unpublished data). Finally, habitat preference for areas near roads did not differ between females that were reproductively successful and females that were reproductively unsuccessful (MJR, unpublished data).

Survival and roads.—We found gravel roads affected annual survival, but not annual fertility. Gravel roads affected annual survival negatively (Chapter 6) at the L-2 level by affecting daily avoidance of mortality factors (i.e., hunters, poachers, and vehicle collisions). In addition, females that were known to have survived avoided areas near gravel roads whereas females that died did not (Chapter 6). We envision the hierarchy for bear survival as follows:

Phylogeny	L + 1
Annual survival rate	L
Daily survival	L-1
Daily energy intake	L-2
Daily avoidance of mortality factors	L-2 (gravel roads)
Foraging efficiency	L-3

Fertility and clearcuts.—We found availability of 2-9 year old clearcuts predicted annual fertility, but not annual survival. Availability of 2-9 year old clearcuts affected annual fertility positively (Chapter 3) at the L-1 level by affecting energy intake. In addition, adult females preferred 2-9 year old clearcuts when selecting resources in summer home ranges (Chapter 4). Moreover, the spatial arrangement of clearcuts may have been effective, so 2-9 year old clearcuts may also have affected annual fertility by influencing foraging efficiency at the L-2 level. We envision the hierarchy for bear fertility as follows:

Phylogeny	L+1
Annual fertility rate	L
Energy intake	L-1 (availability of young clearcuts)
Foraging efficiency	L-2 (spatial arrangement of young clearcuts)

Using hierarchical organization to interpret effects of forest management.— Overall, the availability of 2-9 year old clearcuts affected annual fertility positively at L-1 and the L-2 levels while gravel roads affected annual survival negatively at the L-2 level. According to hierarchy theory, higher levels have a relatively large effect on the focal level. Therefore, positive effects of clearcuts on annual fertility at L-1 level appear to be larger than the negative effects of gravel roads on annual survival at L-2 level.

Individual vital rates (i.e., survival and fertility), however, may not contribute equally to population growth rate (λ) so the overall effect of clearcuts and roads on habitat quality for a bear population may also depend on which vital rate contributes most to changes in λ. For black bears, a long lived species with low reproductive potential, adult survival is the vital rate with the largest potential to contribute to future changes in λ (Brongo 2004; Freedman 2003; Hebblewhite et al. 2003). Therefore, the negative effects of gravel roads on bear survival may outweigh the positive effects of 2-9 year old clearcuts on bear fertility.

CONCLUSIONS

Our results showed the relationship between forest management and habitat quality for black bears in the Southern Appalachians is complex, involving tradeoffs. On one hand, clearcuts can have a positive effect on habitat quality for bears because availability of soft mast (a limiting resource for PBS bears; Chapter 3) can increase, at least for ~7 years (Chapter 2). Bears preferred young clearcuts when selecting resources within summer home ranges (Chapter 4) and availability of young clearcuts affected bear recruitment positively (Chapter 3). On the other hand, clearcuts can have a negative effect because they eliminate availability of hard mast (a limiting resource for PBS bears; Chapter 3) for 25-50 years, the time required for regenerating hardwoods to reach reproductive age in the Southern Appalachians (Burns & Honkala 1990). In addition, clearcuts are spatially associated with gravel roads, which had a negative effect on habitat quality for PBS bears. All PBS bears for 2nd order selection, and adult females for 3rd order selection, avoided areas near gravel roads during summer and fall (Chapter 5). Moreover, habitat preference for areas near gravel roads had negative survival consequences for females (Chapter 6).

Clearcuts cannot exist without gravel roads. Therefore, managers who use clearcuts as a tool to improve bear habitat must consider not only the tradeoffs associated with increased soft mast and decreased hard mast, but also the negative effects of gravel roads on habitat quality. Based on our behavioral and demographic results, the changes in bear habitat due to clearcuts at the stand level (i.e. increased soft mast within clearcuts) may not have been as important as changes due to clearcuts at the landscape level (i.e., increased availability of roads or increased human use of existing roads).

Behaviorally, females preferred young clearcuts when selecting resources within home ranges (i.e., 3rd order selection), but not when establishing home ranges (i.e., 2nd order selection; Chapter 4). Because summer foods were highly available in young clearcuts, yet bears did not prefer young clearcuts for 2nd order selection, indicates something other than foods inside young clearcuts probably influenced 2nd order selection. Minimizing mortality risk, for example, may be more important than maximizing foraging efficiency when bears establish home ranges. That females in PBS avoided areas near gravel roads when establishing home ranges during summer and fall (Chapter 5) indicates road avoidance may have affected 2nd order selection by bears. According to hierarchy theory, avoidance of gravel roads for 2nd order selection may have constrained preference for young clearcuts for 3rd order selection. If so, then the fertility hierarchy we envisioned for PBS bears may be better represented as follows:

Phylogeny	L+1
Annual fertility rate	L
Energy intake	L-1 (availability of young clearcuts) (gravel roads)
Foraging efficiency	L-2 (spatial arrangement of young clearcuts)

Demographically, the availability of young clearcuts affected bear recruitment, but not survival. Habitat preference for areas near gravel roads, however, affected bear survival negatively. Based on life history of bears, the negative effects of gravel roads on bear survival likely outweighed the positive effects of young clearcuts on bear recruitment. This hypothesis is further supported by the fact that availability of young clearcuts alone did not predict population growth (Chapter 3) and bears did not prefer young clearcuts for 2nd order selection (Chapter 4).

CONSERVATION IMPLICATIONS

Strategies which use clearcuts to increase summer foods for bears, but which do not mediate the negative effect of gravel roads on bear behavior and demography, will not necessarily result in increased habitat quality for bears. Our results indicated that gating roads was an effective strategy for minimizing the negative effects of gravel roads on habitat quality for bears. Bears in PBS did not avoid areas near gated roads (Chapter 5) and habitat preference for areas near gated roads did not have negative survival consequences (Chapter 6). If the management goal is to increase bear survival and population growth, therefore, we recommend that managers gate the gravel roads associated with forest stands that are harvested.

For effective conservation, bear research should be conducted at multiple spatial scales and the effects of management should be considered over multiple spatial and temporal scales. The way PBS bears responded behaviorally to young clearcuts differed between the 2 scales of investigation we examined (Chapter 4), which has research and conservation implications. In terms of research, our findings helped resolve conflicting results from previous studies that each evaluated only 1 spatial scale. In terms of conservation, knowing that the changes to bear habitat at the landscape level due to clearcuts (i.e., an increase in gravel roads) may outweigh the changes to bear habitat at the stand level due to clearcuts (i.e., increased soft mast availability) can help streamline conservation efforts. That PBS females avoided intermediate aged stands at the 2 spatial scales we examined (Chapter 4) indicated clearcutting had a negative effect on habitat quality for bears over the longer term. Hence, the effects of clearcutting on bear habitat should be considered over the successional life of clearcuts, not just when clearcuts are young.

Finally, the research approach we used has broad conservation application because it provides a way to distinguish among limiting resources, important resources, and resources that are relatively unimportant for populations of wild animals. By using measures of survival, reproduction, and population growth, our approach provides a rigorous method for testing the effects of disturbances (e.g.,clearcuts, roads, etc.) on habitat quality for wild animals. In addition, our approach is useful for testing whether animal behaviors affect animal fitness, which has implications for both basic and applied research. Within the framework of adaptive management, linking resources or habitat preference with demography can be used to evaluate the efficacy of management strategies and can be used to help streamline conservation efforts to maintain populations of endangered or game species.

FUTURE RESEARCH

Future research could test the behavioral response of bears to clearcuts, with respect to gravel and gated roads. If gating roads minimizes the negative effect of gravel roads on habitat quality, as results from Chapters 5 and 6 suggest, then bears should prefer young clearcuts associated with gated roads more than they prefer young clearcuts associated with non-gated gravel roads.

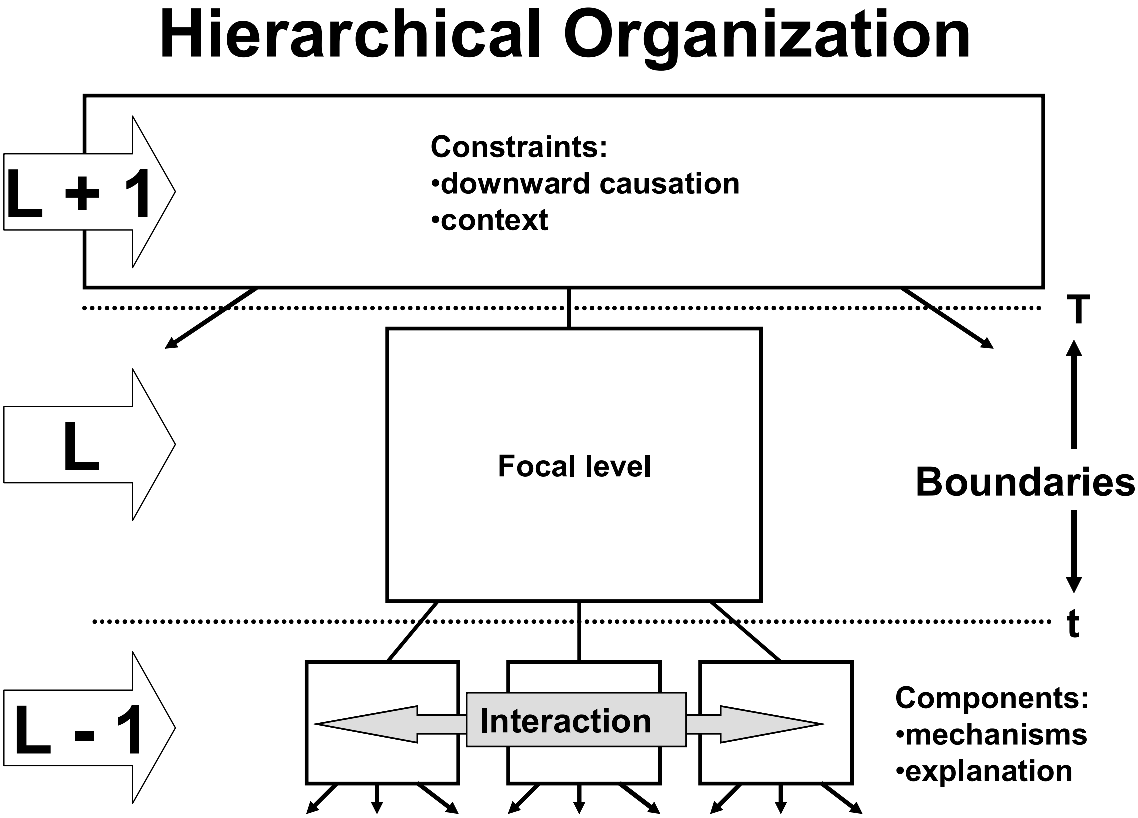
Future research could also focus on understanding how much area should be maintained in young clearcuts in the Southern Appalachians to optimize habitat quality for black bears. In our study, availability of young clearcuts affected habitat quality positively in terms of recruitment (Chapter 3). Biological thresholds, however, may have existed in PBS that we were unable to detect, which could influence the way young clearcuts affected habitat quality for bears. During 1981-2001, the proportion of PBS that comprised 2-9 year-old clearcuts was small (mean = 2% SD = 0.05%). If 2-9 year-old clearcuts are more available (e.g., 25% of the landscape), their effect on bear recruitment may be negative.

Future research could also link estimates of bear survival, recruitment, and λ with estimates of habitat preference for both roads and clearcuts to evaluate the combined effects of road use and clearcut use on bear demography. For reliable results, this analysis should be conducted by incorporating mortality information into estimates of survival, recruitment, and λ. Currently, methods for estimating recruitment and λ when reproduction data are lacking for an animal population (i.e., the Pradel parameteriztion 1996) do not provide a way to inform parameter estimates with mortality data, which is important when evaluating the effects of habitat preference on demographic parameters (Reynolds, unpublished data).

Figure Caption

Figure 1. Hierarchical organization of ecological systems, where the focal level of the ecological process is explained by processes occurring at L-1 levels and constrained by processes occurring at L+1 levels.

Figure 1.


Hierarchical Organization
L + 1
Constraints:
•downward causation
•context
T
L
Focal level
Boundaries
t
L - 1
Interaction
Components:
•mechanisms
•explanation

CHAPTER 8

EVALUATING INTERCEPTS AND ODDS RATIOS FROM SURVIVAL ANALYSES TO UNDERSTAND RESOURCE THRESHOLDS

Abstract: Understanding biological thresholds of resource availability is critical to effective management and conservation of wild animal populations, however resource thresholds are difficult to quantify. We propose current methods for interpreting results from modeling population survival (i.e., evaluating model ranking, model weights, slope estimates, and model averaging) can be expanded to determine biological threshold levels of resources. We demonstrate how interpreting intercepts with respect to odds ratios can yield insights into resource thresholds, assuming logistic regression is used to link estimates of resources with estimates of survival.

Key words: logistic regression**,** odds ratios, population growth rate, resource limitation, resource thresholds, survival

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Recent focus in demographic modeling has shifted from understanding not only how vital rates (e.g., survival, recruitment) change through time, but also why. Modeling tools like Program MARK (White and Burnham, 1999) and Program POPAN-4 (Arnason et al., 1995) are increasingly used by wildlife scientists to link estimates of demography with explanatory variables such as climate (Franklin et al. 1998; Jones et al. 2002), forest fragmentation (Brooker and Brooker 2001; Doherty and Grubb 2002), poison (Armstrong et al. 2001), and edge proximity (Moorman et al. 2002). Similarly, estimates of resource availability can be linked with estimates of demography to yield information about resource limitation (Reynolds et al. submitted$_2$). A resource is limiting if changes in its availability quantifiably affect population growth (Messier 1991), which is a function of survival and reproduction.

Survival is often the vital rate targeted to manage populations of wild animals. On average, survival of wild animals is easier to manage than is reproduction. Moreover, survival often has the greatest potential to contribute to future changes in population growth for long-lived species (Partridge and Harvey 1988). Therefore, knowing the level at which a resource must be maintained to sustain population survival of wild animals would be useful information to wildlife managers.

Because survival rate is bounded between 0 and 1, logistic regression is appropriate for modeling survival and the effects of resources on survival. Therefore, odds ratios associated with logistic regression can be exploited to understand resource thresholds.

Evaluating odds ratios involves understanding the relationship between an explanatory variable and the odds of successful versus unsuccessful outcomes. Analysis of odds ratios is used in several fields, including actuarial science (Al-Ghamdi 2002), economics (Craig and Sandow 2004), engineering (Del Prete and Grigg 1999; Ramirez et al., 1997), epidemiology (Slavin 2002), medicine (Fujiwara et al. 2003), and sociology (Lebel et al. 2002), but it has yet to be applied to demographic modeling to understand resource thresholds. Logistic regression can be used to linearize the sigmoidal relationship between survival and resource availability using the following equation:

$$\ln(\text{survival}/1\text{-survival}) = B_0 + B_i X_i \tag{1}$$

Where B_0 is the y-intercept, B_i is the slope, and X_i is the standardized value of resource *i*. According to Equation 1, if $B_0 = 0$ and $X_i = 0$, the odds of surviving are 50/50:

$$\ln(\text{survival}/1\text{-survival}) = 0$$

$$\text{survival} = e^0\ (1\text{-survival})$$

$$\text{survival} = 0.50$$

$$\text{survival}/1\text{-survival} = 50/50$$

Therefore, if $B_0 = 0$ and $X_i = 0$, the odds of surviving are equal to the odds of dying when resource *i* equals zero. By changing the value of only the y-intercept, the odds of survival also change. For example, if $B_0 = 1$ and $X_i = 0$, the odds of surviving are 73/27, which is greater than the odds of dying (27/73) when resource *i* equals zero. Alternatively, if $B_0 = -1$ and $X_i = 0$, the odds of surviving are 27/73 and the odds of dying are 73/27.

EXAMPLE: RESOURCE THRESHOLDS FOR A HYPOTHETICAL POPULATION

Consider a hypothetical population for which we have estimated annual survival rate. Assume we used capture-recapture data collected over 10 years to model annual survival and recapture probability of adult females. Further assume we *a priori* identified four resources that may be important to the population and we were able to measure annual availability of all four resources as they changed during the study period. We considered each resource a possible covariate to survival and we linked estimates of survival with annual estimates of resources via logistic regression (logit link) in program

MARK (White and Burnham 1999). Prior to analyses, we standardized all covariates by subtracting the mean from each observation and then dividing by the standard deviation, so comparisons among resource effects would be relative. We did not model interaction effects among four resources. We used AIC (Akaike 1973) to rank models and report results in Table 1, which includes four models with resource covariates and one null model with no covariates.

Based on results of our analyses (Table 1), we conclude Resources C, D, and A had relatively little effect on survival because each of these models had relatively high ΔAIC values and low model weights. The model with the covariate Resource B ranked highest for survival and its slope estimate was positive and significant.

To evaluate biological threshold levels of Resource B with respect to survival, we graphed the linear relationship between logit survival and standardized availability of Resource B (Fig. 1). One biological resource threshold should be the level at which the odds of surviving is equal to the odds of dying. Based on Equation 1, the odds of survival are 50/50 when $y = 0$. When $y > 0$, the odds of surviving are greater than the odds of dying and when $y < 0$, the reverse is true. The point where Equation 1 crosses the x-axis, therefore, should represent one biological threshold value for Resource B. Variation in the threshold estimate can be included by plotting the confidence interval around the function and determining where the confidence interval crosses the x-axis. In Fig. 1, a resource threshold level for standardized Resource B = -0.03 (dark rectangle) and the corresponding 95% CI is -2.3 and 0.25 (gray rectangles). If the goal is to manage a population such that the odds of surviving are equal to the odds of dying, then managers could focus efforts on maintaining Resource B at levels between -2.3 and 0.25 standardized units. Real values of Resource B can be estimated by back transformation.

For long-lived species that have low reproductive potential, a biological threshold representing 50/50 chances of survival may not be viable. In these situations, managers can *a priori* set the threshold at a level which corresponds to the survival odds necessary to sustain population growth. For example, if it is known that the survival odds equal to 82/18 is necessary to sustain population growth of our hypothesized population, then the threshold level can be shifted from 50/50 odds to 82/18 odds by shifting the x-axis upward (Fig. 2). Subsequently, the function can be evaluated in terms of where it crosses the shifted x-axis. If the goal is to manage a population such that the odds of survival are 82/18, then managers could focus efforts on maintaining Resource B at levels between -0.0 and 1.7 standardized units.

SUMMARY

Understanding resource threshold levels would be powerful information to wildlife managers. In this paper, we presented methods for analyzing results of modeling population survival that provide information about resource thresholds. Importantly, our methods should be used in conjunction with current methods for analyzing model results. Evaluating model rankings, model weights and slope estimates are critical first steps towards understanding resource thresholds.

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Table 1. Ranking of models of survival, each with a different resource covariate, for a hypothetical population. Only Resource B ranked high and had relatively high model weight.

Model	Δ AIC	AIC Weight	Model Likelihood	Slope	Slope LCL	Slope UCL
Resource B	0.00	0.45	1.00	2.05	1.68	3.78
Resource A	4.67	0.05	0.10	1.16	-0.98	4.02
Resource D	4.70	0.05	0.10	0.50	-1.57	3.79
Null	5.34	0.03	0.07	NA	NA	NA
Resource C	5.39	0.03	0.07	0.40	-0.11	1.97

Figure Captions

Figure 1. Linear relationship between Resource B and logit survival and its 95% confidence interval for a hypothetical scenario. One biological threshold level of Resource B occurs when probability of surviving is equal to probability of dying; where the function crosses the x-axis (dark rectangle). Gray rectangles represent the 95% CI, or the range of variation associated with the threshold point.

Figure 2. Linear relationship between Resource R and logit survival and its 95% confidence interval for a hypothetical scenario, where the threshold level of Resource B has been shifted to occur where survival odds = 82/18. Gray rectangles represent the 95% CI, or the range of variation associated with the threshold point.

Figure 1.

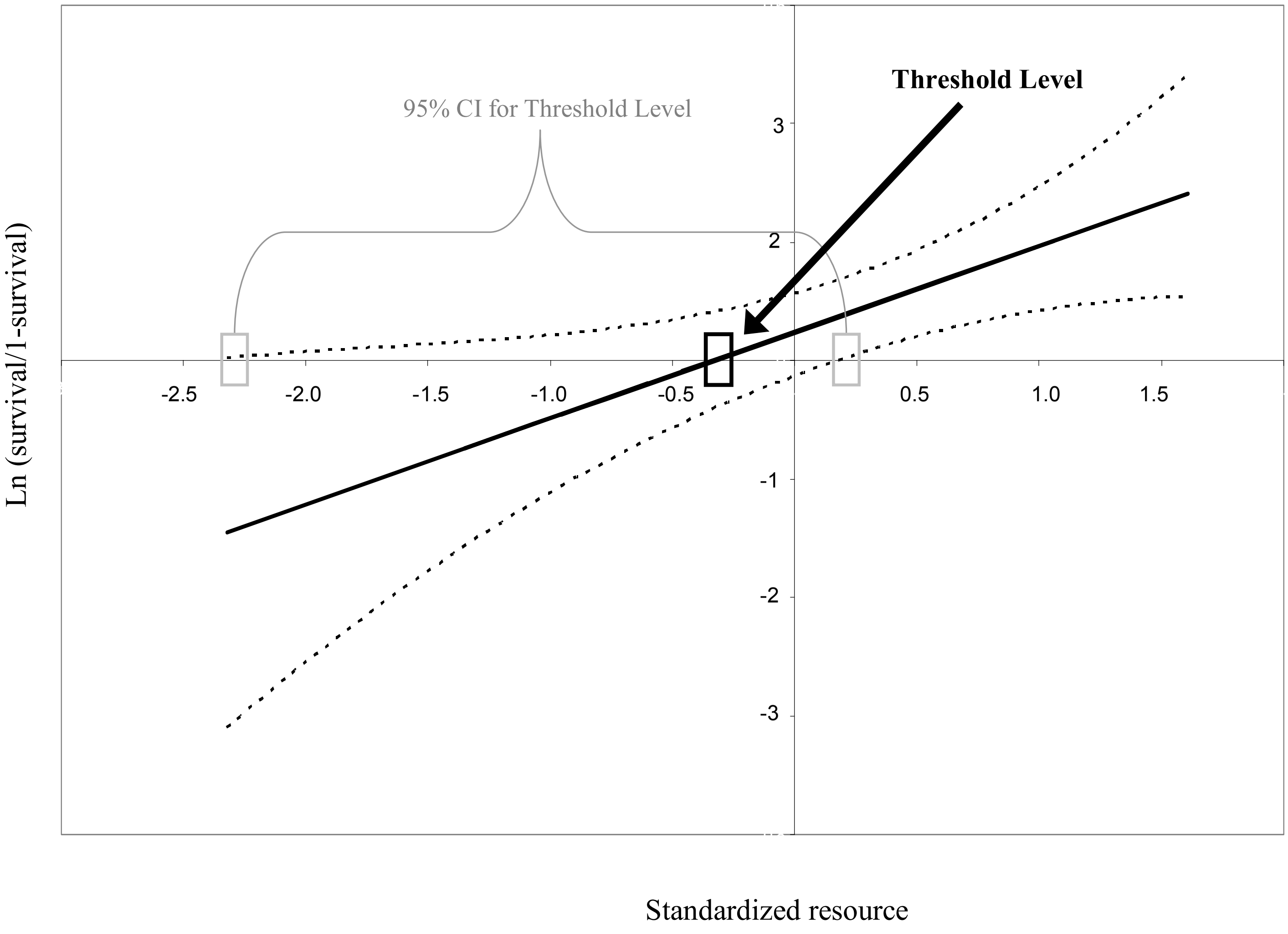
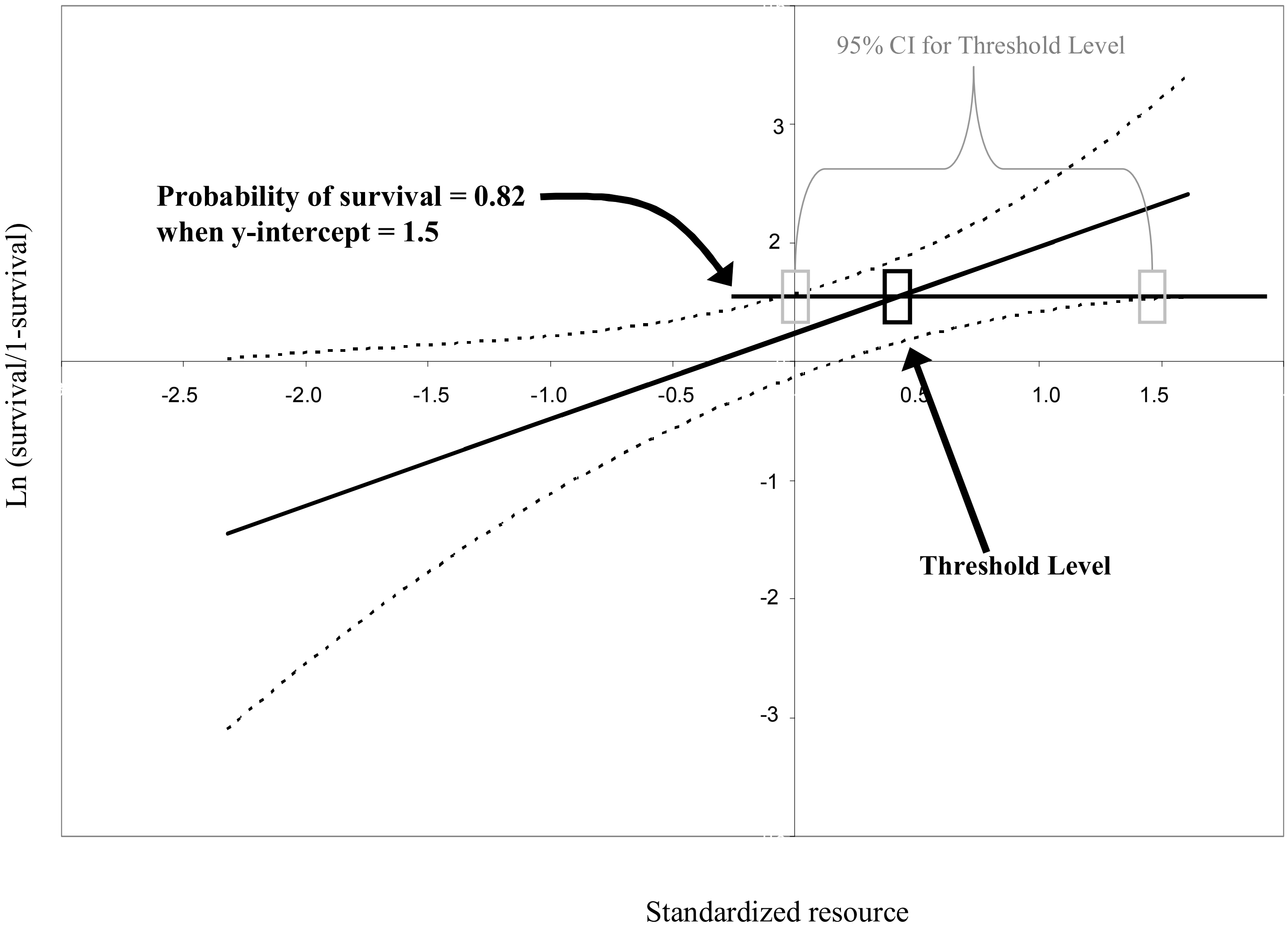

Threshold Level
95% CI for Threshold Level
3
2
-1
-2
-3
-2.5
-2.0
-1.5
-1.0
-0.5
0.5
1.0
1.5
Ln (survival/1-survival)
Standardized resource

Figure 2.


95% CI for Threshold Level
Probability of survival = 0.82
when y-intercept = 1.5
Threshold Level
3
2
-1
-2
-3
-2.5
-2.0
-1.5
-1.0
-0.5
0.5
1.0
1.5
Ln (survival/1-survival)
Standardized resource

CHAPTER 9

DEN SITE SELECTION BY BLACK BEARS IN THE SOUTHERN APPALACHIANS

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

Key words: bears, dens, habitat quality, roads, Southern Appalachians, *Ursus americanus*

Understanding den selection by black bears is important to effective bear conservation (Hellgren and Vaughan 1989; Linnell et al. 2000). Studies on den selection have focused largely on den type (e.g., tree dens, rock dens, etc.; Jonkel and Cowan 1971; Lindzey and Meslow 1976) and whether den type varies among sex and age (Gaines 2003; Johnson and Pelton 1980; Klenzendorf et al. 2002) or whether topography (e.g., slope, elevation, etc.) at den sites varies between sex (Seryodin et al. 2003) or among den types (Johnson and Pelton 1980; Ryan and Vaughan 2004; White et al. 2001). Relatively few studies have evaluated bear use of den characteristics relative to the availability of den characteristics, which is necessary to determine whether bears demonstrate selection. Martorello and Pelton (2002) and Oli et al. (1997) compared microhabitat at dens with that at random sites (Martorello and Pelton 2002) or sites without tree dens (Oli et al. 1997). Johnson and Pelton (1981) and Seryodkin et al. (2003) compared den characteristics at den sites with those at random sites in the study area. Kasbohm et al. (1994) and Gaines (2003) compared categorical data at den sites (e.g., forest cover type) with availability in the study area. No study has compared den characteristics at den sites with availability of den characteristics in home ranges. The objective of our research was to evaluate den selection by bears in the Pisgah Bear Sanctuary (PBS), located in western North Carolina, by comparing den characteristics at known den sites with availability of den characteristics within annual home ranges and within the study area.

Bears in PBS have been shown to use a wide variety of den types (e.g., tree dens, rock cavities, brush piles in clearcuts, open depressions; Powell et al. 1997), indicating den type may not be as important to den selection compared to other variables.

Zimmerman (1992) hypothesized steep slopes may be important to den selection because steep areas provide seclusion and drainage. Although studies have shown black bears den on steep sites (Aune 1994; Huygens et al. 2001; LeCount 1983; Novick et al. 1981; Seryodkin et al. 2003; Tietje and Ruff 1980) we found only 1 study that evaluated whether slope at den sites differed from what was available in the study area (Seryodkin et al. 2003). If steep slopes are important to den selection by black bears, we predicted bear dens in PBS would be located in steep areas relative to availability in home ranges and within the study area.

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

Alternatively, the way bears select dens with respect to road types may be a function of the predictability of human disturbance on roads. Linnell et al. (2000) hypothesized bears would be more likely to den in areas where human disturbance is predictable. We tested two predictions of this hypothesis by evaluating den selection with respect to paved and gravel roads. In PBS, the primary paved road is the Blue Ridge Parkway

(BRP), which provides leisurely motoring opportunities for tourists. On average, motorists who are sight-seeing along the BRP rarely wander more than a few meters from their vehicles. Therefore, human use of paved roads in PBS is predictably high and human use of areas near paved roads is predictably low. Alternatively, gravel roads in PBS are used not only as scenic byways but also for accessing hiking and biking trails, camp sites, and hunting or poaching sites. A motorist driving along a gravel road in PBS might stop at a trailhead, a camp site, a hunting site, or it might not stop at all. Therefore, human use of gravel roads, and areas near gravel roads, is relatively unpredictable. If the Linnell et al. (2000) hypothesis is true, we predicted that bears would den close to paved roads and far from gravel roads, relative to availability.

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

Our final objective was to test an existing model of habitat quality for bears with respect to its ability to predict high quality den sites. Previously, Zimmerman (1992) developed a spatially explicit model of habitat quality that incorporated three life requirements; bear foods, den sties, and escape cover. The overall model was tested using annual home ranges of PBS bears (Mitchell et al. 2002; Powell et al. 1997;

Zimmerman 1992), but the den site component of the model has not been rigorously evaluated. We used known den sites to evaluate the efficacy of the den site component of the habitat model.

MATERIALS AND METHODS

Study area.—We conducted our study in the Pisgah Bear Sanctuary (PBS) in North Carolina (35° 17' N, 82° 47' W) during years 1981-2002. The PBS (235 km^2) was located within the Pisgah National Forest, where topography was mountainous with elevations ranging from 650m to 1800m. The region was considered a temperate rainforest, with annual rainfall approaching 250 cm/yr (Powell et al. 1997).

Roads in PBS included 48.5 km of paved roads, 65.7 km of gravel roads, and 200.3 km of gated roads (Continuous Inventory Stand Condition data base, USDA Forest Service 2001). The Blue Ridge Parkway, administered by the National Park Service, transected the north central portion of PBS, US Highway 276 bounded the western edge of PBS, and State Road 151 (a paved road) ran though a small portion of PBS. Several gravel roads ran through parts of PBS, one of which (Forest road 1206) bisected the Sanctuary. By year 2000, over 80 gated roads ran throughout PBS.

Trapping bears and collecting location data.—We captured bears in PBS from May through mid-August during 1981-2002 (except 1991 and 1992) using Aldrich foot snares modified for safety (Johnson and Pelton 1980) or barrel traps. We immobilized captured bears using a combination of approximately 200 mg Ketamine hydrochloride + 100 mg Xylazine hydrochloride/90kg of body mass (Cook 1984) or Telazol administered with a blow dart or jab stick. We sexed, tattooed, and attached two ear tags to each immobilized bear and extracted a first premolar to determine age. 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 radio transmitter collars (Telonics, Inc. Mesa, Arizona; Sirtrak, Havelock North, New Zealand). All procedures complied with requirements of the Institutional Animal Care and Use Committees for Auburn University (IACUC # 0208-R-2410) and North Carolina State University (IACUC # 88-*** to # 00-018).

From May each year until the bears denned (except 1991 and 1992), we located collared bears using telemetry receivers (Telonics Inc., Mesa, Arizona; Lotek, Newmarket, Ontario; Sirtrak, Havelock North, New Zealand) and a truck-mounted, 8-element yagi antenna. The high elevation of the Blue Ridge Parkway allowed unobstructed line-of-sight with the majority of the study area, reducing the likelihood of signal error due to interference from terrain. Locations were estimated by triangulating compass bearings taken from a minimum of 3 separate locations within 15 minutes (Zimmerman and Powell 1995). Bears were located every 2 hours for 8, 12, or 24 consecutive hours and sampling was repeated every 32 hours to standardize bias from autocorrelation (Swilhart 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 meters. Error did not differ significantly among observers.

Estimating home ranges.— We used the fixed kernel estimator (program KERNELHR; Seaman et al. 1998), with bandwidth determined by cross validation, to estimate annual home ranges of bears. The kernel estimator depicts a bear's use of space 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 (Seaman and Powell 1996), and a grid size of 250 meters was used for kernel estimation to match the resolution of our telemetry data. For analyses, home ranges were defined as the area containing 95% of the estimated utility distribution. We estimated annual home ranges because we wanted to evaluate den selection based on resources available to bears throughout the year.

Mapping roads.—We used a Geographic Information System (GIS; ArcView 3.2 and Spatial Analyst 2.0) to map the distribution of roads in PBS for each year 1981-2001. We partitioned roads into three types (paved, gravel, 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 USDA Forest Service at the Pisgah Ranger District, North Carolina.

Collecting den data.—We tracked radio-collared bears to their dens during most winters 1981-2002. To determine reproductive status of adult females, we visited accessible dens in February and March and immobilized females using a combination of approximately 200 mg Ketamine hydrochloride + 100 mg Xylazine hydrochloride/90kg of body mass (Cook 1984) or Telazol administered with a jab stick. Adult females were categorized as adults with cubs (i.e., cubs were born during the winter following den selection that occured during fall), adults with yearlings (i.e., cubs from the previous year accompanied adult female into den), or adults with no cubs or yearlings.

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

Den characteristics: den sites versus home ranges.—We used a GIS to map values of slope across PBS at a 30 meter resolution. For each known den site, we estimated the slope value to be that for the 30 meter cell within which each den site was located. For each bear that had a known den site, we estimated the mean slope within its annual home range. Because elevation (Mitchell et al. 2005; White et al. 2001) and distance to streams (Johnson and Pelton 1981) may also be important to den selection by bears, we used the same methods to estimate elevation and distance to streams for each den site as well as mean elevation and mean distance to streams within corresponding annual home ranges.

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

To test whether road proximity influenced den selection, we mapped each known den site in a GIS, overlaid each road map (paved, gravel, and gated), and calculated den distance to roads by road type. For each 95% annual home range, we calculated mean distance to roads by road type. We matched distance to roads at each den site with mean distance to roads in corresponding annual home range and conducted paired t-tests, by road type. We also evaluated whether den proximity to roads differed by road type by modeling den proximity as a function of road type. Using Akaike's Information Criterion, with an adjustment for small sample bias (AIC_c; Akaike 1973; Anderson et al. 1994) we compared the ability of this model to explain the data relative to the ability of the null model (i.e. intercept only model).

Den characteristics: den sites versus study area.—To evaluate whether topography at known den sites differed from that available in the study area, we grouped continuous data on slope, elevation, and stream distance into categories (e.g., slope categories; < 10 degrees, 10-15 degrees, 15-20 degrees, etc.) and compared the frequency of categories selected for den sites with the frequency of categories available in PBS using chi squared goodness of fit tests with adjusted confidence intervals (e.g., slope had six categories so $\alpha = 0.10/6 = 0.016$). We did not use paired t-tests because although we had estimates of variance for mean values of each topographic variable at the den sites (n = 53 den sites), we did not have estimates of variance for mean values of topographic variables for the study area (n = 1 study area). To evaluate whether den distance to roads differed from availability in the study area, we grouped den distance into six categories (< 1000 meters, 1000-1500 meters, 1500-2000 meters, 2000-2500 meters, 2500-3000 meters, and < 3000 meters) and compared the frequency of categories selected for den sites with frequency of categories available in PBS using chi squared goodness of fit tests with adjusted confidence intervals.

Sex, age class, and reproductive status.—To determine if den selection differed by sex or age, we compared use of den characteristics with availability of den characteristics in annual home ranges using paired t-tests, by sex and age class. To determine if den selection differed by reproductive status of adult females (i.e., adult females with and without cubs), we compared use of den characteristics with availability of den characteristics for adult females using paired t-tests, by reproductive status.

To compare our results with findings from previous studies, which did not use estimates of den characteristic availability, we evaluated whether den selection differed by sex or age using logistic regression with the Newton-Raphson optimization technique (Proc Logistic; SAS Institute 2000). Using sex as the response variable, we developed a suite of models using age class as a categorical predictive variable and slope, elevation, distance to roads (paved, gravel, gated), and distance to streams as continuous predictive variables. We considered the intercept only model to be the null. We used AICc for model selection and we considered models with ΔAIC value < 2.0 to have substantial support (Burnham and Anderson 2002). We also estimated model likelihoods and model weights, which provide strength of evidence for model selection. We used Hosmer and Lemeshow goodness of fit statistic to test for model fit. We used a similar approach to evaluate whether den selection differed by reproductive status of adult females.

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

Evaluating the den component of the habitat model.—Using the Den Value algorithm from Zimmerman's (1992) habitat model (Table 1), we used a GIS to map den values for every 30 meter cell within PBS during each year 1981-2001. We estimated D_2

(understory in rhododendron and laurel plants) and D_4 (large trees) for each 30 meter cell based on field data collected on percent understory and number of large trees (Reynolds, unpublished data). For each known den site, we considered its den value to be that which was estimated for the 30 meter cell within which the den was located. For each bear that had a known den site, we estimated the mean den value within its annual home range during the year that corresponded to the den site year.

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

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

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

Individual components of Zimmerman's den model included forest contiguity (D_1), area in understory (D_2), slope of terrain (D_3), and availability of large trees (D_4; Table 1). Forest contiguity is a function of distance to roads, so we examined den distance to paved, gravel, and gated roads compared to availability in home ranges and in the study area. We did not compare understory or number of large trees at den sites with availability in home ranges and in the study area because the equations to estimate availability of understory and large trees had relatively low predictive power (Reynolds, unpublished data). To provide some information regarding large trees, we calculated mean dbh of trees when trees were used as dens.

RESULTS

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

Den characteristics: den sites versus home ranges.—Results of paired t-tests showed slope, elevation, distance to gravel roads, and distance to streams were higher at known den sites compared to that available within annual home ranges (Table 2). Errors were normally distributed and variance was constant.

Proximity to roads by road type.—The top ranked model included road type as a variable. Mean den distance to gravel roads was 2145.78 meters (90% confidence interval = 1898.82, 2392.74), whereas mean den distance to paved and gated roads was 1035 (90% confidence interval = 742.96, 1327.04) and 755 meters (90% confidence interval = 621.72, 888.28), respectively (Fig. 1).

Den characteristics: den sites versus study area.—Overall, categories of slope ($X^2 = 41.95$, 5 df, $P < 0.0001$), elevation ($X^2 = 36.5$, 5 df, $P < 0.0001$), distance to paved roads ($X^2 = 24.92$, df 5, $P < 0.0001$), and distance to gravel roads ($X^2 = 36.45$, 5 df, $P < 0.0001$) were used disproportionately to availability in the study area. Dens were located in relatively steep areas at relatively high elevations (Fig. 2). Dens were located in areas that were relatively close to paved roads but not close to gravel roads (Fig. 3).

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

When availability of den characteristics at known den sites was compared with availability of den characteristics in annual home ranges by sex and age class (i.e., paired t-tests), we found no differences between sex and age class. We also examined differences in den characteristics between sex and age class using logistic regression so that we could compare our results with those from previous studies that did not include estimates of den characteristic availability. Based on logistic regression analysis, 2 models had Δ AIC$_c$ values < 2.0. The top ranked model was the null model and the second ranked model included elevation (Δ AIC$_c$ = 0.90). As strength of evidence for model selection, the model weight for the top ranked model was 0.27, indicating the top ranked model was only 1.6 times more likely to be selected over the second ranked model (model weight = 0.17), which was not sufficient to differentiate among models (Burnham and Anderson 2002). Mean elevation for male den sites was 1337.72 (90% confidence interval = 1259.41, 1416.03) whereas mean elevation for female den sites was 1252.68 (90% confidence interval = 1196.79, 1307.88). Results of goodness of fit tests (Hosmer and Lemeshow $X^2 = 7.61$, df = 9; $P > 0.57$) indicated data were not over-dispersed.

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

We also examined differences in den characteristics between adult females with and without cubs using logistic regression so that we could compare our results with those from previous studies that did not include estimates of den characteristic availability. Based on results of logistic regression, two models had Δ AIC$_c$ values < 2.0. The top-ranked model included slope as a variable and the second ranked model was the null model (Δ AIC$_c$ = 0.41). As strength of evidence for model selection, the model weight for the top ranked model was 0.34, indicating it was only 1.2 times more likely to be selected over the null model (model weight = 0.28), which was not sufficient to differentiate among models (Burnham and Anderson 2002). Results of goodness of fit (Hosmer and Lemeshow $X^2 = 4.03$ df = 7; $P > 0.77$) indicate data were not over-dispersed.

Evaluation of the den component of the habitat model.—Mean den values at known den sites ranged from 0.17 to 0.65. Based on paired t-test analysis, den values at known den sites did not differ from mean den values within annual home ranges (Table 2). Errors were normally distributed and variance was constant. Use of den value categories was disproportionate to availability of den value categories in the study area ($X^2 = 37.98$, 9 df, $P < 0.0001$; Fig. 2). Results of regression analysis, based on 58 dens, showed the frequency of den value categories for den sites increased as den value category increased, but only up to den value category 0.60-0.70 (Fig. 4; $F_{1,6} = 3.82$; p = 0.10; $r^2 = 0.43$). The sample size for the regression analysis differed from that for most other analyses, which used only those den sites for which we could estimate home ranges (n = 53). The regression analysis did not require home range estimates so we included all known den sites for which we could estimate den values (n = 58). We collected data on dbh for 14 tree dens; mean dbh = 98.78 cm (90% confidence interval = 91.4, 106.16 cm).

DISCUSSION

Topography and proximity to gravel roads were important to den selection for bears in Pisgah Bear Sanctuary (PBS). Based on availability in both annual home ranges (Table 2) and in the study area (Figs. 2 and 3), bears selected den sites on relatively steep slopes, at high elevations, and in areas that were relatively far from gravel roads. In addition, bears selected den sites away from streams relative to availability in home ranges (Table 2) and near paved roads relative to availability in the study area (Fig. 3).

Roads.—Our results did not support the hypothesis that den proximity to roads varies inversely with traffic volume. Traffic volume was highest on paved roads and lowest on gated roads, but mean den distance to paved roads did not differ from mean den distance to gated roads (Fig. 1). Mean den distance to gravel roads, however, was higher than mean den distance to paved and gated roads (Fig. 1). In addition, den distance to gravel roads was greater than mean distance to gravel roads within annual home ranges (Table 2) and bears avoided areas within 1000 meters of gravel roads relative to availability within the study area (Fig. 3).

Our results regarding den distance to paved roads provided evidence in support of the Linnell et al. (2001) hypothesis, which posits that bears will be more likely to den in areas where human disturbance is predictable. Dens should have been located relatively close to paved roads and relatively far from gravel roads if the “disturbance predictability” hypothesis was true. Assuming “close” is defined as areas within 1 km (Linnell et al. 2001), bear dens in PBS were located close to paved roads but not close to gravel roads (Fig. 3). Den distance to paved roads did not differ from mean distance to paved roads in annual home ranges (Table 2), indicating bears did not avoid areas near paved roads when selecting den sites. On the contrary, PBS bears preferred to den in areas close to paved roads relative to availability in the study area (Fig. 3). Our results corroborated those by Klenner and Kroeker (1990) and Tietje and Ruff (1983) who reported black bears denned close to regularly traveled roads in Canada.

Although our results regarding den distance to gravel roads (Table 2; Table 3; Fig. 3) supported the Linnell et al. (2001) hypothesis, they do not prove it conclusively. Human disturbance on gravel roads was relatively unpredictable, but only because motorists traveling on gravel roads might stop at trailheads, camping sites, hunting sites, poaching sites, or they may not stop at all. Motorists traveling on gravel roads, however, were more likely than motorists traveling on paved roads to get out of vehicles and use areas near roads for hiking, hunting, etc. The argument could be made, therefore, that human use of areas near gravel roads was predictably high compared to human use of areas near paved roads. Hence, bears may have avoided denning in areas near gravel roads simply to avoid relatively high human disturbance.

How bears select den sites in late fall may be influenced by their behavior during the rest of the year. Previously, we found PBS females avoided areas near gravel roads more than they avoided areas near paved roads during both summer and fall (Reynolds and Mitchell, submitted$_1$). We hypothesized 2 reasons to explain our findings for fall. Bears may have avoided areas near gravel roads during fall to avoid non-lethal human contact, such as hikers, campers, bikers, and legal hunters of deer (*Odocoileus virginianus*) and small game. Alternatively, bears may have avoided areas near gravel roads to minimize risk of mortality due to poaching. Although bears were legally protected in PBS, poaching occurred in bear sanctuaries in North Carolina (Beringer et al.

1989; Brody and Pelton 1989). Moreover, legal bear hunting in North Carolina was usually done with the aid of hounds (Collins 1983), which were often released into bear sanctuaries (Beringer et al. 1989). In addition, some hunters used illegal bait piles to lure bears out of sanctuaries so they could be hunted along sanctuary perimeters (Beringer et al. 1989). Poachers in PBS likely use gravel roads to access bears because doing so lowers their risk of detection by enforcement officers or other drivers who may report them to enforcement officers. That we found habitat preference for areas near gravel roads by females affected female survival negatively (Reynolds and Mitchell, submitted$_2$) lends support for the hypothesis that females avoided areas near gravel roads during fall to avoid poachers.

In terms of fitness, the behavioral response of females to gravel roads during fall had survival consequences (Reynolds and Mitchell, submitted$_2$) and results from this paper show the way females selected dens, with respect to gravel roads, may have had reproductive consequences. Adult females with cubs selected dens in areas that were far from gravel roads, relative to what was available to them in their home ranges (Table 3). Alternatively, den distance from gravel roads did not differ from mean distance to gravel roads in home ranges for adult females without cubs or yearlings (Table 3).

This result, combined with bear biology, indicates that adult females who select den sites far away from gravel roads may increase reproductive success. Black bears are polygynous, they mate during summer, and adult females can produce litters bi-annually (Powell et al. 1997). Therefore, most, if not all, adult females who do not have cubs during mating season should breed during the mating season. Bred females delay implantation until fall and a female will abort her fetus if she does not have sufficient stores of energy and protein (Bunnell and Tait 1981; Elowe and Dodge 1989).

Den disturbance can affect reproductive success negatively by increasing cub abandonment (Linnell et al. 2000) and over-winter weight loss (Teitje and Ruff 1980), energy that might otherwise be allocated towards reproduction. Selecting den sites away from gravel roads may decrease the risk of den disturbance. For our analyses, we defined adult females with cubs to be those females who bore cubs during the winter following den site selection. Importantly, these females selected den sites prior to bearing cubs. It is significant that adult females with cubs did not appear to select den sites based on any other variable (e.g., slope, elevation, etc.; Table 3), indicating distance to gravel roads was the most important criterion for den selection. Adult females classified as those with neither cubs nor yearlings did not bear cubs, even though they likely mated during the previous summer.

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

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

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

Den component of the habitat model.—Our results regarding the den component of Zimmerman's (1992) habitat model were mixed. Den values (estimated using the habitat model; Table 1) at den sites did not differ from mean den values available within annual home ranges (Table 2). These results suggest bears did not prefer areas with high den values based on what was available to them in home ranges. Based on availability of den values in the study area, however, bears preferred areas with den values between 0.5 and 0.6 (Fig. 2). Moreover, results of regression analysis showed the frequency of den sites generally increased as den value category increased (Fig. 4). These results indicate the den component of the habitat model captured at least part of the functional relationship between habitat and den value, but it could be improved.

Distance to gravel roads, slope, and elevation were important to den selection based on availability in home ranges (Table 2) and in the study area (Figs. 2 and 3), so the way these variables were modeled for the den component should be re-evaluated. The habitat model assumed areas > 1225 meters from all roads provide high quality den sites (Table 1), but we found den proximity to roads depended on road type. PBS bears preferred to den in areas < 1000 meters from paved roads but they avoided denning in areas < 1000 meters from gravel roads (Fig. 3). Mean den distance to gravel roads was 2145 meters, indicating the habitat model over-estimated den values for areas near gravel roads. Fig. 5 shows the hypothesized relationship between proximity to roads and den value based on Zimmerman's (1992) habitat model. On a scale of 0 to 1, areas that are within 1000 meters of gravel roads are hypothesized to have a den value = 0.78. Our results indicate that this relationship should be modified.

We present one possible modification in Fig. 5. No den was located closer than 322 meters from gravel roads, so we defined the den value to be zero when distance to gravel roads < 322 meters. Because we did not know the optimal den distance to gravel roads, we used the mean den distance to gravel roads (2145 meters; SE = 126 meters) to define the upper asymptote for gravel roads. Bears in PBS preferred denning in areas < 1000 meters from paved roads and they showed no denning preference or avoidance for areas < 1000 meters from gated roads. No den was located closer than 16 meters from paved roads and mean den distance to paved roads was 1035 meters (SE = 149 meters), so we used these values to define the lower and upper asymptotes for paved roads. No den was located closer than 54 meters from gated roads and mean den distance to gated roads was 755 meters (SE = 68 meters), so we used these values to define the upper and lower asymptotes for gated roads.

The habitat model assumed areas with slopes > 45 degrees have the highest den value because human access is limited on these areas (Table 1). We found mean slope for den sites was 23.5 degrees, indicating the habitat model under-estimated the value of moderately steep slopes. Based on the equation for slope, the den value for areas with 23.5 degree slope is only 0.43 (i.e., tan (23.5) = 0.43; Table 1). We recommend that the slope equations for the den component of the habitat model be downward adjusted to reflect the den value of areas with slopes < 45 degrees. The habitat model did not incorporate elevation as a possible predictor, but we found bears preferred to den at elevations > 1400 meters and avoided denning at elevations < 1100 meters (Table 2; Fig. 2). Therefore, we recommend that an elevation equation, which reflects our results, is included in the den component of the habitat model. Subsequently, the adjusted habitat model should be tested using den data that are independent of those we used to explore the efficacy of the den component of the habitat model.

The habitat model assumed areas with large trees provided quality den sites for bears. We did not estimate number of large trees in PBS, but we did find that tree dens were relatively large (mean dbh =98.78cm; SE = 4.5), indicating large trees were probably important to bears who denned in trees.

CONCLUSIONS AND CONSERVATION IMPLICATIONS

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

Overall, we found gravel roads had a strong influence on den selection by black bears in Pisgah Bear Sanctuary (PBS). These findings 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 (i.e., fleshy fruits; Clark et al. 1994; Mitchell et al. 2002; Perry et al. 1999; Reynolds et al. submitted$_1$), a food important to bear fitness (Elowe and Dodge 1989; Reynolds et al. submitted$_2$; Rogers 1976, 1987), harvested stands are usually spatially associated with gravel roads. That habitat preference for areas near gravel roads had negative survival consequences for females during fall (Reynolds and Mitchell, submitted$_2$), and adult females with cubs avoided areas near gravel roads for denning, indicates gravel roads had a negative effect on habitat quality for bears in PBS. Therefore, managers must consider the tradeoffs associated with timber harvesting in terms of increased habitat quality due to increased bear foods in summer and in terms of decreased habitat quality due to the negative effects of gravel roads on fall habitat and denning habitat.

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Table 1. The den component of Zimmerman's (1992) model of habitat quality for black bears in the Southern Appalachian Mountains. The overall den value is a function of conterminous forest (D_1), understory (D_2), slope (D_3), and availability of large trees (D_4).

DEN VALUE = $\{[D_1 + D_2)/2](D_3 + D_4)\}^{0.5}$, when $\{[D_1 + D_2)/2](D_3 + D_4)\}^{0.5} < 1.0$

DEN VALUE = 1.0, when $\{[D_1 + D_2)/2](D_3 + D_4)\}^{0.5} \geq 1.0$

Den model component	value	x
D_1 (conterminous forests)	0.0	$x^a \leq 200$
	0.00098 x - 0.20	$200 < x^a < 1225$
	1.0	$x^a > 1225$
D_2 (understory)	0.0333 x	$x^b < 30$
	1.0	$x^b \geq 30$
D_3 (slope)	tan (x)	$x^c \leq 45$
	1.0	$x^c > 45$
D_4 (large trees)	0.564 (log x) - 0.352	$x^d \leq 250$
	1.0	$x^d > 250$

x^a = distance to roads in meters; x^b = area covered in rhododendron and laurel plants;
x^c = slope degrees of terrain; x^d = number of large trees > 90 cm dbh

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

Variable	Mean difference[1]	90% LCL	90% UCL	p-value
Slope	3.66	2.27	5.05	0.001
Elevation	111.28	54.61	167.95	0.002
Distance to streams	63.68	30.73	96.63	0.002
Distance to paved roads	-65.40	-279.10	148.34	0.611
Distance to gravel roads	188.68	4.49	372.88	0.092
Distance to gated roads	32.54	-90.31	155.39	0.659
Den value	0.00	-0.02	0.03	0.839

[1] Mean difference between variable value at den site and mean value of variable in annual home range
Positive differences indicate variable value at den site was larger than that in home range

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

Reproductive status	Variable	Mean difference[1]	90% LCL	90% UCL	p-value
Without cubs or yearlings	Slope	4.80	2.51	7.01	0.002
	Elevation	92.76	11.15	174.36	0.065
	Distance to streams	55.55	2.24	108.86	0.088
	Distance to paved roads	-426.30	-760.10	-92.46	0.040
	Distance to gravel roads	16.36	-407.50	440.23	0.950
	Distance to gated roads	-20.38	-184.20	143.39	0.831
	Den value	0.14	-0.02	0.05	0.537
With cubs	Slope	0.96	-2.58	4.49	0.636
	Elevation	19.97	-76.90	116.83	0.718
	Distance to streams	43.56	-42.38	129.51	0.382
	Distance to paved roads	249.65	-184.20	683.49	0.324
	Distance to gravel roads	218.21	31.99	404.43	0.059
	Distance to gated roads	-70.12	-404.10	263.87	0.713
	Den value	0.012	-0.03	0.06	0.657

[1] Mean difference between variable value at den site and mean value of variable in annual home range
Positive differences indicate variable value at den site was larger than that in home range

Figure Captions

Figure 1. Mean den distance (with 90% CI) to paved, gravel, and gated roads for 53 black bear dens in Pisgah Bear Sanctuary, western North Carolina during 1981-2002.

Figure 2. Frequency of slope, elevation, and den value categories used at black bear dens (n = 53) compared with frequency of categories available in Pisgah Bear Sanctuary in western North Carolina. Den values were estimated using the den component of Zimmerman's (1992) habitat model.

Figure 3. Frequency of road (paved, gravel, gated) distance categories used at black bear dens (n = 53) compared with frequency of road distance categories available in Pisgah Bear Sanctuary in western North Carolina.

Figure 4. Frequency of den value categories for 58 black bear dens in Pisgah Bear Sanctuary in western North Carolina. Den values were estimated using the den component of Zimmerman's (1992) habitat model. Category labels represent the midpoint of the category range (e.g., 6.5 = den values between 6.0 and 7.0).

Figure 5. Hypothesized relationships between den distance to roads (m) and den value. The solid line represents the relationship for all road types hypothesized by Zimmerman (1992) for the den component of the habitat model. The dashed lines represent proposed modifications to the relationship based on findings from this paper.

Figure 1.

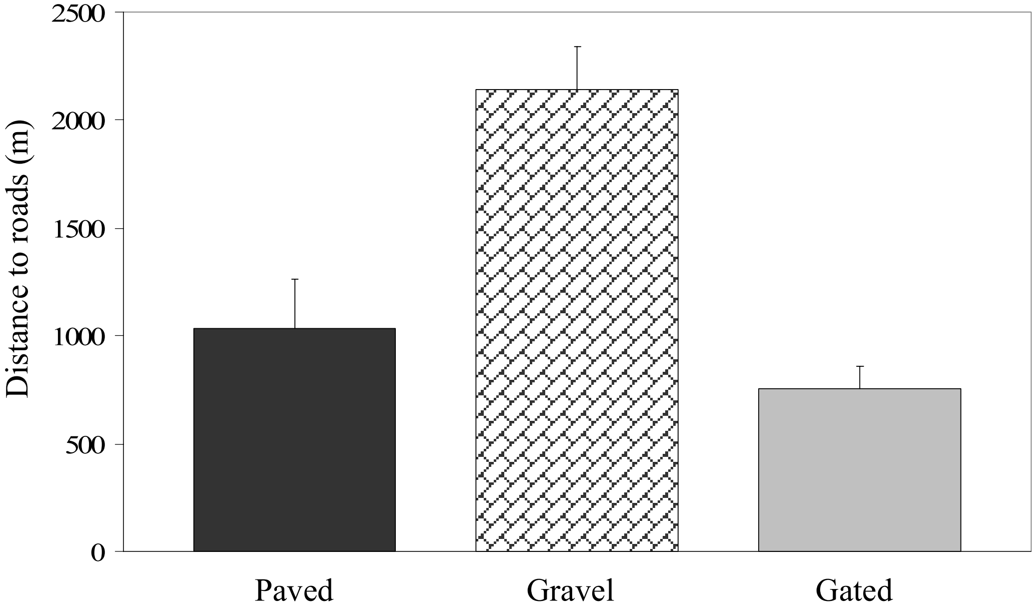
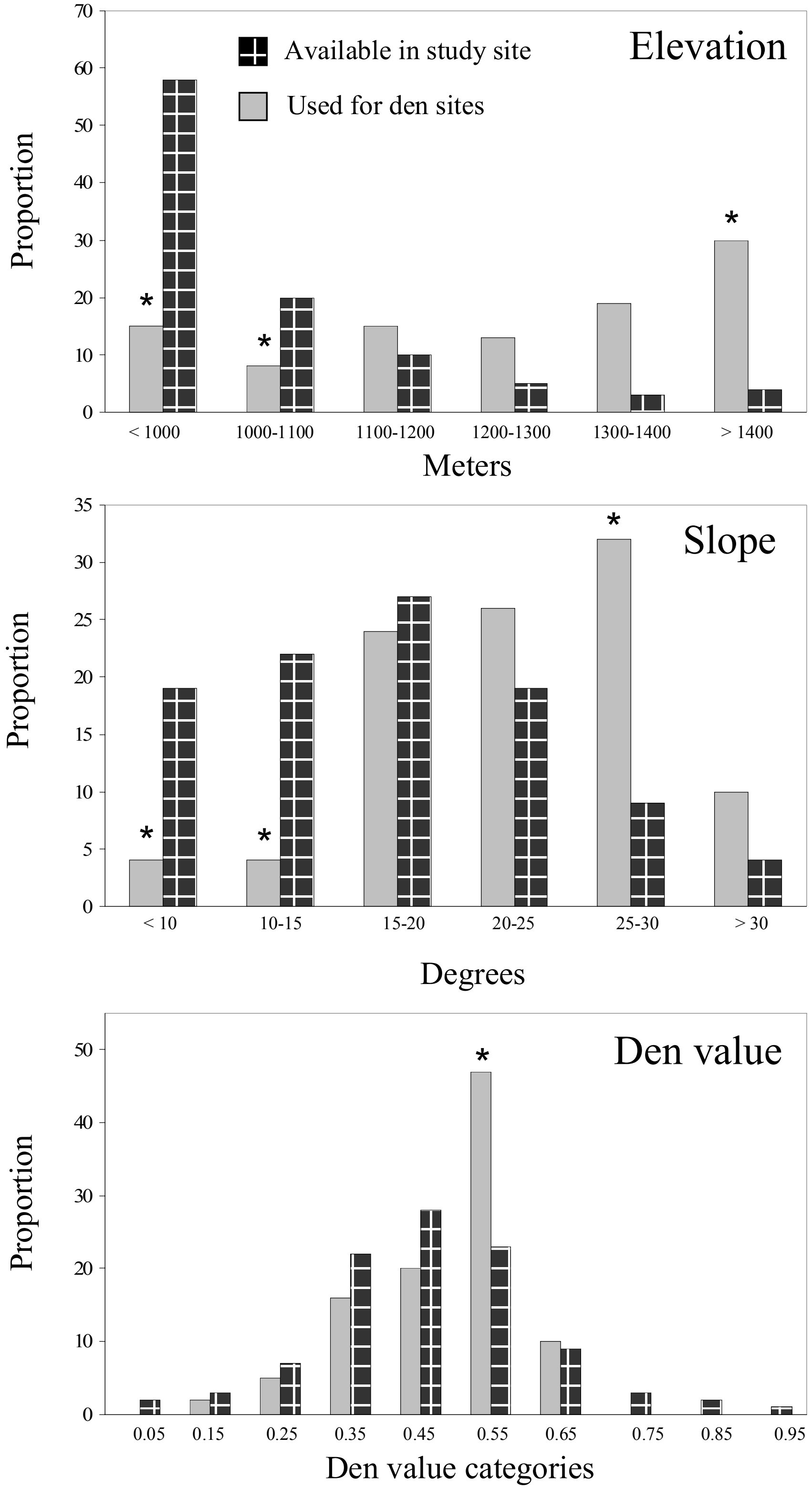
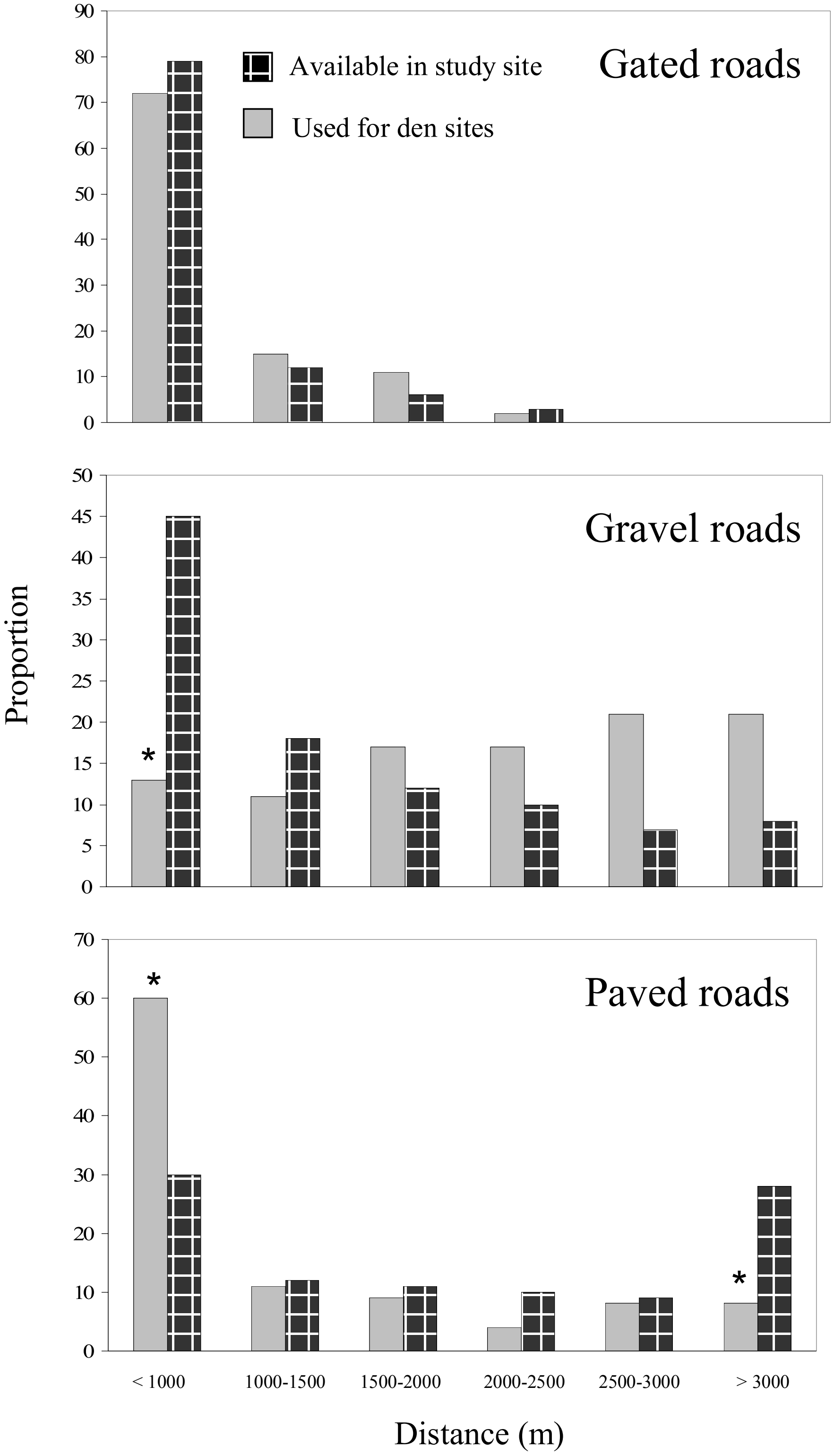

2500
2000
1500
1000
500
0
Distance to roads (m)
Paved
Gravel
Gated

Figure 2.



* indicates use was in greater proportion than availability ($P < 0.01$)

Figure 3.



* indicates use was in greater proportion than availability (P < 0.01)

Figure 4.

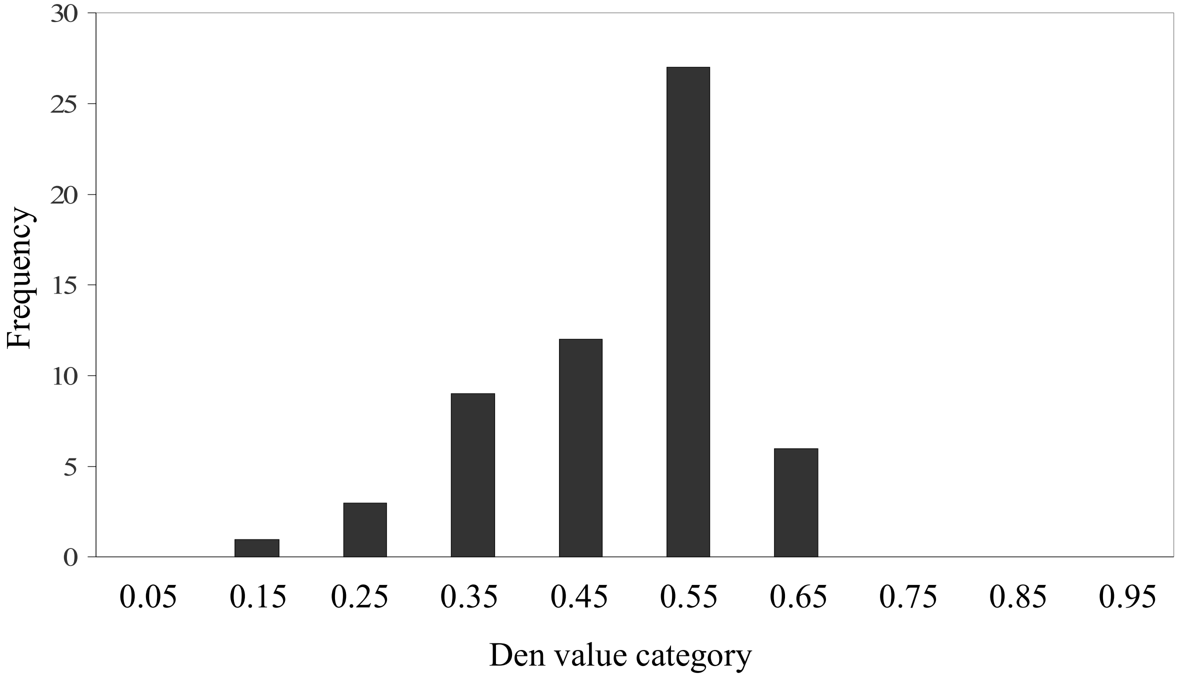
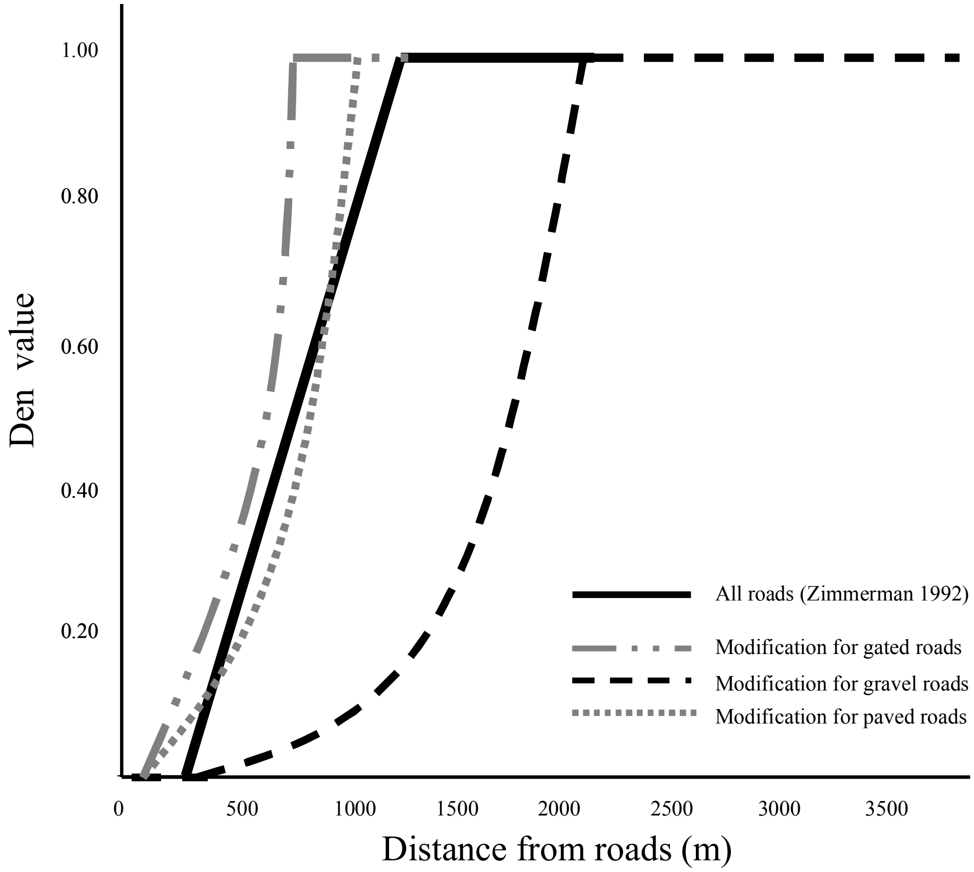

30
25
20
15
10
5
0
Frequency
0.05
0.15
0.25
0.35
0.45
0.55
0.65
0.75
0.85
0.95
Den value category

Figure 5.


Den value
1.00
0.80
0.60
0.40
0.20
0
500
1000
1500
2000
2500
3000
3500
Distance from roads (m)
All roads (Zimmerman 1992)
Modification for gated roads
Modification for gravel roads
Modification for paved roads

CHAPTER 10

SUMMARY OF ROAD RESULTS WITH RESPECT TO A MODEL OF HABITAT QUALITY FOR BEARS

Our results regarding bear response to roads are useful for understanding previous findings from research on habitat quality for black bears. Previously, Zimmerman (1992) developed a spatially explicit model of habitat quality that incorporated three components of bear habitat (i.e., foods, den sites, and escape cover). Zimmerman tested his model using location data from bears in Pisgah Bear Sanctuary (PBS) and found his model predicted habitat selection reasonably well. Powell et al. (1997) and Mitchell et al. (2002) developed and tested a 2nd generation habitat model, which included only the food and den site components. The 2nd generation model outperformed the 1st generation model, but researchers didn't know why (Mitchell et al. 2002).

The way roads were modeled to affect each habitat component (foods, den sites, escape cover), coupled with our results regarding bear response to roads (Chapters 5, 6, and 9), help explain, in part, why the 2nd generation model outperformed the 1st. For the food component of the habitat model, all areas within 1600 meters of all road types were modeled to have a negative effect on fall foods, but areas near paved roads were devalued the most and areas near gated roads were devalued the least (Table 1). For the den site component of the habitat model, areas within 1225 meters of all road types were modeled to have an equally negative effect on den value (Table 1). For the escape cover component of the habitat model, areas within 1600 meters of all road types were modeled to have an equally negative effect on escape cover (Table 1).

We found that PBS bears avoided areas near gravel roads more than they avoided areas near paved or gated roads (Chapters 5 and 9), which did not match predictions based on the habitat model (Table 1). Although areas near paved roads were devalued more than were areas near gravel roads for both the 1st and 2nd generation models, the 2nd generation model devalued areas near paved roads less than did the 1st generation model, overall. For example, areas within 200 meters of paved roads were devalued by 34% in the 1st generation model, whereas the 2nd generation model devalued the same areas by only 12% (Appendix 1). Given both habitat models were tested using location data by PBS bears (Mitchell et al. 2002; Powell et al. 1997; Zimmerman 1992), and PBS bears did not avoid areas near paved roads (Chapters 5 and 9), the model with the lowest devaluation for areas near paved roads (i.e., 2nd generation model) should have performed relatively well.

RECOMMENDATIONS FOR 3RD GENERATION MODEL

We propose a 3rd generation model, which devalues areas near roads by road type and which includes all 3 habitat components (i.e., foods, escape cover, and den sites). Figure 1 shows the hypothesized relationship between proximity to roads and fall food value based on Zimmerman’s (1992) habitat model. Areas near paved roads are devalued more than are areas near gravel roads, which should be modified based on our findings. We present one possible modification in Fig. 1. Because most PBS bears avoided areas within 1600 meters of gravel roads for 2nd order selection during fall (Chapter 5) and avoidance of areas within 1600 meters of gravel roads during fall had positive survival consequences for females (Chapter 6), areas within 1600 meters of gravel roads should be heavily devalued. Because PBS bears did not avoid areas near paved or gated roads during fall (Chapter 5) and preference for areas near paved and gated roads during fall did not have negative survival consequences for females (Chapter 6), areas > 250 meters from paved and gated roads should not be devalued for the fall food component. We used 250 meters as a conservative estimate of the lower asymptote for paved and gated roads because although we found bears did not avoid areas within 250 meters of paved and gated roads, the resolution of our data (250 meters) precluded us from determining how close bears traveled to roads during fall. Our proposed modification in Fig. 1 is further limited by the extent of our data. We did not evaluate whether bears avoided areas > 1600 meters from roads. If areas > 1600 meters from gravel roads affect habitat quality negatively for black bears, then our proposed function over-estimates the value of areas > 1600 meters from gravel roads.

Figure 2 shows the hypothesized relationship between proximity to roads and den value based on Zimmerman's (1992) habitat model. Areas that are 1000 meters from all roads are only slightly devalued, which should be modified based on our findings. We present one possible modification in Fig. 2. Because bears in PBS avoided denning in areas < 1000 meters from gravel roads and mean den distance to gravel roads was 2145 meters (Chapter 9), areas < 1000 meters from gravel roads should be heavily devalued. No den was located closer than 322 meters from gravel roads, so we defined the den value to be zero when distance to gravel roads < 322 meters. Because we did not know the optimal den distance to gravel roads, we used the mean den distance to gravel roads (2145 meters; SE = 126 meters) to define the upper asymptote for gravel roads. Bears in PBS preferred denning in areas < 1000 meters from paved roads and they showed no denning preference or avoidance for areas < 1000 meters from gated roads. No den was located closer than 16 meters to paved roads and mean den distance to paved roads was 1035 meters (SE = 149 meters), so we used these values to define the lower and upper asymptotes for paved roads. No den was located closer than 54 meters to gated roads and mean den distance to gated roads was 755 meters (SE = 68 meters), so we used these values to define the upper and lower asymptotes for gated roads.

The 2nd generation model did not include the escape cover component (Powell et al. 1997; Mitchell et al. 2002), but escape cover should be an important life requirement for bears. Figure 3 shows the hypothesized relationship between proximity to roads and escape cover value based on the 1st generation model (Zimmerman 1992). Areas within 800 meters of all roads were devalued, but only moderately (value = 0.50). Based on our findings, the escape cover function should be modified. We present one possible modification to the escape cover function in Fig. 3. Bears avoided areas within 800 meters of gravel roads during both summer and fall for 2nd order selection and they avoided areas within 800 meters of gravel roads during summer for 3rd order selection (Chapter 5). Moreover, avoidance of areas within 800 meters of gravel roads during fall had positive survival consequences for females (Chapter 6). Therefore, areas < 800 meters from gravel roads should be heavily devalued. Because bears did not avoid areas near paved or gated roads during summer and fall (Chapter 5) and preference for areas near paved and gated roads did not have negative survival consequences for females

(Chapter 6), areas > 250 meters from paved and gated roads should not be devalued for the escape cover component of the habitat model.

Future research could test the 3rd generation habitat model using location data that are independent of those we used to suggest model modifications. In addition, future research could evaluate how bears respond, behaviorally and demographically, to areas > 1600 meters from roads. Finally, research could take advantage of satellite technology to evaluate how bears respond behaviorally to areas within 250 meters of roads.

Table 1. The hypothesized effects of roads on habitat components (i.e., foods, den sites, escape cover) for a model of habitat quality for black bears in the Southern Appalachians (Zimmerman 1992).

Habitat model component	Road type	Road function	x (meters)
Fall Food	Paved	0.33	$x \leq 200$
		$0.000454\ x + 0.273$	$200 < x < 1600$
		1.0	$x \geq 1600$
	Gravel	0.44	$x \leq 200$
		$0.0004\ x + 0.36$	$200 < x < 1600$
		1.0	$x \geq 1600$
	Gated	0.50	$x \leq 200$
		$0.000357\ x + 0.429$	$200 < x < 1600$
		1.0	$x \geq 1600$
Den Sites	All roads	0.0	$x \leq 200$
		$0.00098\ x - 0.20$	$200 < x < 1225$
		1.0	$x \geq 1225$
Escape Cover	All roads	0.0	$x = 0$
		$0.156\ (x/1000) + 0.195\ (x/1000)^2 + 0.25$	$0.00 < x < 1600$
		1.0	$x \geq 1600$

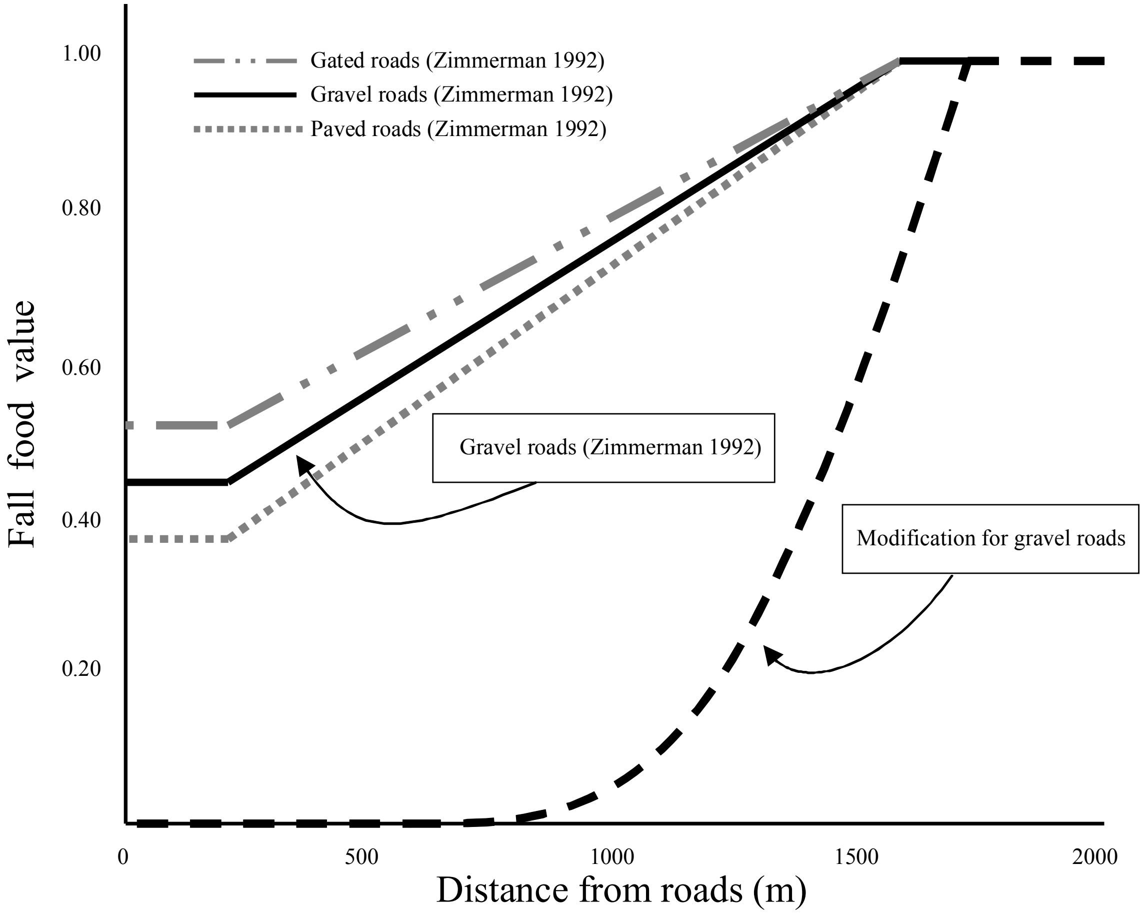
Figure captions

Figure 1. Hypothesized relationships between proximity to paved, gravel, and gated roads and fall food value for black bears in the Pisgah Bear Sanctuary, North Carolina. The gray dashed lines and the solid line represent the relationships hypothesized by Zimmerman (1992) for the fall food component of the habitat model. The black dashed line represents a modification to the relationship based on findings from this dissertation.

Figure 2. Hypothesized relationships between proximity to roads and den value for black bears in the Pisgah Bear Sanctuary, North Carolina. The solid line represents the relationship for all road types hypothesized by Zimmerman (1992) for the den component of the habitat model. The dashed lines represent modifications to the relationship based on findings from this dissertation.

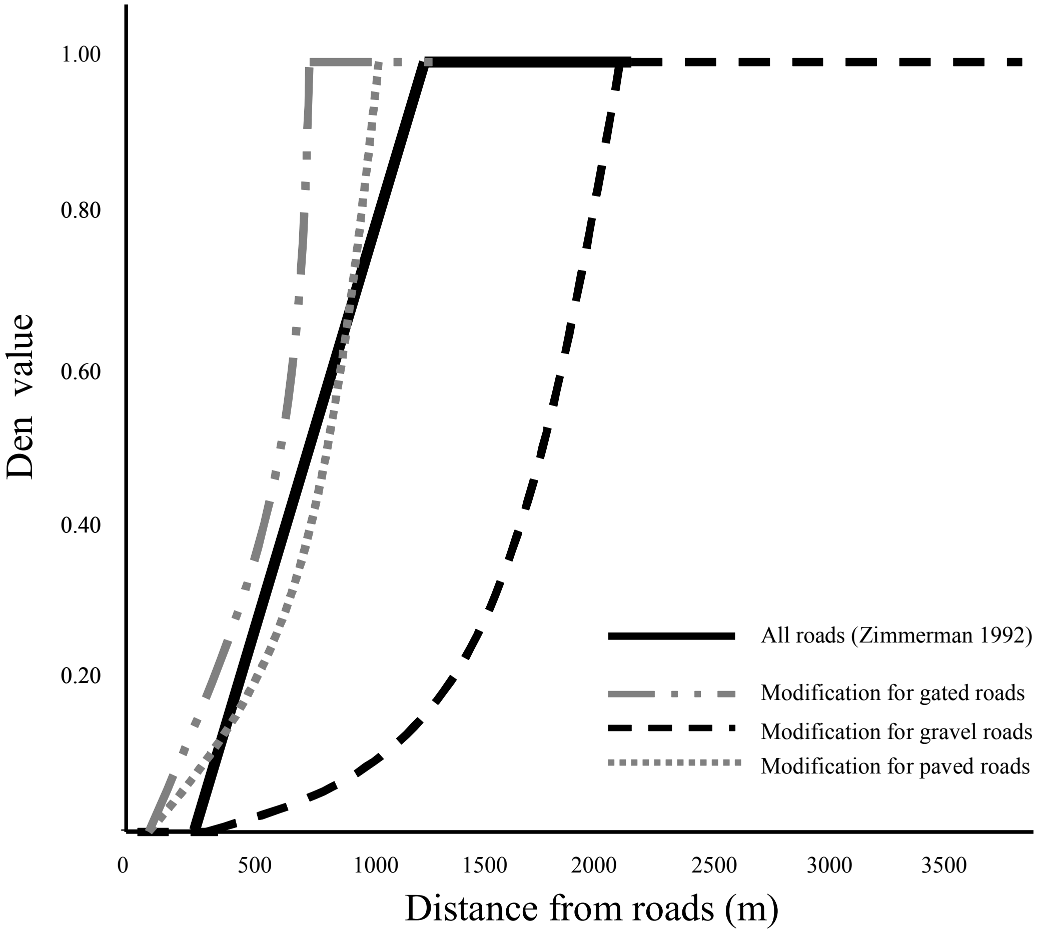
Figure 3. Hypothesized relationships between proximity to roads and escape cover for black bears in the Pisgah Bear Sanctuary, North Carolina. The solid line represents the relationship for all road types hypothesized by Zimmerman (1992) for the escape cover component of the 1st generation habitat model. The dashed lines represents a modification to the relationship based on findings from this dissertation.

Figure 1.



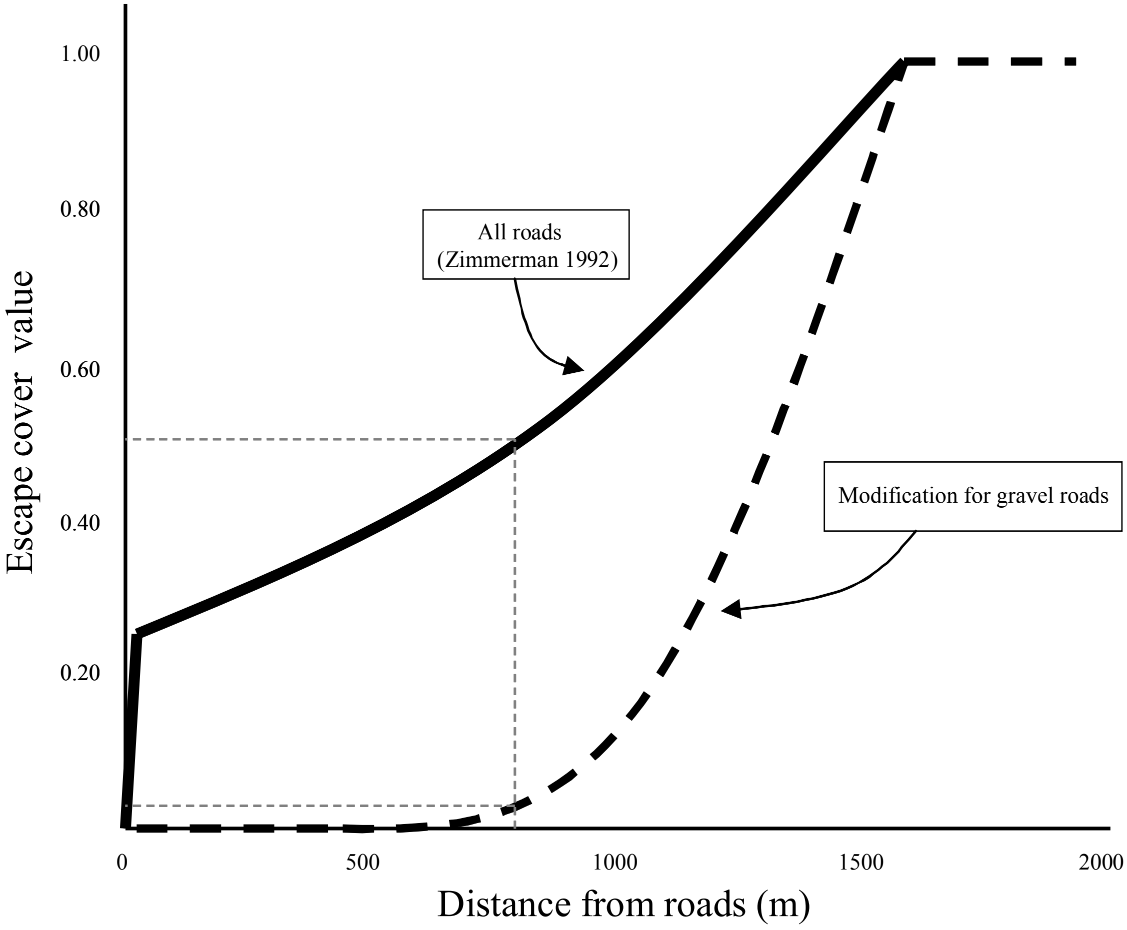
Gated roads (Zimmerman 1992)
Gravel roads (Zimmerman 1992)
Paved roads (Zimmerman 1992)
Gravel roads (Zimmerman 1992)
Modification for gravel roads
Fall food value
1.00
0.80
0.60
0.40
0.20
0
500
1000
1500
2000
Distance from roads (m)

Figure 2.



Den value
1.00
0.80
0.60
0.40
0.20
0
500
1000
1500
2000
2500
3000
3500
Distance from roads (m)
All roads (Zimmerman 1992)
Modification for gated roads
Modification for gravel roads
Modification for paved roads

Figure 3.


1.00
0.80
0.60
0.40
0.20
Escape cover value
0
500
1000
1500
2000
Distance from roads (m)
All roads
(Zimmerman 1992)
Modification for gravel roads

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APPENDIX

Equations for the 1st generation (Zimmerman 1992) and 2nd generation (Powell et al. 1997, Mitchell et al. 2002) models for predicting habitat quality for black bears within 200 meters of paved roads in the southern Appalachian Mountains. Habitat values are based on 3 Life Requirement Values (LRV); foods, den sites, and escape cover.

1st generation model: habitat quality = $1/3\ \mathrm{LRV}_{\text{food}} + 1/3\ \mathrm{LRV}_{\text{den site}} + 1/3\ \mathrm{LRV}_{\text{escape cover}}$
2nd generation model: habitat quality = $1/2\ \mathrm{LRV}_{\text{food}} + 1/2\ \mathrm{LRV}_{\text{den site}}$

$$\mathbf{LRV}_{\textbf{food}} = \frac{\text{nonseasonal food}}{7} + \left(\frac{\text{spring food}}{7} + \frac{\text{2 summer food}}{7} + \frac{\text{4 fall food}}{7}\right) * \text{interspersion}$$

Fall foods are devalued when they are close to roads

Equation for fall foods = $\left(\frac{\text{2 hard mast}}{3} + \frac{\text{grapes}}{3}\right) * \text{road function}$

1. Road function for fall foods located within 200m of paved roads = **0.33**

$$\mathbf{LVR}_{\textbf{den sites}} = \left\{\frac{(\text{conterminous forest + understory})}{2} * (\text{slope + large trees})\right\}^{2}$$

Den sites are devalued when areas are close to roads

1. Conterminous forest = **0.00** when areas are within 200m of roads

$$\mathbf{LVR}_{\textbf{escape cover}} = \left(\text{conterminous forest} + \frac{\text{understory}}{2} + \frac{\text{slope}}{4}\right) * \text{road function}$$

Escape cover is doubly devalued when areas are close to paved roads

1. Conterminous forest = **0.00** when area is within 200m of roads
2. Road function when area is within 200m of roads =
$0.156\ (0.2) + .195\ 0.2^{2} + .25 = \mathbf{0.29}$

Holding constant all components of the habitat model that are not affected by proximity to roads, the following values are calculated for LRVs when an area is within 200 meters of a paved road:

$\mathbf{LRV}_{\textbf{food}} = 1/7 + (1/7 + 2/7 + (4/7*\mathbf{0.33})) = 0.76$
$\mathbf{LVR}_{\textbf{den site}} = \{(\mathbf{0.00} + 1)/2 * (1 + 1)\}^{.5} = 1.00$
$\mathbf{LVR}_{\textbf{escape cover}} = (\mathbf{0.00} + 1/2 + 1/4) * \mathbf{0.29} = 0.22$

1st generation habitat model = (0.76 + 0.22 + 1)/3 =0.66 **total devaluation =** 0.34
2nd generation habitat model = (0 .76+1)/2 = 0.88 **total devaluation =** 0.12