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A multi-scale assessment of den selection of Louisiana black bears (Ursus americanus luteolus) in northern and central Louisiana

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A MULTI-SCALE ASSESSMENT OF DEN SELECTION OF LOUISIANA BLACK BEARS (*URSUS AMERICANUS LUTEOLUS*) IN NORTHERN AND CENTRAL LOUISIANA

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ABSTRACT

Understanding den selection for the Louisiana black bear (*Ursus americanus luteolus*) may provide insight into habitat requirements of the subspecies and assist in conservation and management efforts. With that goal, I assessed den selection of female Louisiana black bears at multiple spatial scales in northern and central Louisiana. I used 230 den-years to examine den type (tree or ground), microhabitat characteristics at dens, and effects of landscape characteristics on den selection. We also evaluated tree availability and reuse. Solitary and parturient females selected tree dens more frequently (65%) than ground dens. However, tree dens were not required for successful denning and reproduction. Ground dens were consistently located in upland habitat with dense understory. An evaluation of ground den locations relative to landscape composition and configuration indicated that ground dens were positively associated with proximity to water, greater proportions of water, and smaller patch sizes of water. Tree dens were predominantly located in baldcypress (86%) surrounded by water (80%), likely selected for the presence of a suitable cavity and were positively associated with proximity to edge and higher proportions of swamp and water habitat than surrounding areas. A survey of available tree dens indicated that densities of tree dens were comparable to other southeastern areas with sustainable bear populations, which suggested that tree den densities are likely adequate to support a population. Tree dens were associated with similar landscape characteristics across my northern and central study areas, which suggested that landscape variables may be used by managers to identify where tree dens should occur and may prioritize conservation efforts in these areas. Due to the variety of habitat types suitable for ground dens, it was not feasible to identify optimal habitat for ground dens based solely on variables that reflected land cover.

INTRODUCTION

Historically, the range of the Louisiana black bear (*Ursus americanus luteolus*), a subspecies of American black bear (*Ursus americanus*) included forested regions of Louisiana, western Mississippi and eastern Texas (Hall 1981). Because of a loss of >80% of bear habitat to agriculture (Neal 1990), Louisiana black bear populations have declined throughout their historic range. The subspecies is now only present in 3 isolated subpopulations in Louisiana. One subpopulation is located in the Tensas River Basin (TRB), and 2 subpopulations are found in the Atchafalaya River Basin (ARB; Weaver et al. 1990). As a result, in 1992 the United States Fish and Wildlife Service (USFWS) listed the Louisiana black bear as federally threatened (Neal 1992). As part of the management strategy for the Louisiana black bear, a multi-agency repatriation project was initiated in 2001 (Van Why 2003). To establish gene flow between the TRB and ARB subpopulations and increase bear abundance, female bears with cubs from the TRB were relocated to the Red-River Complex (RRC; USFWS 1995) in central Louisiana. To ensure persistence of black bears in Louisiana, an understanding of habitat requirements is essential (Clark et al. 1993).

Suitable den sites are a basic habitat requirement for black bears (Powell et al. 1997, Pelton 2003). Bears use winter dens to cope with food shortages and inclement weather (Lindzey and Meslow 1976, Johnson and Pelton 1980); moreover, dens are the site of birth and early maternal care of offspring (Johnson and Pelton 1981, Wathen et al. 1983). Because dens play such a significant role in survival and reproduction, understanding the various factors that influence den selection is valuable for black bear management.

Most studies of black bear denning have examined den use at a single spatial scale, for example studies will either focus on microhabitat characteristics (Martello and Pelton 2003) or landscape-level characteristics (Reynolds-Hogland 2007). However, habitat selection by animals may occur at various spatial scales and may be viewed as a hierarchical process (Johnson 1980); therefore, an examination of den use at multiple spatial scales may provide insight into how factors at different spatial scales interact to influence den selection.

At a small spatial scale the type of den and its characteristics are important factors, as they help mitigate effects of weather and disturbance on denned bears (Hayes and Pelton 1994). In Louisiana, both ground nests and elevated tree cavities are most commonly used (Weaver and Pelton 1994, Benson 2005). Bears, especially those with cubs of the year (COY) are thought to prefer tree dens because they offer substantially more protection than ground dens (Johnson and Pelton 1981). Not all bears, however, may have tree dens available. Den availability may influence den selection and a lack of suitable tree dens could limit population growth (Oli et al. 1997). Additionally, den reuse (the use of a single den in different years) also may provide insight into den selection as reuse is thought to reflect den availability (Alt and Gruttadauria 1984) and den type preference (Schwartz et al. 1987). Evaluating den selection at a broad scale may be useful in determining the effects of landscape-level characteristics on black bear den selection in Louisiana. Because of low topographic relief, a very small change in elevation over a short distance may create very different hydrologic conditions, often resulting in different soils and plant communities (Sharitz and Mitsch 1993). Hence, using variables that reflect land cover may be used to examine black bear den selection in Louisiana. The purpose of the research was to provide a comprehensive assessment of den selection of female Louisiana black bears at multiple spatial scales by examining den type preference, microhabitat characteristics of dens, the effect of reproductive status on den selection, tree dens availability and reuse, and the effect of landscape characteristics on den selection. This information may be useful for identifying areas with high denning potential so that appropriate conservation strategies could be established.

Specifically, I sought to evaluate the following hypotheses:

- At a small spatial scale bears likely prefer tree dens because they offer increased protection from disturbance and flooding. Therefore, I hypothesized that bears would select tree dens more frequently than ground dens, consistently select to use tree dens, that tree den reuse would be high, and that a female would continue to use a tree den once she had access.
- Because dens are used to protect bears from inclement weather and disturbance (Lindzey and Meslow 1976), I hypothesized that some microhabitat characteristics may be more important than others and characteristics that are consistently selected would reflect those characteristics that are most important to a denning bear. Additionally, if trees are being selected for based on specific microhabitat characteristics, I hypothesized that characteristics would differ between trees that were used once and trees that were used multiple times.
- Den requirement may be more specific for females with COY because energy requirements are significantly more demanding (Teitje and Ruff 1980, Alt and Gruttadauria 1984). Therefore, I hypothesized that females with COY would use tree dens more frequently than solitary bears and those with yearlings, that females that used the same den would have the same reproductive status, that reproductive output would be higher for females using tree dens, and that den

selection at a broad spatial scale would differ between females with COY and those without COY.

- Because the use of tree dens has been documented in several regions in Louisiana, and that most tree dens were located in baldcypress trees (*Taxodium distichum*; Weaver 1999, Hightower 2002, Benson 2005) I hypothesized that tree dens would not be tree dens would not be evenly distributed across habitat types on my study areas. In addition, because reuse is thought to reflect availability, I hypothesized that reuse would be highest in areas where tree den densities were lowest.
- Habitat selection may occur at a broad scale, and in Louisiana land cover may be important to den selection at the landscape-level. Therefore, I hypothesized that most dens of the same type (tree or ground) would be located in similar habitat types, the composition of the landscape around the den site would differ in comparison to the surrounding area, and that I could model den selection using variables that reflect landscape composition and configuration.

STUDY AREA

This study was conducted in the TRB in northern Louisiana and the RRC in central Louisiana, both located in the Mississippi Alluvial Valley (MAV). I studied bears in 2 areas in the TRB: Tensas River National Wildlife Refuge (25,900 ha; hereafter, Tensas; Figure 1) and 2) 2 privately owned, isolated woodlots northeast of Tensas: Blue Cat (640 ha) and Wade Bayou (690 ha; hereafter, Deltic). Deltic and Tensas were approximately 10 km apart and separated by agricultural land and Interstate 20.

The RRC encompassed several wildlife management areas (WMA), a national wildlife refuge (NWR) and blocks of privately owned land which comprises a total of >72,000 ha of suitable bear habitat (USFWS 2001). I studied bears in 3 areas in the RRC, which were the designated release sites of relocated bears: 1) Red River WMA (16,868 ha, hereafter Red River), 2) Three Rivers WMA (11,080 ha; hereafter Three Rivers; Figure 1), and 3) Lake Ophelia NWR (7,082 ha; hereafter, Lake Ophelia). Lake Ophelia is separated from Red River and Three Rivers by the Red River. Other public lands included in RRC were: Grassy Lake WMA (5,540 ha), Spring Bayou WMA (4,925 ha), and Pomme de Terre WMA (2,863 ha). Historically, 10-year flooding events would inundate 75-100% of the RRC (USFWS 2001). However, hydrology of the RRC has been altered in recent years by the Army Corps of Engineers Old River control structure, the Red River, Atchafalaya and Bayou Jeansonne levees, and the Tensas-Cocodrie pumping plant which have reduced the amount and duration of flooding (LDWF 1998).

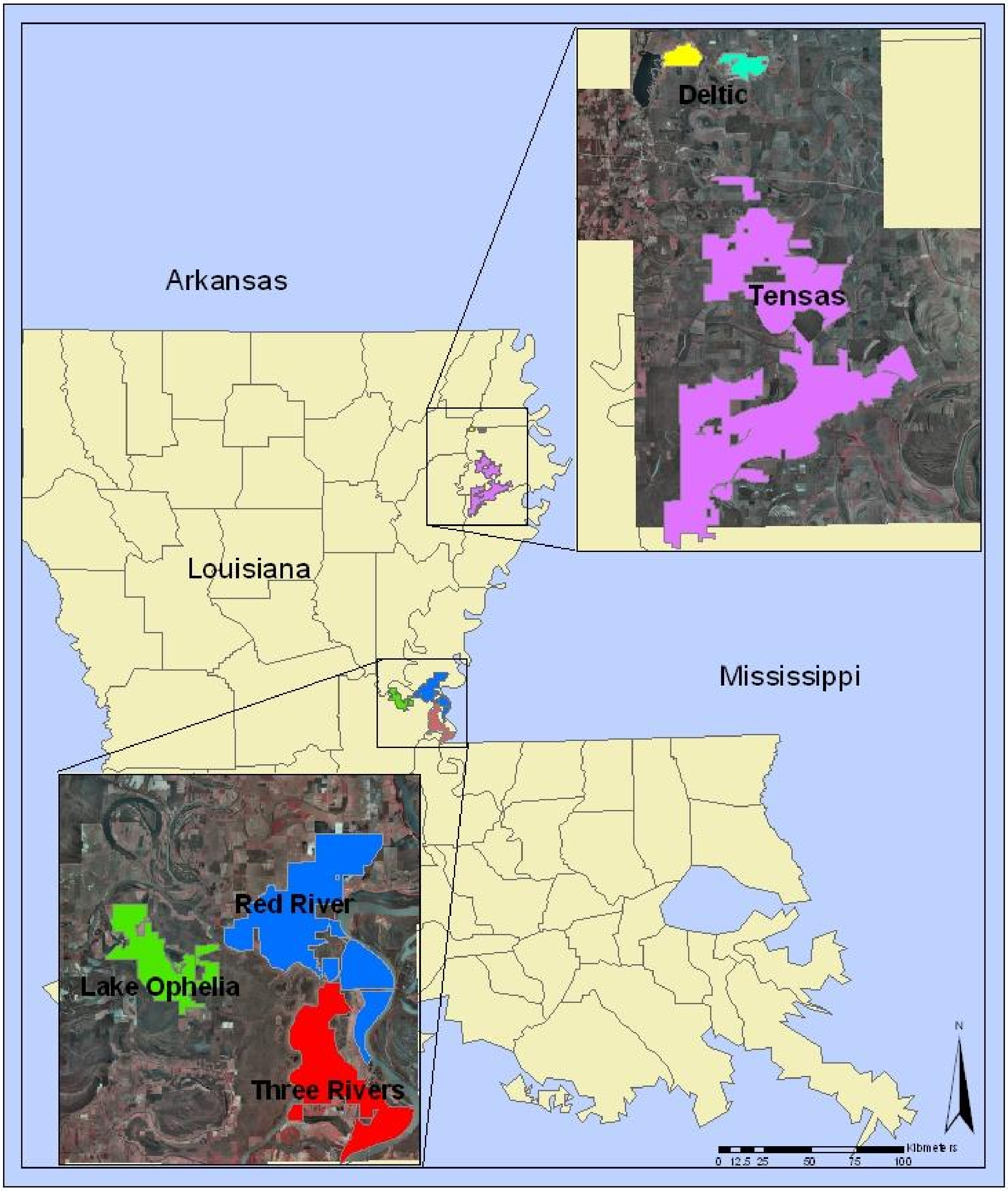

Figure 1. Locations of northern study areas (Tensas and Deltic) which are part of the current range of the Louisiana black bear, and southern study areas (Lake Ophelia, Red River, and Three Rivers) which are part of the Red River Complex and were the release sites of relocated bears.

Land Features and Vegetation Characteristics

Study areas were primarily composed of bottomland hardwood forests fragmented by agricultural land. Seasonal and permanent swamps were common, as were lakes, rivers and bayous. Topographically, the MAV was relatively flat but slight changes in elevation resulted in a variety of habitat types. Forest management practices differed among study areas. In Deltic, selective harvest was used to increase hard mast production (Benson and Chamberlain 2006), whereas a variety of timber harvest practices were used in Red River and Three Rivers to promote species and age class diversity within management compartments (LDWF 2007). Comparatively, efforts were focused on reforestation in Tensas and Lake Ophelia, and minimal timber harvest occurred in recent years.

Overstory consisted predominantly of American elm (*Ulmus americana*), sweetgum (*Liquidambar styraciflua*), willow oak (*Quercus phellos*), water oak (*Q. nigra*), Nuttall oak (*Q. texana*), overcup oak (*Q. lyrata*), persimmon (*Diospyros virginiana*), sugarberry (*Celtis laevigata*), sweet pecan (*Carya illinoinensis*), and water hickory (*C. aquatica*), interspersed with low-lying baldcypress and water tupelo (*Nyssa aquatica*) breaks. Primary understory plant species include palmetto (*Sabal minor*), greenbrier (*Smilax* spp.), blackberry and dewberry (*Rubus* spp.), poison ivy (*Toxicodendron radicans*), and Japanese honeysuckle (*Lonicera japonica*). Because of reduced flooding and continued timber harvest, Deltic exhibited dense and diverse understory, rich in soft mast producing species including French mulberry (*Callicarpa americana*), pokeberry (*Phytolacca americana*), pawpaw (*Asimina parviflora)*, and muscadine (*Vitis rotundifolia*), whereas Tensas was characterized by closed canopies and reduced understory (Benson and Chamberlain 2006). Surrounding agriculture that may have acted as a food source for black bears included corn, grain sorghum, rice, wheat, and soybean.

Bear Subpopulations

Tensas, Deltic, and the RRC were considered to have separate subpopulations. Both subpopulations in Tensas and Deltic appear to be stable and possibly increasing in size (Anderson 1997). However, the estimated bear density in Tensas (1 bear/1.43 km^2; Boersen et al. 2003) was considerably lower than in Deltic (1 bear/0.35 km^2; Beausoleil 1999), which was the highest density reported in the southeastern coastal plain. This high density was likely due to high food availability supplemented by surrounding agriculture. It has not been shown if the RRC subpopulation is viable, although reproduction of relocated bears has been observed.

METHODS

From 2005 to 2007 I collected data at dens of female Louisiana black bears that had been captured and radio-collared from 2003 to 2005 (see Benson 2005). I considered bears that were captured on Tensas or Deltic and not relocated to the RRC as part of the Tensas or Deltic subpopulations. I considered bears that were relocated as part of either Tensas or Deltic subpopulations until they were relocated. All bears that were relocated were classified as part of the RRC subpopulation, although many did not remain within the defined boundaries of the RRC. Dens of radio-collared bears were located January-March by ground-based telemetry using a receiver (Telonics© TR-4, Advanced Telemetry Systems© R4000) and antenna (Telonics© 4-element H). Den visits were attempted for all radio-collared bears. I considered bears to be denned if a ground den or tree den was located. Bears were classified as active if: 1) I saw the bear mobile and not at a den site or 2) I attempted to approach the bear ≥ 2 times and was unable to locate a den or see the bear and suspected the bear was moving based on telemetry.

At each den site I recorded universal transverse mercator (UTM) coordinates using a Garmin© hand-held global positioning system (GPS), general behavior of the bear, and reproductive status of the bear as solitary, with COY or with yearlings (cubs from the previous year). Because female black bears generally give birth biennially in January or early February (Pelton 2000), den visits for females confirmed to have reproduced the previous year began prior to 15 February, whereas females that were confirmed not to have reproduced the previous year were visited after 15 February. I determined reproductive status by either visual or auditory confirmation of COY. When reproductive status could not be confirmed at the den site, bears were approached after den emergence to determine if COY or yearlings were present. Reproductive status of a bear that remained active was classified as unknown unless a yearling was positively identified; however, as these bears appeared to remain active throughout the den season it is assumed that they did not have COY.

When bears were denned inside tree cavities, I climbed trees using the single rope technique (Jepson 2000). I attempted to see all bears, which required a spotlight for deeper tree cavities. I measured 12 microhabitat characteristics at each tree den (Table 1). When bears were denned on the ground, I attempted to approach them slowly and quietly to avoid flushing the bear. If I was unsuccessful and the bear fled the den, I recorded microhabitat characteristics (Table 2). However, if the bear remained at the den, I did not collect microhabitat data until after she permanently left the den in March or April. In those cases, I did not measure canopy cover where it was obscured by spring vegetation growth.

Den Type

To address my hypothesis that females selected tree dens more frequently than ground dens, I partitioned dens by type (tree and ground) and assessed the proportion of females that selected each of these den types. I excluded non-collared bears because I was actively looking for bears in tree dens to estimate den reuse, thus inclusion of non-collared bears would have biased results. Because all bears in the RRC (n =22) were from Tensas (n=15) or Deltic (n =7) an individual bear may have had den locations representing different subpopulations.

Fidelity to Tree Dens

To determine if bears showed fidelity to tree dens, I examined multiple years of den data for each bear. For every den season, each bear was classified as either in a tree or on the ground, which included both denned and active bears.

Table 1. Microhabitat characteristics recorded for tree dens used by radio-collared female Louisiana black bears during 2003-2007 in the Tensas River Basin and central Louisiana.

Diameter at breast height (DBH)	Diameter of the tree at breast height
Canopy cover	Percentage of closed canopy, measured using a densiometer and calculated as the mean of 4 reading taken with my back to the tree in cardinal directions
Tree height (m)	Height of the tree, measured using a clinometer and calculated as the height difference between the highest branch and the base of the tree
Cavity entrance height (m)	Height of cavity entrance measured using a clinometer and calculated as the height difference between the middle of the cavity opening and the base of the tree
Water percentage	Estimated percentage of the tree's circumference that was submerged in water
Water depth (cm)	Average estimated depth of water at the base of the tree
Cavity opening direction	Direction in which the entrance of a side cavity faced
Cavity depth (cm)	Depth of the cavity measured from the base of the cavity entrance to the platform
Cavity entrance width (cm) entrance	Width of the entrance to a side cavity measured at the widest point of the opening
Cavity entrance length (cm)	Length of a side cavity entrance measured at the longest point of the opening
Inside cavity width (cm)	Width across the inside of the tree at the cavity entrance
Tree species	Identification of the tree to species

Table 2. Types of ground dens and microhabitat characteristics recorded for ground dens used by female Louisiana black bear during 2003-2007 in Tensas River Basin and central Louisiana.

Types of ground dens	
Nest	Open dens not associated with any additional structures
Nest at the base of a tree	Nest dens within 1 m of a tree that is >10cm DBH.
Slash Pile	Dens within piles of woody debris, often the product of timber harvest
Under a downed tree	Dens positioned below or adjacent to a downed tree
Microhabitat characteristics recorded for all types of ground dens	
Species and description of vegetation	Identification of species and description of vegetation primarily used to construct the den
Canopy cover	Percentage of closed canopy, measured using a densiometer and calculated as the mean of 4 readings taken from the edge of the nest in each cardinal direction
Microhabitat characteristics recorded for dens classified as nests at the base of a tree	
Diameter at breast height	Diameter of the tree at breast height
Tree height	Height of the tree, measured using a clinometer and calculated as the height difference between the highest branch and the base of the tree
Tree species	Identification of the tree to species

I calculated the proportion of bears that consistently denned in trees over multiple years. However, this proportion of bears does not account for the possibility that some bears remained on the ground because surrounding trees were occupied by other bears and thus unavailable during that particular den season. Therefore, to account for this possible lack of availability, I determined whether trees were occupied when I surveyed for den reuse in 2006-2007 (see Tree Den Reuse). Then I calculated the proportion of bears that remained on the ground during a den season in which a tree previously by the bear remained unoccupied.

Tree Den Reuse

To address my hypothesis that tree den reuse would be high, I first estimated den reuse by checking for bears in tree dens that had been used at least once from 2003 to 2005, in 2006 and 2007; new tree dens from 2006 also were checked in 2007. I began climbing trees to check for reuse in late January. If a bear was located in a tree in January or early February, I climbed the tree again after 15 February to determine reproductive status of the bear. Because different studies have used different methods to calculate reuse, I calculated reuse 3 ways. In method 1, I estimated reuse using den-years of radio-collared bears, whereby 1 den-year=1 den season of 1 bear. Percent reuse was calculated by dividing number of den-years of bears that denned in a previously used tree den by the total number of den-years of bears denned in any tree den. In method 2, I estimated reuse by examining the number of times each tree den had been used by a radio-collared bear. I calculated percent reuse by dividing the number of tree dens used >1 year by total number of known tree dens. In method 3, I estimated reuse by examining the number of years that a tree den was available where for each year a tree was classified as either empty or occupied. I determined the number of empty and occupied trees in 2006 and 2007 by checking all tree dens that had been previously used; occupied tree dens included both radio-collared bears and non-collared bears. I calculated percent reuse by dividing the sum of all occupied trees from each year, by the sum all trees from each year (Alt and Gruttadauria 1984). Estimates were calculated for each subpopulation and across subpopulations. To determine whether my estimated percentage of den reuse should be considered high, I compared estimates among subpopulations and previous studies. I also examined den data over multiple years, to determine whether reuse occurred primarily by the same bear that had initially denned in the tree, and whether bears more frequently selected new tree dens or reused a den that they had used in a previous year.

Den Characteristics

To determine whether specific microhabitat characteristics were consistently selected for, I first calculated mean, standard error, and minimum and maximum values for each microhabitat characteristic of tree and ground dens measured in this study. Tree species, percent water, and cavity direction, were summarized by partitioning data into relevant categories and provided the percent occurrence for each category. I then reviewed data to determine whether characteristics were consistent among dens of the same type.

Reproductive Status and Den Selection

To assess whether females with COY selected tree dens more frequently than solitary bears and those with yearlings, I examined the proportion of bears using each den type relative to reproductive status of the bear. To further assess whether den selection reflected reproductive status, I reviewed multiple years of den data to determine whether reuse of a particular tree occurred primarily by bears with the same reproductive status.

To assess differences in litter size relative to den type, I used an analysis of variance (ANOVA) to test if litter size differed between tree dens and ground dens. To determine if differences in den selection at a broad scale differed by reproductive status of the female, I used a compositional analysis (Aebischer et al. 1993; see Effects of Landscape Characteristics on Den Selection) partitioned by den type to test if the composition of the landscape around the den site relative to the surrounding area differed between parturient and non-parturient bears for each den type. For this analysis females with yearlings were classified as non-parturient and only bears in Tensas were included because sample sizes were too small on Deltic and the RRC.

Tree Den Availability

To assess tree den availability across study areas and habitat types, I estimated availability of tree dens on Tensas, Deltic, Red River, and Three Rivers by conducting random plot surveys. I generated random points across each area using the Spatial Analyst extension in ArcView® 3.3. Number of sites surveyed reflected the relative size of each area (see Study Area) and were as follows: 60 points on Tensas, 30 on Three Rivers, 50 on Red River and 10 on each woodlot on Deltic (20 total). In accordance with methods outlined by Hersey et al. (2005), I surveyed a 100 m × 100 m plot at each point. Trees that were ≥84 cm DBH were recorded as potential tree dens (Johnson 1978). Additionally, I recorded tree species, DBH, presence of claw marks, presence of a cavity, and size of the cavity opening classified as small (0-15 cm), medium (15-30 cm), or large(>30 cm). Tree counts were scaled into densities according to habitat type and study area. Because baldcypress trees swell at the base of the trunk, those with a DBH of 84 cm are generally not large enough to accommodate a bear. Therefore, I only used baldcypress trees with a DBH ≥ 145 cm to calculate density of tree dens by study area as this was the minimum recorded DBH for a baldcypress tree used as a den in this study.

I estimated tree den availability for Lake Ophelia using data collected in 2002 by USFWS personnel. Seven evenly spaced transect lines that extended between the east and west boundaries of the refuge were surveyed. Trees with a DBH of ≥ 86 cm within sight of the transect line were recorded in addition to DBH, tree species, cavity size, and UTM coordinates. Although all trees that were visible at any distance were recorded, I only included those within 50 m because this was the approximate range of consistent visibility based on my experience surveying random plots. Using ArcGIS® 9.0, I overlaid the line transects, and tree location coordinates on my land cover layer (see Effects of Landscape Characteristics on Den Selection). I used the X-tools extension to create a 50 m buffer around each transect line and calculate the total area and area of each habitat type within the buffers, which comprised 381 ha. I counted all trees located within the buffers. Tree counts were scaled into densities according to habitat type and across study area.

I assessed den availability according to 1) number of large trees, 2) number of large trees with any size cavity, and 3) number of large trees with a cavity that could potentially be used by a bear (large cavity opening and above the flood line; Hersey et al. 2005). I considered large trees with cavities suitable for a bear to be potential current tree dens, whereas large trees without cavities or with small or medium cavities could be tree dens in the future. I categorized trees by species as baldcypress, oak, or other species and reported the proportion of trees found in each category. To further investigate tree den availability, I compared reuse estimates with estimated densities of tree dens for each study area.

Effects of Landscape Characteristics on Den Selection

To examine den selection at a landscape-level, I created a Geographic Information System (GIS) land cover layer using ArcView® 3.3 software (Environmental Systems Research Institute Inc., Redlands, California, USA) by digitizing habitat patches using Digital Ortho Quarter Quadrangle (DOQQ; 2004) aerial photographs of Tensas, Deltic, Lake Ophelia (Benson 2005), Red River, and Three Rivers. I also digitized areas around bear dens that were outside the designated study areas to the spatial extent that analyses could be performed. I classified land cover patches according to 6 habitat types: upland forest, lowland forest, swamp, water, agriculture, regenerating forest (Table 3). Any references made to habitat types are based on this GIS land cover layer. To determine the habitat type in which dens were located, I overlaid spatial coordinates of den sites on my digitized land cover layer and spatially joining them using ArcView® 3.3. I reported the number of den sites located within each habitat type for both ground dens and tree dens. I subsequently investigated den selection at a broader spatial scale based on *a-priori* knowledge of black bear space use. I used ArcGIS 9.0 to create 2 different sized buffers around each den site, one was the size of the mean annual 95% fixed kernel home range estimate, the other was the size of the mean annual 50% fixed kernel core area estimate reported by Benson (2005; buffer radii rounded to the nearest 100m). As areas of space use differed among subpopulations (Benson 2005), I used buffer sizes that were specific to each subpopulation. Radii of small and large buffers for Tensas, Deltic, and the RRC were 700m and 2000m, 400m and 1000m, and 800m and 2400m, respectively. I intersected buffers with the land cover layer and calculated percent composition of each habitat type within buffered areas using the X-tools extension in ArcView® 3.3. I assumed that females selected den sites at a scale consistent with the core use area (50%

estimate of space use) because size of the core area represents a scale at which habitat configuration and composition is most important to an animal (Samuel et al. 1985). Additionally, I assumed that females were selecting for habitat around the den site from habitat available to bears at a scale consistent with the size of female home ranges (95% estimate of space use).

Table 3. Description of 6 habitat types used to investigate den selection of female Louisiana black bears in northern and central Louisiana, 2003-2007 (adapted from Benson 2005).

Upland forest	Bottomland hardwood forests in relatively high elevation not subject to frequent or lengthy flooding, includes ridges, natural levees, terraces and higher hardwood flats
Lowland forest	Bottomland hardwood forests in relatively low elevation subject to seasonal flooding, includes lower hardwood flats and first bottoms
Swamp	Forested areas generally flooded throughout the year, vegetation is predominantly baldcypress, tupelo and other flood tolerant taxa
Water	Bodies of water including lakes, rivers, bayous, sloughs and ditches
Agriculture	Human altered landscapes devoid of forest, such as crop fields and pastures
Regenerating forest	Early successional (0-12 years) forests planted with trees or regenerating naturally, characterized by open canopy and dense understory of shrubs, vines and/or saplings

I used compositional analysis (Aebischer et al. 1993) to compare habitat composition at the core area scale to that at the home range scale. I tested differences of log ratio of proportions of each habitat type found at both spatial scales with a multivariate analysis of variance (MANOVA). A ranking matrix of *t*-tests was constructed to evaluate habitat type preferences. I partitioned data by den type because I had *a priori* knowledge that ground dens and tree dens were associated with different habitat types (see Results), and by subpopulation, because of reported differences in habitat selection among subpopulations (Benson and Chamberlain 2007).

To further assess den selection at the landscape scale, I modeled black bear den selection using variables that reflected composition and configuration of selected habitat types. Spatial coordinates of den sites were overlaid on the land cover layer in ArcGIS 9.0 and buffers with a 500m radius were created around each den location. The size of the buffer was selected because it was between the mean 50% core area sizes reported for Tensas and Deltic (Benson and Chamberlain 2007). I quantified landscape structure within each buffer by calculating landscape and class-level metrics using the patch analyst extension (Elkie et al. 1999) within ArcView® 3.3 (Table 4) and I used ArcView® 3.3 to calculate distances from each den site to selected landscape features.

I developed 7 *a priori* models that predicted tree den locations as a function of landscape structure and composition (Table 5). These models represented research hypotheses regarding factors that influence tree den locations and were based on results of this study and previous research. Most models were based on results of my compositional analysis which suggested that water and swamp habitats were preferentially selected, that tree den availability is highest in these habitats, and the knowledge that most dens were baldcypress (see Results). Four models were based on the hypothesis that den selection reflected both swamp and water habitat in varying degrees of composition and structure.

Table 4. Landscape metrics used to develop a spatial model of den selection for female Louisiana black bears in northern and central Louisiana, 2003-2007.

Parameter	Description	Level
UCA	Area of upland forest	Class
UPS	Upland mean patch size	Class
LCA	Area of lowland forest	Class
SCA	Area of swamp	Class
SPS	Swamp mean patch size	Class
WCA	Area of water	Class
WPS	Water mean patch size	Class
SDI	Shannon diversity index	Landscape
DWA	Distance to water feature	Landscape
DED	Distance to edge	Landscape

Table 5. *A priori* candidate models developed to assess selection of tree dens by female Louisiana black bears in northern and central Louisiana, 2003-2007.

Model	Metric Included
Swamp and water 1	SCA, WCA
Swamp and water 2	SCA, DWA
Swamp, water and edge	SCA, WCA, DED
Swamp	SCA, SPS
Water	WCA, WPS
Swamp, water, lowland and edge	SCA, WCA, LCA, DED
Shannon Diversity index and edge	SDI, DED

My swamp model and water model were developed to determine whether one of those habitat types was most influential. Edge was included in 3 models because land use practices often create edge around bodies of water, thus the location of baldcypress may be related to the presence of edge.

I developed 9 *a priori* models that predicted ground den locations as a function of landscape structure and composition (Table 6). These models represented research hypotheses regarding factors that influence ground den locations and were based on results of this study which indicated that most ground dens were located in upland habitat, and in areas with greater proportions swamp, lowland and water than surrounding areas (see Results). Models were based on the hypothesis that bears in ground dens selected for dense vegetation and reduced probabilities of inundation, which are often found on ridges adjacent to topographically low lying areas. The location of such ridges may be related to upland, lowland, swamp and water habitat types in varying degrees of composition and structure, therefore I used different combinations of these variables to model the location of ground dens.

I calculated landscape metrics and distances to landscape features for an equal number of random points as den sites within Tensas and Deltic. I used logistic regression to develop predictive models based on den sites and random points for each den type (ground and tree) using data from Tensas and Deltic. I used the information theoretic approach to select the best approximating model (Burnham and Anderson 1998). I used AIC_c values for model selection and calculated ΔAIC_c values to compare relative distances between the best approximating model and each competing model (Burnham and Anderson 1998). I also calculated normalized Akaike weights (w_i), which provided additional means to evaluate relative strength of each model (Burnham and Anderson 1998) given the data and the set of candidate models. After the best approximating model was selected, I validated both the tree den model and ground den model using den locations from the RRC. I developed cross-classification rates by applying parameter estimates from the original model to each validation data set. The number of den locations used to assess landscape-level den selection differed from the number of den locations used to evaluate den type because I included dens of non-collared bears that were confirmed as female (n=7) and I excluded den locations from Mississippi (n=5) because habitat types did not conform to those delineated in this study. All statistical tests were performed using SAS 9.1 (SAS Institute, 2003, Cary, North Carolina, USA).

Table 6. *A priori* candidate models developed to assess ground den selection by female Louisiana black bears in northern and central Louisiana, 2003-2007.

Model	Metric Included
Water 1	DWA
Water 2	WCA, DWA
Water 3	WCA, WPS, DWA
Upland and water	UCA, DWA
Upland and swamp	UCA, SCA
Swamp	SCA, SPS
Upland, Swamp and water,	UCA, SCA, WCA
Upland	UCA, UPS
Upland, lowland, swamp and water	UCA, LCA, SCA

RESULTS

Den Type

Den data were recorded for 230 den-years of 72 individual bears (Table 7). Most dens used by females in Tensas and Deltic were tree dens (67%; Table 8). The proportion of bears that used tree dens was lower in the RRC (42%). The RRC had a greater proportion of bears that were classified as active (20%), compared to Tensas and Deltic (≤15%).

Tree Den Fidelity

Most (52%) bears used both ground dens and tree dens (Table 9). The proportion of bears that exclusively used tree or ground dens was relatively similar (22% and 26%, respectively). There was no apparent trend for bears to switch from ground to tree or vice versa. Additionally, I examined the den history of 27 bears that remained on the ground in 2006 and/or 2007 for a total of 40 den-years. I found that 58% of den-years in which bears remained on the ground, bears did so despite that a tree den that the bear had used in a previous year was unoccupied.

Table 7. Number of den-years[1] of data recorded for radio-collared female Louisiana black bears from 2003-2007 by subpopulation in the Tensas River Basin (Tensas and Deltic) and central Louisiana (RRC).

	Tensas	Deltic	RRC	**Total**
Number of den-years	102	73	55	**230**
Number of individual bears	44	26	22	**72**[2]
Mean number of den-years/ bear	2.3	2.8	2.5	**3.2**

[1]One den-year= 1 den season of 1 individual bear.
[2] Not equal to the sum total because bears in the RRC came from Tensas and Deltic.

Table 8. Den types of radio-collared female Louisiana black bears during 2003-2007 by reproductive status and subpopulation in the Tensas River Basin (Tensas and Deltic) and central Louisiana (RRC).

	Bears with cubs of the year				Solitary bears			
	Tensas	Deltic	RRC	**Total**	Tensas	Deltic	RRC	**Total**
Tree den	34	18	1	**53**	23	18	14	**55**
Ground den	11	7	9	**27**	6	9	14	**29**
No den (active)	0	0	0	**0**	0	0	0	**0**
Total	**45**	**25**	**10**	**80**	**29**	**27**	**28**	**84**

	Bears with yearlings				Bears with unconfirmed reproductive status			
	Tensas	Deltic	RRC	**Total**	Tensas	Deltic	RRC	**Total**
Tree den	2	4	3	**9**	1	0	0	**1**
Ground den	9	4	2	**15**	0	0	0	**0**
No den (active)	3	2	2	**7**	13	11	10	**34**
Total	**14**	**10**	**7**	**31**	**14**	**11**	**10**	**35**

Table 9. Fidelity of tree den use for female Louisiana black bears[1] during 2003-2007 by subpopulation in the Tensas River Basin (Tensas and Deltic) and central Louisiana (RRC).

	Tensas	Deltic	RRC	**Percent total**
Number of bears that exclusively used tree dens	10	5	2	**26%**
Number of bears that remained exclusively on the ground as denned or active	5	3	6	**22%**
Number of bears that used both tree dens and remained on the ground as denned or active	15	12	7	**52%**

[1]Included only bears for which data was collected for multiple (2-5; $\overline{x}$ =3.2) years

Tree Den Reuse

Tree den reuse was based on 118 den-years of 54 radio-collared bears and 7 den-years of 7 non-collared bears. Bears used 94 different tree dens. During the 2006 and 2007 den seasons, I climbed 55 tree dens that had been occupied by a radio-collared bear from 2003 to 2005 to check for the presence of a bear. An additional 18 trees occupied by radio-collared bears in 2006 were checked in 2007. Eight non-collared bears were found in tree dens, 4 in both 2006 and 2007. Six of the 8 non-collared bears were confirmed as female by the presence of ear tags or cubs and 2 were of unknown sex. Twenty seven tree dens were used >1 time (6 were used 3 times, and 21 were used twice). Data were recorded for all tree dens in 2006 and 2007, but only recorded for tree dens used by radio-collared bears from 2003-2005, thus it is possible that some trees were used >3 times.

Each method used to calculate percent reuse provided slightly different estimates. Methods 1 (Table 10) and 2 (Table 11) both produced similar estimates of den reuse in Tensas and Deltic (22%-24%). The reuse estimate calculated using Method 3 (Table 12) was similar to that of other methods for Tensas (20%), however for Deltic, reuse estimate was half that of other methods (11%). According to all 3 methods, reuse was lowest in the RRC (0%-17%).

Dens were reused more frequently by different bears than by the same bear that had initially used the den. One hundred percent (n=3) of den reuse in the RRC was by the same bear that had previously used the den, whereas in Tensas and Deltic only 46% and 11% of reuse was by the same bear, respectively (Table 10). Most bears were found to use different tree dens, rather than reusing one from a previous year. In 2006 and 2007 there were 24 instances where a bear that had previously (2003-2005) used a tree den, denned in a tree again. Of those 24 instances, 29% of bears reused their tree den; whereas 71% selected a different tree despite that their tree den from a previous year remained unoccupied.

Table 10. Percentage of radio-collared female Louisiana black bears that reused a tree den known to have been used in a previous year from 2003-2007, by subpopulation in the Tensas River basin (Tensas and Deltic) and central Louisiana (RRC).

	Tensas	Deltic	RRC	**Total**
Total den-years[1]	60	40	18	**118**
Total reuse-years[2]	13	9	3	**25**
Percent reuse	22%	23%	17%	**21%**
Number of reuse-years that were by the same bear	6	1	3	**10**
Percent of reuse that was by same bear	46%	11%	100%	**40%**

[1] One den-year=1 den season of 1 individual bear.
[2] One reuse-year= 1 season that a bear is denned in a tree that had been occupied in a previous year; if a tree was used 3 times then the number of reuse-years would be 2.

Table 11. Percentage of tree dens used >1 year during 2003-2007 by radio-collared female Louisiana black bears by subpopulation in the Tensas River Basin (Tensas and Deltic) and central Louisiana (RRC).

	Tensas	Deltic	RRC	**Total**
Total number of different tree dens used	46	31	17	**94**
Number of tree dens used >1 time	11	7	2	**18**
Percent reuse	24 %	23%	12%	**19%**

Table 12. Percentage of known tree dens reused by female Louisiana black bears by subpopulation in the Tensas River Basin (Tensas and Deltic) and central Louisiana (RRC) in 2006 and 2007.

	Tensas	Deltic	RRC	**Total**
Number of tree dens checked for reuse	64	37	13	**114**
Number of tree dens reused	13	4	0	**17**
Percent Reuse	20%	11%	0%	**15%**

Tree Den Characteristics

Microhabitat characteristics associated with tree dens were recorded for 94 individual tree dens used by a female bear at least once from 2003 to 2007 (Table 13). Most (86%) tree dens were found in baldcypress. Other tree species housing dens included oak spp., hickory, sweetgum, and cottonwood (*Populus deltoides*). The narrowest width of a side entrance was 23 cm, but the overall smallest entrance was 29 cm × 55 cm. Canopy cover varied substantially, from almost completely open to closed. Most (68%) tree dens were completely surrounded by water, which was usually (69% of dens) ≤ 61cm deep. Tree dens located in water >121cm of depth (n=9) were either in a bayou or a lake. Most (57%) tree dens had side entrances although there was no apparent trend in the direction in which they opened. Many (50%) cavities were <3m deep, and several (31%) trees with open top cavities were <1m deep. In comparing characteristics of trees used multiple times to those only used once, I found that tree dens that were reused had a larger mean DBH (223.8 ± 9.5), than trees that were known only to be used once (189.6± 7.4).

Ground Den Characteristics

Microhabitat characteristics were recorded at 71 ground dens. Most ground dens were associated with standing or downed trees (55%; Table 14). Nest dens at the base of trees were most commonly (53%) found at the base of oak spp.; other trees for which species was identified were sweetgum, sugarberry, and American elm. Mean DBH of trees adjacent to nests was 42 (SE=8.4, range= 17-117cm), and mean height was 19.5 (SE=2.8, range= 3 - 35m). In general ground dens were located in areas of thick understory, primarily comprised of palmetto (*n*=23), greenbrier and *Rubus* spp. (*n*=12), or switchcane (*Arundinaria gigantea*; *n*=4). Most (88%) nests were oval in shape and built up with surrounding vegetation and debris. Less elaborate nest dens may have been day beds that were only used temporarily during the den season. Data that may support this include multiple ground dens found for a single bear (*n*=10), presence of scat adjacent to ground nests (*n*=8) and 3 instances when I located a bear in a ground den and subsequently found the same bear active (not denned) within the same den season.

Reproductive Status and Den Selection

Parturient females selected tree dens more frequently (66%) than non-parturient females (43%), assuming that females that remained active during the winter do not have COY. Although, only 10% (*n*=10) of females with COY used tree dens in the RRC. In Tensas, females with yearlings used ground dens most frequently (64%), whereas in Deltic and the RRC females with yearlings used ground dens and tree dens with similar frequency, although samples sizes were much smaller in these areas.

Table 13. Microhabitat characteristics of tree dens used by female Louisiana black bears during 2003-2007 in the Tensas River Basin and central Louisiana.

	n	Mean ±SE	Min	Max	Percent total
Canopy cover (%)	84	51.4 ± 2.1	3.4	95.3	-
DBH (cm)	83	200.0 ± 6.1	64.0	320.0	-
Height (m)	83	24.0 ± 0.8	1.8	45.4	-
Cavity entrance height (m)	82	11.9 ± 0.7	1.1	28.3	-
Cavity depth from entrance (m)	82	3.9 ± 0.4	0.2	5.3	-
Cavity entrance width (cm)	64	49.2 ± 3.2	23.0	160.0	-
Cavity entrance height (cm)	63	137.6 ± 13.4	35.6	462.2	-
Inside diameter at entrance (cm)	50	75.8 ± 3.1	33.0	152.4	-
Water depth at base of tree (cm)	56	62.2 ± 6.1	18.0	200.0	-
Tree species:					
Baldcypress	80	-	-	-	86
Oak species	9	-	-	-	10
Other	4	-	-	-	4

(table continued)

Surrounding water:					
Not surrounded by water	19	-	-	-	20
Partially surrounded by water	7	-	-	-	8
Completely surrounded by water	68	-	-	-	72
Direction of cavity entrance:					
North (315°-45°)	17	-	-	-	35
East (45°-135°)	12	-	-	-	25
South (135°-225°)	9	-	-	-	19
West (135°-225°)	10	-	-	-	21

Table 14. Types of ground dens used by radio-collared female Louisiana black bears during 2003-2007 by subpopulation in the Tensas River Basin (Tensas and Deltic) and central Louisiana (RRC).

	Tensas	Deltic	RRC	**Total**
Nest den	14	9	9	**32**
Nest at the base of a tree	12	5	2	**19**
Under a downed tree	0	1	8	**9**
Slash pile	0	5	6	**11**
Total	**26**	**20**	**25**	**71**

Most (44%) tree dens that were used multiple times were used by both parturient and non-parturient females, compared to 37% that were used exclusively by non-parturient females (1 with yearlings), and 19% that were used exclusively by parturient females. To determine whether litter size was related to den type, the number of cubs in 43 litters (27 Tensas, 8 Deltic and, 8 RRC) 2003 to 2007 was determined from. All litters were from different females, and therefore independent. I pooled litter sizes across years because sample sizes were small within year; therefore, litter sizes were assumed to be independent of year (Hightower et al. 2002). Litter size did not differ among subpopulations ($F_{2,40}$=1.90, P= 0.16; Welch's ANOVA for heterogeneous variance) therefore litters were pooled across subpopulations. Litter sizes were similar between tree dens (n=19, $\bar{x}$ =2.37) and ground dens (n=24, $\bar{x}$ =2.17; $F_{1,41}$= 0.39, P= 0.54).

At the landscape-level, reproductive status did not affect selection of ground dens ($F_{5,28}$= 2.09, P=0.11), but did affect selection of tree dens ($F_{5,56}$=15.31, P<0.0001). Non-parturient females (n=36) selected (in order of preference based on the t-statistics between habitat types) swamp, lowland forest, water, regenerating forest, upland forest and agriculture, whereas parturient females (n=26) selected swamp, water, lowland forest, upland forest, regenerating forest, and agriculture.

Tree Den Availability

Deltic had the highest density of trees without cavities or cavities of any size and Red River had the highest density of trees with large cavities (Table 15). Lake Ophelia had the lowest density of tree dens regardless of cavity size, about a tenth of that of Red River. Baldcypress comprised 52% of all trees with a DBH ≥84cm and 87% of trees with cavities suitable for a bear (Table 16). Oaks were the second most abundant species of trees with large cavities, followed by other species including hackberry, honey locust

(*Gleditsia triancanthos*), green ash (*Fraxinus pennsylvanica*), and sycamore (*Platanus occidentalis*), which together only comprised 3% of tree dens with large cavities. Density estimates of tree dens were not evenly distributed across habitat types (Table 17). Swamp habitat had the highest density tree dens. Densities of tree dens with large cavities were similar in water, upland forest, and lowland forest habitats, whereas density of trees without cavities or with cavities of any size was greater in lowland forest habitat. In comparing tree den availability estimates to reuse estimates, I found that reuse was higher where tree den density was lower, which was in Tensas. Reuse in the RRC could not be compared with den availability because most tree dens (*n*= 14; 88%) were outside the designated study areas for which tree den availability was estimated.

Table 15. Mean density of tree dens[1] (trees/ha) with 95% confidence limits (CL) by study area according to tree den surveys in the Tensas River Basin (Tensas and Deltic) and central Louisiana (Red River, Three Rivers and Lake Ophelia) and densities of tree dens in the Mobile-Tensaw Delta, Alabama and White River National Wildlife Refuge, Arkansas (Hersey et al. 2005)

	Tensas		Deltic	
	Mean	CL	Mean	CL
Large trees	1.12	0.76-1.47	2.65	1.97-3.33
Large trees with a cavity	0.35	0.19-0.51	0.85	0.36-1.34
Large trees with a cavity suitable for a bear	0.15	0.06-0.24	0.20	0.01- 0.39

(table continued)

	Red River		Three Rivers	
	Mean	CL	Mean	CL
Large trees	1.32	0.89-1.75	0.63	0.24-1.02
Large trees with a cavity	0.72	0.41-1.02	0.26	0.01-0.52
Large trees with a cavity suitable for a bear	0.24	0.92-0.38	0.13	0.00-0.35

	Lake Ophelia		Mobile-Tensaw Delta	
	Mean	CL	Mean	CL
Large trees	0.02	0.00-0.02	0.91	0.58-1.25
Large trees with a cavity	0.02	0.00-0.02	0.13	0.02-0.23
Large trees with a cavity suitable for a bear	0.02	0.00-0.03	0.00	0.00-0.09

	White River North		White River South	
	Mean	CL	Mean	CL
Large trees	0.91	0.41-1.40	0.91	0.58-1.25
Large trees with a cavity	0.16	0.01-0.32	0.38	0.02-0.23
Large trees with a cavity suitable for a bear	0.11	0.00-0.24	0.28	0.19-0.38

[1] Data collection methods differed for Lake Ophelia (see Methods)

Table 16. Number and corresponding percentage of potential tree dens by tree species located through tree den surveys during 2006-2007 in the Tensas River Basin and central Louisiana.

	Baldcypress		Oak Species		Other Species	
	Number	Percent	Number	Percent	Number	Percent
Large trees	199	52%	129	34%	53	14%
Large trees with a cavity	120	74%	37	23%	5	3%
Large trees with a cavity suitable for a bear	67	87%	8	10%	2	3%

Table 17. Mean tree den density (trees/ha) with 95% confidence limits (CL) by habitat type according to tree dens surveys in the Tensas River Basin and central Louisiana.

	Upland forest		Lowland forest	
	Mean	CL	Mean	CL
Large trees	1.57	1.28-1.97	2.50	1.51-3.48
Large trees with a cavity	0.58	0.39-0.76	1.22	0.63-1.81
Large trees with a cavity suitable for a bear	0.23	0.12-0.35	0.22	0.06-0.38
	Swamp		**Water**	
	Mean	CL	Mean	CL
Large trees	4.55	-0.33-9.43	1.38	-0.30-3.04
Large trees with a cavity	1.27	-0.07-2.62	0.62	-0.55-1.80
Large trees with a cavity suitable for a bear	0.36	-0.09-0.82	0.25	-0.14-0.64
	Regenerating forest		**Agriculture**	
	Mean	CL		
Large trees	0.75	-0.71-2.22	0	-
Large trees with a cavity	0.25	-0.14-0.64	0	-
Large trees with a cavity suitable for a bear	0.13	-0.17-0.42	0	-

Effects of Landscape Characteristics on Den Selection

I used 190 den locations from 74 bears to investigate landscape-level selection of dens. The greatest proportion of tree dens was located in swamp habitat (41%; Table 18). In Tensas many tree dens were located in water (25%) and an equal proportion of tree dens were located in upland forest and lowland forest (20%). In Deltic, a higher proportion of tree dens were located in upland forest and water (≥23%) than lowland forest (5%). By comparison, the RRC had a lower proportion of tree dens located in upland forests, lowland forest, and water (≤16%), and a greater proportion of tree dens located in regenerating forest (16%). Most ground dens were located in upland habitat in Tensas, Deltic, and the RRC (≥70%). Several ground dens were also located in lowland forest habitat in Deltic and the RRC (≥14%), whereas Tensas did not have any. Conversely, Tensas and RRC had ground dens in regenerating forest (≥14%) but Deltic did not.

Results of the compositional analysis, partitioned by den type and subpopulation, indicated non-random selection of den sites ($F_{5,179}$=21.22, P<0.0001). Both ground dens and tree dens were located in areas with greater proportions of swamp than surrounding areas (Table 19).

I used 102 tree dens from Tensas (n=62) and Deltic (n=40) and an equal number of random points to develop my model for tree den selection relative to landscape metrics and distances to landscape features. The best approximating *a priori* model (ΔAIC_c=0, w_i= 0.999) included four parameters: an intercept term (β= -0.16, SE=0.24, χ^2= 0.44, P=0.51), distance to edge (β= -0.009, SE=0.003, χ^2= 12.12, P<0.001), area of swamp (β= 0.13, SE=0.30, χ^2= 18.54, P<0.0001), and area of water (β= 0.66, SE=0.22, χ^2= 9.34, P=0.002). The model correctly classified 76.2% of den locations and 68.9% of random points. This model ranked considerably greater than all other models (Table 14). I used 19 tree dens from the RRC to validate the model, and the model correctly classified 14 of 19 (73.7%) den sites in the RRC subpopulation.

I used 47 ground dens from Tensas (*n*=27) and Deltic (*n*=20) to develop my model for ground den selection relative to landscape metrics and distances to landscape features. The best approximating *a priori* model (ΔAIC_c=0, w_i= 0.997) included 4 parameters, an intercept term (β= 1.27, SE=0.45, χ^2= 8.15, *P*=0.004), distance to water (β= -0.002, SE=0.001, χ^2= 5.70, *P*=0.012), area of water (β= 0.22, SE=0.095, χ^2= 5.13, *P*<0.024), and mean patch size of water (β= -1.07, SE=0.32, χ^2= 10.91, *P*=0.001). The model correctly classified 63.8% of den locations and 72.3% of random points. This model ranked considerably greater than all other models (Table 15). I used 20 ground dens from the RRC to validate the model and the model correctly classified 6 of 20 (30%) known den sites in the RRC subpopulation.

Table 18. Number of dens occupied by female Louisiana black bear across habitat types from 2003-2007 in the Tensas River Basin (Tensas and Deltic) and central Louisiana (RRC) by den type and subpopulation.

	Tensas		Deltic		RRC		**Total**	
	Tree	Ground	Tree	Ground	Tree	Ground	**Tree**	**Ground**
Upland forest	11	23	11	16	3	15	**25**	**54**
Lowland forest	12	0	2	4	1	3	**15**	**7**
Swamp	21	0	19	0	10	0	**50**	**0**
Water	16	0	9	0	2	0	**27**	**0**
Agriculture	0	0	0	0	0	0	**0**	**0**
Regenerated forest	2	4	0	0	3	3	**5**	**7**
Total	**62**	**27**	**41**	**20**	**19**	**21**	**122**	**68**

Table 19. Habitat types selected by denned female Louisiana black bears from 2003-2007 ranked in order of preference according to *t*-statistics of a compositional analysis partitioned by den type and subpopulation in the Tensas River Basin (Tensas and Deltic) and central Louisiana (RRC).

	Tensas		Deltic		RRC	
	Ground (n= 27)	Tree (n=62)	Ground (n=20)	Tree (n=41)	Ground (n=20)	Tree (n=19)
Upland forest	3	4	5	4	2	5
Lowland forest	2	3	1	3	5	4
Swamp	1	1	3	2	1	1
Water	4	2	4	1	3	3
Regenerating forest	5	5	2	5	4	2
Agriculture	6	6	6	6	6	6

Table 20. The -2 Log likelihood, number of parameters, AIC_c values, Δ AIC_c values and weights (w_i) for all *a priori* models of tree den selection by female Louisiana black bears using Akaike information criterion modeling, in the Tensas River Basin, Louisiana, 2003-2007.

a priori model	-2 Log	K	AIC_c	ΔAIC_c	w_i	Correct Classification (%)
Swamp, water and edge	218.394	4	226.593	0.000	0.999	76.2
Swamp, water, lowland and edge	231.219	5	241.519	14.926	0.001	71.4
Swamp and water 1	235.885	3	242.004	15.411	4.51E-04	68.4
Swamp and water 2	239.132	3	245.251	18.658	8.87E-05	70.9
Swamp	247.568	3	253.687	27.094	1.31E-06	66.5
SDI and edge	252.108	3	260.307	33.714	4.77E-08	67.0
Water	271.675	3	277.794	51.201	7.61E-12	57.8

Table 21. The -2 Log likelihood, number of parameters, AIC_c values, Δ AIC_c values and weights (w_i) for all *a priori* models of ground den selection by female Louisiana black bears using Akaike information criterion modeling, in the Tensas River Basin, Louisiana, 2003-2007.

a priori model	-2 Log	K	AIC_c	ΔAIC_c	w_i	Correct Classification (%)
Water 3	108.587	5	117.269	0.000	0.997	63.8
Water 1	127.642	3	131.909	14.640	0.001	58.5
Water 2	126.100	4	132.549	15.281	4.81E-04	52.1
Swamp	127.045	4	133.494	16.226	2.99E-04	18.1
Upland and water	127.595	4	134.044	16.776	2.27E-04	52.1
Upland and swamp	129.993	4	136.442	19.174	6.86E-05	42.8
Upland	130.059	4	136.508	19.239	6.62E-05	35.1
Upland, swamp and water	129.418	5	138.100	20.831	2.99E-05	37.2
Upland, lowland, swamp and water	138.950	6	139.000	21.681	1.95E-05	40.1

DISCUSSION

Den Type

At a small spatial scale my results were consistent with previous research in the Southeast, most female black bears selected tree dens (Pelton et al. 1980, Carlock et al. 1983, Smith et al. 1985, White et al 2001). Females likely preferentially select tree dens because tree dens offer protection against flooding (Smith 1985, Oli et al. 1997), heat loss (Johnson et al. 1978, Johnson and Pelton 1980) and disturbance (Linnell et al. 2000). Because thermal insulation is likely not a threat to denning females in the warm climate of Southeast (Hellgren and Vaughan 1989), protection from flooding and disturbance likely drive selection of tree dens in Louisiana. Due to flood control of the Mississippi River, flooding is currently not a prevalent concern in my study areas, although historic flood conditions have likely contributed to the use of tree dens in the MAV. Disturbance likely poses a larger threat in mild climates because bears may abandon dens more readily since energetic cost of relocating is lower (Linnell et al. 2000). This is important considering Teitje and Ruff (1980) found that black bears that changed dens suffered a 56% increase in weight loss compared to undisturbed bears. Moreover, even if bears do not abandon their dens, disturbances that cause frequent waking or rises in body temperature may have a considerable cumulative effect on energy consumption (Linnell et al. 2000). In previous studies, bears in ground dens were observed to be more alert and aware than those in tree dens (Hightower et al. 2002), and were therefore probably more sensitive to disturbances. It is likely that bears prefer tree dens because trees reduced likelihood of disturbance compared with ground dens (Johnson and Pelton 1981, Alt and Guttadauria 1984).

Fidelity to Tree Dens

Despite this likely preference for tree dens it appears as though bears may sometimes select to den on the ground. Most bears did not consistently select tree dens through time, but rather had a history of using both tree dens and ground dens with no apparent tendency to switch from one type to the other. In examining fidelity to tree dens I found that most bears that denned on the ground in 2006-2007 did so even though their tree den from a previous year was unoccupied. This lack of fidelity to tree dens counters the idea that bears would select a tree den if it is available and when the bear has knowledge of it. Although most bears appeared to preferentially select tree dens, some bears occasionally to selected ground dens despite the availability of tree dens.

Tree Den Reuse

I found that estimates of tree den reuse calculated from radio-collared bears alone may produce biased results because accuracy is dependent on the proportion of the population that is radio-marked. Assessing reuse using den-years of radio-collared bears is inherently flawed because the number of tree dens is finite, thus over a long enough period of time, all tree dens would be classified as a previously used den. Assessing reuse according to the number of trees that are used >1 time may also produce an inaccurate estimate of reuse because multiple years of reuse of the same tree are not accounted for. Based on my results, assessing reuse by checking all available tree dens (method 3) provided the most accurate reuse estimates because it was the only one that accounted for all known tree dens and included non-collared bears. Although the reuse estimate for Tensas did not change appreciably among methods, assessing reuse by checking all available tree dens produced a considerably lower estimate for Deltic.

Tree den reuse for Tensas was relatively high compared to numerous studies outside Louisiana, as many have reported reuse to be <10% (Jonkel and Cowan 1971, Tietje and Ruff 1980, Alt and Gruttadauria 1984, Kolenosky and Strathearn 1987, Oli et al. 1997, Ryan and Vaughan 2004). However, caution should be used when comparing reuse estimates among studies in which bears used different den types. As noted by Alt and Gruttadauria (1984) some den types are reused more than others. Reuse would likely be lower in excavated dens, brush piles, and ground nests because they often collapse or deteriorate after 2 years, making reuse impossible (Alt and Gruttadauria 1984). Furthermore, excavated dens and nest dens can be constructed every year, whereas bears can only use tree dens that already exist. Due to such differences in available den types, and in methods used to estimate reuse, comparing reuse among studies is tenuous. However, it is likely that higher reuse provides further support that tree dens are the preferred den type and thus are selected repeatedly (Schwartz et al. 1987).

I expected that a bear would continue to reuse a tree den for as long as it had access to it, especially if the tree had previously provided adequate protection for successful denning and reproduction. However, reuse was most often by a different female and most females changed tree dens between years, rather than reuse one from a previous year, even if the tree from a previous year remained unoccupied. Alt and Gruttadauria (1984) suggested that bears may select different dens because it may reduce likelihood of predators locating denned bears, make them less vulnerable to hunting, and lower chances of spreading disease. Alternatively, bears may change trees in an effort to upgrade to better quality den that offers increased protection from disturbance. If that were the case, tree den reuse may have been higher if bears had not been subjected to disturbance by the researcher. This hypothesis, however, would be difficult to test and would require additional research.

Characteristics of Tree Dens

A suitable cavity is the most essential feature of a potential tree den (Oli et al 1997). In Louisiana, cavity suitability requirements have most frequently led to the selection of a baldcypress tree, with a large DBH and an elevated cavity that is surrounded partially or completely by water (Weaver and Pelton 1994, Benson 2005). Other characteristics were variable suggesting they likely have a minimal effect on den selection and simply reflect the types of trees that meet cavity suitability requirements. I hypothesized that microhabitat characteristics may differ between tree dens that were only used once those reused because bears may cue on a particular characteristic at the den site. I found that dens reused multiple times had a higher mean DBH, suggesting that larger trees (with presumably larger den cavities) are favored.

Characteristics of Ground Dens

Consistent with previous studies, bears tended to select ground dens that provided adequate cover (Johnson and Pelton 1981, Beecham et al. 1983, Smith 1985, Hellgren and Vaughn 1989). Denning in thick vegetation, at the base of trees, under downed trees, or in slash piles was likely an effort to ensure presence of protective cover (Lombardo 1993). The high degree of variability in canopy cover suggests that overhead cover may not as important in selection of ground dens as lateral cover. Although density of understory vegetation was not quantified, vegetation surrounding ground dens, such as palmetto, certainly provided dense lateral cover. Dense understory vegetation not only provides concealment (Hamilton and Marchinton 1980, Beecham et al. 1983, Smith 1985, Hellgren and Vaughn 1989, Lombardo 1993), but also may discourage traffic and allow bears to detect intruders (Hamilton 1978, Lombardo 1993, Martorello and Pelton 2003). Because protection appears to be important in the selection of ground dens, slash piles may be preferentially selected because they are more secure than other types of ground dens (Hightower et al. 2002). Availability of slash piles increases in forest stands managed with timber harvest, which may explain why slash piles were used more frequently in Deltic and the RRC than Tensas.

Reproductive Status and Den Selection

Parturient females may be selecting tree dens more frequently that non-parturient females because the risks of disturbance and flooding associated with ground dens are more of a threat to females with COY as energy requirements are significantly more demanding and cub survival is at stake (Teitje and Ruff 1980). Following a 10-year study of den reuse by black bears in Pennsylvania, Alt and Gruttadauria (1984) found that 23% of dens that were reused had been used for whelping consecutive litters, and suggested that this may be because parturient females are more specific in their individual den preference. I found that only 19% of tree dens that were used multiple times were used exclusively by parturient females, which may be a random occurrence. It is likely that parturient females are more likely to select to use a tree den, but that the specific tree reflects availability rather than the selection of a specific characteristic.

Although parturient females appeared to preferentially select tree dens, successful parturition also occurred in ground dens across my study areas and litter size was not reduced in ground denning females (Rogers 1987, Hellgren and Vaughan 1989). Although cub survival was not assessed in my study, McDonald and Fuller (1998) did not observe reduced survival of cubs when females selected ground dens. Hence, the potential detrimental effects of disturbance and flooding associated with ground dens may have encouraged bears with COY to preferentially select trees dens in my study, but may not have been severe enough translate to differences in reproductive success of females using different den types. However, because flooding can be unpredictable, it is possible that during extreme flood events, bears may not be as successful at denning and bearing cubs in ground dens.

Reproductive status of females may also affect den selection because that size restrictions may limit den use (Klenzendorf et al. 2002) which may be why most females with yearlings selected ground dens, in that trees large enough to house multiple bears were likely limited. Furthermore solitary bears and those with yearlings may remain on the ground rather than den in an available tree because of intermittent activity (use of several day beds rather than one den site) through winter. Winter activity has been reported in other studies in the Southeast (Hellgren and Vaughan 1989, Weaver and Pelton 1994, Oli et al. 1997, Hightower et al. 2002). For bears without COY in areas with a mild climate and sufficient food resources, denning behavior may be circumvented (Hellgren and Vaughan 1989, Graber et al. 1990). I observed scat at several ground dens, as have other researchers in Louisiana (Weaver and Pelton 1994, Hightower et al. 2002, Benson 2005) suggesting that feeding may have continued through winter.

At a landscape-level, both parturient and non-parturient females selected tree dens in areas with greater proportions of swamp, lowland forests, and water habitat and with lesser proportions of upland forest, regenerating forest, and agriculture habitat. Parturient females may have selected areas with greater proportions of water than non-parturient females because deeper water may limit access to a tree by potential predators (human or otherwise) and reduce the likelihood of disturbance. Likewise, regenerating forest was likely ranked low for parturient females because tree dens in regenerating forests may be more exposed to disturbance.

Tree Den Availability

Den type preference may be important, but the use of tree dens is dependent on availability of an adequate tree. Dens in baldcypress trees surrounded by water is a direct reflection of availability; results from tree den surveys indicated baldcypress trees in swamp and water habitats were the most abundant dens on the landscape. The relationship between den use and availability is evidenced by the similarity between the proportions of different species of tree dens that were used and those identified through availability surveys as potential tree dens.

Den availability plays an important role in den selection and a lack of suitable tree dens may limit population growth (Oli et al. 1997). Densities of potential current tree dens in Deltic and Tensas were comparable to those found in Arkansas at White River NWR North and South (Table 15), where a viable population of black bears exists. These results suggest that there is an adequate supply of tree dens across study areas. However, as tree dens were not evenly distributed across the landscape, some bears may not have access to a tree den within their home range, requiring them to use ground dens. Despite the fact that densities of tree dens in Red River and Three Rivers were similar to those found in Tensas and Deltic, a lower proportion of females selected tree dens in the RRC (42%), similar to that reported for the Inland ARB (51%; Hightower et al. 2002). Since most (89%) relocated bears denned outside the delineated study areas, tree den densities where bears denned were not estimated and may have been lower than within study areas. The similarity between tree den use in the RRC and in the Inland ARB may be a reflection of timber harvest practices used in that region of the state. Lake Ophelia had a low density of tree dens compared to other areas, which may indicate that tree dens are a limited resource. This probably does not pose a threat to bears in the RRC because many bears that inhabited the Lake Ophelia area found available tree dens (n=10) on private land adjacent to the refuge. Additionally, Lake Ophelia had a large proportion of regenerating forest habitat, which is characterized by dense understory and thus may provide suitable cover for ground dens.

Because den availability is so influential in den selection, studies often report den reuse as a reflection of den availability (Alt and Gruttadauria 1984). I expected reuse to be greater where there was a lower density of tree dens, which was the case with Tensas. This suggests that reuse may be related to availability. A relationship between tree den reuse and availability could not be inferred for the RRC. However, both trees that were reused in the RRC were on or adjacent to Lake Ophelia, which had the lowest overall tree den density estimate. This observed reuse may have been a result of low tree den availability on Lake Ophelia.

Effects of Landscape Characteristics on Den Selection

Most tree dens were found in swamp and water habitats regardless of study area. The selection of tree dens associated with swamp and water habitat was supported by the results of my compositional analysis and my landscape model. Bears are likely constrained in their selection of dens because suitable tree dens are primarily only baldcypress trees which are available in swamp and areas of standing water. The model also suggested that tree den sites are closer to edge than random points. This is likely because land use has created the edge around swamps and water. As my model correctly classified most dens, it is likely that landscape metrics could identify areas in Louisiana in which tree dens should occur which may be used by managers to conserve denning habitat.

Elevation is an important characteristic influencing selection of ground dens because bears need to select sites with reduced probability of inundation (White et al. 2001). Ground dens were consistently located in upland forest, surrounded by areas with relatively greater proportions of lowland forest and swamp habitat than surrounding areas. Additionally, as indicated by my model, bears selected ground dens adjacent to water. The selection of upland sites adjacent topographically low areas is related the local topography. Microelevational relief creates ridges juxtaposed to water and swamps which are elevated enough to avoid inundation, yet remain moist enough to support dense vegetation, which may be a prerequisite for ground nests (Martello and Pelton 2003). This was supported by the predominant use of palmetto in ground dens, which is most common in seasonally flooded habitats and on moist bluffs (Miller and Miller 1999).

Predicted classification values were reasonably accurate for Tensas and Deltic, but the model had poor predictability for the RRC. Selecting areas with reduced probabilities of inundation is required, after which microhabitat characteristics are likely selected for. Because favorable microhabitat, primarily dense vegetation, is found in a variety of habitat types. Based on these results it is not feasible to accurately predict ground den locations based on land cover variables.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Female Louisiana black bears demonstrate plasticity in den requirements. Through the selection of optimum ground dens, including dense cover and micro-elevational relief, risks associated with ground dens may be mitigated allowing a bear to den and reproduce successfully (Hellgren and Vaughn 1989). However, data from other studies indicate that in areas that flood extensively a lack of suitable tree dens may be limiting to black bears (Oli et al. 1997, Hersey et al. 2004). Given that some areas in Louisiana may flood more than my study areas (such as the ABR) and because flooding events may be unpredictable, tree dens may still be required. Additionally, tree dens appear to be preferred and offer increased protection from disturbance. Therefore I recommend that tree dens continue to be protected within the historical range of the Louisiana black bear. By protecting tree dens there is an economic loss to the landowner that would otherwise harvest the trees. However, the Louisiana black bear is a threatened subspecies, and current management goals include the restoration and persistence of the bear population, thus the benefit of tree dens to the restoration effort need to be considered when evaluating the severity of economic loss.

Potential tree dens are defined by the USFWS as baldcypress or tupelo >92cm DBH with a visible cavity occurring along rivers, lakes, streams, bayous, sloughs or other bodies of water (Neal 1992). Because tree dens may be 1 of many different species and may be associated with a range of habitat types, Hightower (2002) recommended that protection be extended to include any species of tree with a suitable cavity regardless of location relative to a body of water. Although this may benefit bears by increasing denning opportunities, such extensive protection of trees may not be economically feasible across the range of the Louisiana black bear. As an alternative to protecting all species with suitable cavities, an effort could be made to preserve these trees on public land, and states could try to encourage landowners to leave large trees with cavities if they are of low value (Hersey et al. 2004).

Even with the protection of candidate trees, some bears may not have access to available tree dens, and under certain circumstances others may select to use ground dens. Therefore, I encourage forest management practices leave logging debris in topographically higher areas (White et al. 2001) and current timber harvest practices that provide canopy gaps to promote understory growth, such as selective cuts and shelterwood cuts. Dense cover can also be improved by protecting switchcane, and palmetto thickets (Weaver and Pelton 1994).

Reuse of tree dens may reflect availability and therefore reuse may possibly be used as a relative measure of availability. However potential biases inherent in estimating den reuse should be considered prior to interpreting results or making comparisons among studies. Current tree den availability appears to be adequate in all study areas except Lake Ophelia. This does not seem to be threat to the RRC subpopulation because there appears to be adequate habitat for ground dens, and bears can access tree dens on lands adjacent to Lake Ophelia, provided trees remain protected and are not harvested.

Based on tree den densities, it appears there will continue to be an adequate supply of trees in my study areas. However, attrition needs to be considered in managing for future tree den availability (Johnson and Pelton 1981). The existence of future tree dens requires that the rate of attrition be less than or equal to the rate of cavity formation, which may take 8-30 years (Carey and Sanderson 1981). Attrition would ultimately eliminate tree dens if protecting those already suitable cavities was the only management strategy (Johnson and Pelton 1981). Therefore, I support forest management recommendations that ensure minimum of 5%-10% of the forest be maintained in the age class at which large cavity formation occurs to ensure presence of future tree dens (Pelton 1985).

In this study, tree dens were predominantly located in baldcypress. Changes to hydrology such as drainage of deepwater swamps, may cause reestablishment of species that could not tolerate flooding (Marois and Ewel 1983), reduction in growth rates of trees, and thinning of the canopy (Conner 1994). Additionally, changes resulting in permanent inundation of swamps will cause reduced growth and eventual death of cypress trees (Eggler and Moore 1961). Therefore, I recommend that managers consider how changes in hydrology might affect tree dens prior to further manipulating the hydrologic regime.

My results support the importance of examining den selection at multiple scales. Bears select tree dens based on both small scale and broad scale habitat characteristics. Tree dens appear to be selected for based on availability, which at a small scale requires the presence of a suitable cavity, and at a broad scale reflects the landscape characteristics consistently associated with large trees. Because den availability is closely related to habitat composition, habitat variables may be used to identify areas that have high probabilities of having tree dens for future Louisiana black bear populations. Knowledge of denning habitat may be valuable for managing land use (Clark et al. 1998) and for scheduling forest-related activities so that denned bears are not disturbed (Clark et al. 1993). Bears also appear to select ground dens based on both small and broad scale habitat characteristics. At a small scale bears select areas with dense cover as it may be crucial in protecting ground denning bears from disturbance. On a broad scale bears select sites with a reduced probability of becoming inundated. The models constructed and detailed herein only included broader scale habitat characteristics, which explain poor model performance when attempting to correctly classify ground dens based on landscape characteristics. A model that included both broad scale characteristics and microhabitat characteristics may be more effective at predicting potential ground den sites. Because ground denned bears may also be more easily disturbed, limiting winter activities may be beneficial especially in the RRC, at least until the subpopulation becomes established.

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VITA

Annelie Clare Crook was born in Frankfurt, Germany, to British parents in 1978. She was moved to Vancouver, British Columbia, (Canada) at the age of 2. In 1996 she graduated high school and began attending the University of Victoria (also in Canada). After graduating with a Bachelor of Science in biology with a minor in environmental science Annelie headed south. She worked on a variety of field research projects over several years including: radio tracking coyotes in northern California, tracking lynx by snowshoe and trapping black bears in Maine and trapping Island foxes off the coast of southern California. After working as a field technician on a black bear project in Louisiana she was accepted into the graduate school in August 2005. Annelie will be awarded a degree of Master of Science in wildlife in May of 2008.