SPATIAL ECOLOGY OF FEMALE FLORIDA BLACK BEARS

By

MELISSA ANN MOYER

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By

Melissa Ann Moyer

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An understanding of how a wildlife species utilizes space and habitat is critical to ensure its persistence in an increasingly human dominated landscape. The Florida black bear (*Ursus americanus floridanus*) is state listed as a threatened species and occupies fragmented and geographically isolated habitats within a matrix of heavy human development. Using 35 radio-collared female black bears from the Ocala bear population during 2000-2003, I investigated the patterns of space use in Ocala National Forest (ONF) and the adjacent residential community of Lynne in north central Florida. I examined factors influencing home range dynamics, hierarchical habitat selection, and the relationship between spatial organization and genetic relatedness.

Annual home range size (95% fixed kernel density estimator) ranged from 3.8 km^2 to 126.9 km^2, and averaged (±SE) 24.2 ± 3.55 km^2. Home ranges were largest during the year 2000 when a drought led to a forest-wide acorn mast failure. During this year females with cubs had significantly larger home ranges than females without cubs (p = 0.011). Home range sizes during fall (19.92 ± 4.59 km^2) were substantially larger than

home ranges during summer (8.26 ± 0.99 km^2). The seasonal difference in home range size was more pronounced in Lynne than in ONF, perhaps due to differences in anthropogenic activities and habitat types between the two study sites.

Using a distance-based habitat analysis method, I examined habitat selection by female Florida black bears within ONF at two spatial scales: the selection of a home range from the study area and the utilization of habitat within that home range. Female black bears used habitat types in proportion to their availability at both spatial scales for multi-year annual and fall home ranges. However habitat selection was detected for summer home ranges ($p = 0.026$) and for habitat types used within summer home ranges ($p = 0.026$). Xeric oak scrub and sand pine forest were the most preferred habitat types when selecting a home range. They provide both substantial escape cover and abundant fall food sources. Conversely, within the summer home range, pine flatwoods and swamp forests were the most preferred habitat types for the abundant summer foods that they provide.

I also tested the hypothesis that the genetic relatedness among individuals influenced female spatial organization. I estimated relatedness between individuals using microsatellite DNA and the program Kinship. For each year and season (except fall 2000), relatedness decreased significantly ($\alpha = 0.1$) as the distance between female core home ranges increased. Additionally, females that had overlapping core home ranges were more closely related than females whose home ranges did not overlap. My data are consistent with the hypothesis that genetic relatedness does influence spatial organization, although this pattern may be subsequently modified by resource availability.

CHAPTER 1
INTRODUCTION

One of the primary goals in the field of wildlife ecology is to understand the space and habitat use patterns of species across multiple spatial scales. Species are not distributed uniformly across a landscape but are believed to select environments that are conducive to their survival and reproduction. Many factors can influence whether an area is hospitable or inhospitable for an animal, but two widely accepted explanations (aside from historical processes) are the availability of food resources and the interactions within and between species (Krebs 1978). Animals must have resources available to promote their own survival and the survival of the species. To survive and reproduce an animal also must select habitat that adequately minimizes competition and predation. A cohesive understanding of the spatial ecology of a species requires the synthesis of many interacting processes, and a multi-faceted approach may yield a more complete picture than analysis from a single perspective.

The home range is a common way to conceptualize the use of space by one animal, nested in the larger landscape, within which the animal should be able to obtain food, shelter, and access to mates (Burt 1943). Resource availability greatly influences home range dynamics and habitat use, and species with large geographic ranges may have different space and habitat use strategies in different parts of this range depending on habitat quality and population density (Carpenter and MacMillen 1976; Krebs 1978; Morrison et al. 1992; McLoughlin et al. 2000). Interactions of individuals within a species may further influence spatial organization in a variety of ways (Macdonald 1983;

Sandell 1989; Gompper and Wayne 1996). Examining only one source of variation in space use and habitat selection patterns may not explain complex dynamics.

Conclusions of research on the spatial ecology of a species in one part of the larger geographic range may not be directly applicable to the same species elsewhere. Not only do food abundances and specific habitat types differ within a species' geographic range, but the impact of human activities on the landscape also is highly variable. Loss, modification, and fragmentation of habitat are relatively recent developments. Their effects on the spatial ecology of wildlife species are often unknown and may further impede extrapolation of conclusions from one part of a species' geographic range to another.

The black bear (*Ursus americanus*) in the eastern United States has suffered from tremendous habitat loss and fragmentation due to human activities (Maehr 1984). Within Florida, the Florida subspecies of the black bear (*U. a. floridanus*) has experienced similar pressure from anthropogenic sources. Once contiguous, the bear population now exists in nine genetically distinct subpopulations within the state (Dixon 2004). The Ocala National Forest in north central Florida supports one of the largest of these subpopulations. It has been suggested, however, that public lands alone may not provide enough habitat to ensure long-term persistence of the black bear in Florida (Maehr and Wooding 1992). Home range placement and utilization also provide the framework within which to interpret an animal's response to changes in the landscape at multiple spatial scales.

Anthropogenic changes and development are occurring at a rapid pace in Florida. Moreover, the sand pine/scrub oak dominated forest composition within the Ocala

National Forest is unique to inland Florida. Thus, it is of interest to know how black bears use space and habitat within the forest. Do they exhibit space use patterns similar to other black bear populations in the southeastern United States? How do they respond to the influences of human activities? Florida black bears have been less thoroughly studied than black bears in other parts of the southeastern United States, so their space and habitat use patterns, and responses to human activities are not well documented. The human population of Florida is rapidly increasing, so evaluation of black bear spatial ecology is essential to develop and implement management plans for the Ocala bear population.

The objective of this study is to examine three interrelated aspects of the spatial ecology of the Florida black bear within the Ocala National Forest. Female black bears were the focus of the study because they are thought to select their home ranges based on resources, while males are thought to select their home ranges based predominantly on access to females for mating. In Chapter 2, I examine the temporal and spatial variation in home range size of female black bears, and investigate the influence of several factors on home range size. How black bears use habitat can also influence their space use pattern, and information on habitat selection by bears is necessary for habitat management for black bears. In Chapter 3, I examine the pattern of habitat use by black bears at multiple spatial scales within the forest. I first consider how bears select home ranges within the forest, and then examine how habitat types within the home range are utilized. It has been hypothesized that space use pattern in female black bears is influenced by the relatedness among individuals. Rigorous tests of this hypothesis are rare. In Chapter 4, I test the hypothesis that genetic relatedness influences the spatial organization of female black bears in Ocala. Finally, conclusions are summarized and management recommendations based on my findings are proposed in Chapter 5.

CHAPTER 2
FACTORS INFLUENCING SPACE USE PATTERNS OF FEMALE FLORIDA BLACK BEARS

Introduction

Detailed knowledge of the spatial distribution of any wildlife species is essential to a cohesive understanding of its ecology. The space use pattern of mammalian species, in particular the size of the home range, can be roughly projected based on body size (Gompper and Gittleman 1991; Biedermann 2003) and mating system (Clutton-Brock 1989). Intraspecies variation in home range size has further been shown to be influenced by resource availability (Mares et al. 1982; Ford 1983; Macdonald 1983; Van Orsdol et al. 1985; South 1999; Lariviere and Messier 2001; Oehler et al. 2003), population density (Young and Ruff 1982; Lindzey et al. 1986; Oli et al. 2002; Kjellander et al. 2004), social factors (Grigione et al. 2002; Boydston et al. 2003), and anthropogenic influences such as habitat fragmentation (Crooks 2002; Beckmann and Berger 2003; Riley et al. 2003; Admasu et al. 2004; Gehring and Swihart 2004).

The black bear (*Ursus americanus*) is a large solitary carnivore with an extensive space requirement and a polygynous mating system. Given this mating system, female black bears are thought to select a home range based on the abundance of resources, while male bears establish a home range in relation to the presence of females (Clutton-Brock 1989; Sandell 1989). The spatial pattern of females is influenced at multiple scales, directly or indirectly, by the abundance and temporal availability of resources throughout the United States and Canada (Lindzey and Meslow 1977; Smith and Pelton

1990). Within the broad geographic range, home range size decreases along the latitudinal gradient from north to south (Powell 1987; Gompper and Gittleman 1991; Schenk et al. 1998). Local environmental variation further influences home range size and smaller home ranges are commonly documented in more productive habitats (Smith and Pelton 1990; Oli et al. 2002; Koehler and Pierce 2003).

The distribution of resources across the landscape also can affect home range size. Bears inhabiting a diverse landscape will often have smaller home ranges compared to those occupying productive and homogeneous habitats because availability of food resources varies with plant phenology (Reynolds and Beecham 1980; Garshelis and Pelton 1981; Klenner 1987). Annual and seasonal fluctuations in resource availability due to normal seasonal variation, drought, or mast failure also may add temporal variation to female home range size (Jonkel and Cowan 1971; Garshelis and Pelton 1981; Rogers 1987; Schooley 1994). Female black bears may further adjust their home range size to meet resource and safety requirements specific to being accompanied by cubs (Lindzey and Meslow 1977; Alt et al. 1980; Hellgren and Vaughan 1990; Smith and Pelton 1990).

The Florida subspecies of the North American black bear (*U. a. floridanus*) is listed as a threatened species by the state of Florida and exists in isolated populations centered on public land holdings. While long-term studies have been conducted in many parts of the country (e.g., Alt et al. 1980; Reynolds and Beecham 1980; Powell 1987; Rogers 1987), less is known about spatial ecology of Florida black bears and factors influencing home range size. Because of the latitudinal gradient of home range size (Powell 1987; Gompper and Gittleman 1991), one would expect the home range size of the Florida black bear, near the southern tip of the geographic distribution, to be smaller than in populations occupying northern habitats. However, habitat types, resource availability, and fragmentation of black bear habitat in Florida differ substantially from regions where the majority of black bear research has been conducted. These factors may offset the expected effect of latitude on home range size.

Many studies of black bear spatial ecology that have documented home range sizes also noted that multiple factors may influence home range size (Jonkel and Cowan 1971; Lindzey and Meslow 1977; Young and Ruff 1982; Koehler and Pierce 2003). Most of these studies have only considered the effect of one factor at a time on the size of the home range. However, several factors may have synergistic or confounding effects on home range size, which could be revealed if multiple factors and interaction effects were analyzed simultaneously.

Using data from female black bears radio-collared between 2000-2003, I investigated their home range dynamics in north central Florida. Specifically, I asked the following questions: (1) Are home range sizes of Florida black bears similar to those of the other populations of black bears? (2) Do sizes of black bear home ranges in north central Florida show annual or seasonal variation? (3) Is the pattern of space use by bears inhabiting a forested habitat different from those inhabiting a fragmented residential area? (4) What factors or combinations of factors influence the home range size of Florida black bears?

Study Area and Methods

Study Area

The study was conducted in the Ocala National Forest in north central Florida. Ocala National Forest is the largest public land holding in central Florida and supports one of the largest of the 9 subpopulations of black bears in Florida (Dixon 2004). Two study sites were designated within Ocala National Forest: “ONF” designates the study area that is fully within the Ocala National Forest while “Lynne” designates the study area that includes the residential community of Lynne (Fig. 2.1). The ONF study area is approximately 500 km^2 and is centered on State Road 40 along a ridge of ancient sand dunes primarily vegetated by sand pine forest and xeric oak scrub (for a more thorough description see Chapter 2 of this thesis and Myers and Ewel (1990)). Human disturbance due to selective logging, clear-cutting, prescribed burning, and road building practices within the forest provide much of the heterogeneity in the forest cover type and stand age. Elevations range from 15 m above sea level near Juniper Springs to 53 m above sea level in the north central part of the forest. The forest as a whole sustains a high degree of recreational activity such as camping, hunting, and off road vehicle use.

The Lynne study area is located to the west of ONF and encompasses a matrix of US Forest Service and privately owned land in the residential community of Lynne. Elevations in Lynne were lower than those in ONF and ranged from 0 m-12 m above sea level. The predominant forest cover types are swamp forests and pine flatwoods and there is a greater degree of fragmentation due to human developments such as roads, businesses, and houses. Because both the degree of urbanization and available food resources have been shown to influence home range size, bears in the two study areas were analyzed separately.

North central Florida experienced substantial variation in rainfall and drought conditions over the course of the study. The Palmer Drought Severity Index (DPSI) ranges from - 4 to + 4, where - 4 and below signifies extreme drought conditions, 0 signifies near normal conditions, and + 4 and above signifies extreme moist conditions. The DPSI in north central Florida at the beginning of September was - 4.41, - 2.57, 2.73, and 3.94 in 2000, 2001, 2002, and 2003, respectively (Southeast Regional Climate Center 2004). An acorn mast failure in 2000 resulted from these extreme drought conditions.

Field Methods

Trapping and radio-collaring of black bears began in summer 1999 and continued through fall 2002. Although bears were trapped from May through December, the most intensive trapping occurred during summer months. Bears were trapped using spring activated Aldrich foot snares disguised in natural vegetation and baited with donuts or a combination of corn and donuts. Traps were set near dusk and monitored continuously to ensure that trapped bears were processed immediately. Bears were anesthetized with Telazol® delivered through a CO_2 charged low-impact dart delivery system. Once sedated, bears were ear tagged and lip-tattooed for individual identification. Hair and blood samples were collected for genetic analyses, and a pre-molar tooth was extracted to estimate age (Willey 1974). Morphometric measurements and body mass as well as physical and reproductive condition scores also were recorded. Most females, and some males, were fitted with a motion-sensitive radio-collar (150-151 MHz; Telonics, Mesa, Arizona). Radio-collars included a leather connector, which would allow the collar to fall off within two to three years. Reproductive females or those $\geq$ 3 years of age were considered adults and included in analyses (Garrison 2004). Male bears were not included in this study because data were insufficient for estimation of home ranges.

Adult female bears were located on average once per week during 1999-2001, twice per week in 2002, and three times per week in 2003. The majority of locations were obtained from the ground during daylight hours (0900-1800) using a 4-element hand held antenna and a Telonics® receiver, but bears were also tracked 1-4 times per month from a fixed wing aircraft. For each bear, $\geq$ 3 compass bearings were obtained within 30 minutes to minimize location error due to movements. Point locations from ground telemetry were estimated using the program Locate II (Pacer 1990). Telemetry error was estimated by comparing estimated locations of dropped collars and female natal dens to their actual locations. The average ground telemetry error was 157 m, based on 303 locations on 19 dens and 7 test collars. In these cases observer distances varied from 0.25-1 mile from the actual location. The average aerial telemetry error was 251 m, based on 25 dropped and deployed collar locations.

Data Analysis

It is well documented that the number of locations used to estimate a home range affects the size of the home range (White and Garrot 1990; Seaman and Powell 1996; Seaman et al. 1999; Belant and Follmann 2002). Recommendations as to how many locations are necessary for robust estimates of home range size differ among publications. Most authors recommend about 50 locations per home range (Seaman and Powell 1996; Gehrt and Fritzell 1998), although others suggest that 25-30 locations are sufficient (Seaman et al. 1999; Koehler and Pierce 2003). Koehler and Pierce (2003) found that an asymptote in black bear home range size estimated using the fixed kernel density method was reached at 25 locations. Therefore, I required a minimum of 25 locations per female annual or seasonal home range for these analyses. Due to sample size constraints, a minimum number of locations greater than 25 locations would have reduced the sample sizes substantially.

For each bear, by year and season, I estimated home range size using both the 95% fixed kernel density estimator (kernel home ranges) and the 95% minimum convex polygon (MCP home ranges) for comparison to other studies and to evaluate differences in results based on the home range estimation method (Millspaugh and Marzluff 2001). I used the program CALHOME (Kie et al. 1994) to estimate 95% MCP home ranges and the Animal Movement extension of ArcView 3.2 (Hooge et al. 1999) to estimate 95% fixed kernel home ranges with least squares cross validation (LSCV) (Seaman and Powell 1996). I estimated annual home ranges using locations collected from May-December. Locations for an annual home range had to span at least 75% of the 8-month period. For seasonal analysis, summer was designated as May-August and fall was designated as September-December. I required that the locations span at least 50% of each season. The beginning of September was chosen as the transition between summer and fall based on the start of the availability of acorns at this time, the end of the breeding season, and to distribute sampling effort evenly across seasons. I did not use locations collected during the winter/spring months of January-April due to substantial variation in dates of den entrance and den emergence among females (Garrison 2004).

I used general linear models (SAS procedure GLM; SAS Institute Inc. 1999) to simultaneously assess the influence of several factors on home ranges estimated using MCP and kernel methods. Annual and seasonal home ranges were analyzed separately. The independent variables included in the annual home range models were the year of study (2000, 2001, 2002, or 2003), study area (ONF or Lynne), and female reproductive status (with or without cubs). Seasonal home range models were slightly different in that season (summer or fall) also was included, and I only included data collected in 2002 and

2003 due to insufficient data prior to 2002. As previously mentioned, the number of locations has been shown to influence home range size (Seaman et al. 1999; Millspaugh and Marzluff 2001; Belant and Follmann 2002). In order to remove any potential effect of the number of locations on home range size, I used the residuals of the regression of log-transformed home range size on the number of locations as the response variable in each model.

Initially, I included all main effects and all two-way interactions in each GLM model. I then removed non-significant ($\alpha = 0.05$) interaction terms in a step-wise fashion such that the least significant interaction term was removed each time. The model was refitted sequentially until all main effects and only significant interaction effects remained in the model (Slade et al. 1997). I further explored the significant interaction effects in the final model using the least squares means multiple comparisons (LSMEANS), although for graphical representations the actual home range sizes (km^2) are presented.

Results

Of the 53 radio-collared females, 35 met criteria for estimation of at least one annual or seasonal home range. The average (±SE) number of locations per annual home range varied from 36 ± 2 in 2000 to 79 ± 4 locations per bear in 2003 (Table 2.1). The average number of locations per seasonal home range varied from 32 ± 1 for summer 2002 to 43 ± 1 for summer 2003 (Table 2.2).

Annual home range size estimated using the 95% kernel density estimator ranged from 3.8 km^2 to 126.9 km^2, and averaged 24.2 ± 3.55 km^2 (Fig. 2.2). Likewise, annual home range size estimated using the 95% minimum convex polygon method ranged from 3.3 to 231.1 km^2, and averaged 22.6 ± 5.18 km^2 (Fig. 2.3). Although kernel home range estimates were slightly larger than MCP estimates, the two methods yielded similar estimates (Tables 2.1, 2.2). The average home range size was much greater in 2000 than in subsequent years. Combining data across years, average home range size was larger for females with cubs than females without cubs. Using the kernel method home ranges in ONF were larger than those in Lynne; however, the home range sizes estimated using MCP were similar between sites.

Average home range size during summer was smaller than that during fall (Table 2.2). Summer home range size varied from 0.34 km^2 to 21.35 km^2 and averaged 8.26 ± 0.99 km^2 using the kernel method, and ranged from 0.63 km^2 to 31.18 km^2 and averaged 5.80 ± 1.04 km^2 using the MCP method. Fall home range size varied from 1.78 km^2 to 119.32 km^2 and averaged 19.92 ± 4.59 km^2 using the kernel method, and ranged from 2.68 km^2 to 114.1 km^2 and averaged 16.28 ± 4.17 km^2 using the MCP method. Females with cubs had smaller home ranges during the summer than females without cubs, while the average fall home range was larger for females with cubs. Female bears in ONF had larger summer home ranges, but smaller fall home ranges, than those in Lynne.

Factors Influencing Annual Home Ranges

The final GLM models for annual home ranges estimated using both kernel and MCP home range estimation methods included the main effects of year, study area, and reproductive status, and the two-way interaction effect between year and reproductive status (Table 2.3). Although exact *p*-values differed based on the method of home range estimation, significant factors were identical between the models. No main effect had a significant influence on home range size. However, the interaction between year and reproductive status was significant, indicating that reproductive status did influence home range size, yet the pattern of influence varied with year.

During 2000 and 2002, LSMEANS comparisons indicated that females with cubs had larger home ranges than females without cubs (*p* = 0.011 and *p* = 0.035, respectively) (Fig. 2.4). This pattern appears to be reversed during 2001 and 2003, although differences between home range sizes within these years were not significant. The most striking difference was that the average home range size of females with cubs during the year 2000 was not only significantly larger than females without cubs during the same year but was significantly larger than home ranges for females without cubs in 2001 (*p* = 0.026), females without cubs in 2002 (*p* = 0.001), and females with cubs in 2003 (*p* = 0.006). Results were similar in the analysis of home ranges estimated using MCP except that there was no significant difference between home range sizes of females with and without cubs in 2002 (*p* = 0.272), and during 2003, females without cubs had significantly larger home ranges that females with cubs (*p* = 0.012).

Factors Influencing Seasonal Home Ranges

Season was the only significant main effect in the final GLM model using the kernel home ranges, indicating that home ranges during fall were larger than home ranges during summer (Table 2.4). Reproductive status by year and season by study area interaction effects were both significant. The significant interaction of reproductive status and year reflects the pattern seen for the annual home ranges. LSMEANS comparisons indicated that females without cubs had significantly larger home ranges than females with cubs during 2003 (*p* = 0.012). During 2002, females with cubs appeared to have larger home ranges (Table 2.4), although the difference was not significant (*p* = 0.543).

The interaction of season and study area suggested that the effect of season differed between study areas. LSMEANS comparisons indicated that fall home ranges in Lynne were larger than summer home ranges ($p < 0.001$) (Fig. 2.5); however, the seasonal difference in home range size was not significant in ONF ($p = 0.545$). Additionally, fall home ranges were significantly larger in Lynne than in ONF ($p = 0.024$), while during summer, average home range size in ONF was larger than that in Lynne ($p = 0.032$). Results of LSMEANS comparisons for the MCP home ranges were similar for both interaction terms.

Discussion

Revealing the spatial requirements of the Florida black bear and how these requirements change with fluctuations in the environment is necessary for a complete understanding of the ecology and behavior of this threatened subspecies. Ultimately, this information is needed to guide conservation and management of this subspecies within an increasingly human dominated landscape. The Florida black bear is already restricted to 17% of its historic range in Florida (Wooding 1993), and only 40% of currently available potential black bear habitat is in public ownership (Maehr et al. 2001). The bears in ONF occupy primarily federal lands; however, the bears in Lynne use a matrix of publicly and privately owned land and are highly susceptible to further encroachment. As the human population of Florida continues to expand, and space becomes an increasingly limited commodity, understanding both average and extreme spatial use patterns, as in times of drought, becomes critical to preserving the Florida black bear.

Published reports indicate that home ranges of black bears vary substantially in North America such that bears occupying northern habitats have larger home ranges than those occupying more productive habitats in the southeast (Powell 1987; Schenk et al. 1998). For example, home ranges of female black bears averaged 295 km^2 in Manitoba, Canada (Pacas and Paquet 1994) and 72 km^2 in Pennsylvania (Alt et al. 1980). Further south, home ranges of female black bears averaged 15 km^2 in the Smoky Mountains of Tennessee (Garshelis and Pelton 1981) and 5 km^2 in Arkansas (Oli et al. 2002).

The average home range size of females in the Ocala black bear population (Kernel: 24.2 ± 3.55 km^2; MCP: 22.6 ± 5.18 km^2) was not as small as expected based solely on latitude. The productive habitat in the floodplains of Arkansas and the eastern forests of the Smoky Mountains likely allowed for smaller home ranges than documented in this study. However, if the average home range size in Ocala is recalculated excluding data from the year 2000 (drought year), the average more closely approximates home range size in other southeastern populations (Kernel: 16.64 ± 1.80 km^2; MCP: 15.45 ± 3.56 km^2). I believe this estimate is more reflective of home range size during “normal” years in Ocala because the drought, and subsequent acorn mast failure, during fall 2000 led black bears, and in particular female bears with cubs, to search for food over a vast area as compared to what they typically use during normal years. Still, this finding is important because understanding how females adjust home range size during drought conditions may assist managers to amend management activities in order to minimize the impact of future drought conditions.

Resource availability and habitat productivity have a tremendous influence on home range size (Lindzey and Meslow 1977; Reynolds and Beecham 1980; Smith and Pelton 1990; Samson and Huot 1998; Koehler and Pierce 2003). Based on the composition of swamps and riparian habitats in Lynne compared to the xeric scrub habitats of ONF, I expected the home ranges in Lynne to be smaller than in ONF. Conversely, the greater degree of fragmentation and associated anthropogenic effects in Lynne would lead me to believe that home ranges would be larger than in ONF in order to meet nutritional needs, as has been shown in other carnivores (Riley et al. 2003). Therefore, I expected that these effects would be nullified to yield equal home range sizes in the two study areas.

While there was no difference in annual home range size between study sites, there was a difference in seasonal home range usage. Female black bears in Lynne experienced a much larger seasonal effect on home range size than black bears in ONF. Female black bears in Lynne utilized summer home ranges that were half the size of those in ONF, while fall home ranges in Lynne were twice as large as fall home ranges in ONF. From a resource utilization standpoint, peak food production in Lynne may occur during the summer months because of high soft mast and berry production, while a higher density of hard mast species, especially acorns, in ONF may explain the comparably smaller fall home ranges.

Contrary to my expectations, the human presence in Lynne may have actually resulted in smaller summer home ranges than in ONF. Black bears living near urban environments have been shown to increase nocturnal activity and supplement their nutritional requirements with food items from human sources such as dumpsters (Jonkel and Cowan 1971; Rogers 1987; Beckmann and Berger 2003). Female bears in this study were primarily located during the day and thus their full range of daily movement was perhaps underestimated. Increased nocturnal behavior in order to avoid contact with humans and exploit artificial food sources would explain the smaller home range size in Lynne. However, a lack of nighttime radio-locations leaves this conclusion open to interpretation.

The larger fall home ranges in Lynne may be related to habitat fragmentation as well as temporal fluctuations in resource availability. Habitat fragmentation would reduce the total amount of forest cover within a given area as compared to contiguous habitat. During fall, bears in Lynne primarily traveled out of the residential part of Lynne to the less developed banks of the Ocklawaha River or into ONF (Figs. 2.1-2.3), most likely to take advantage of food sources not available within their summer home ranges. A more thorough investigation of home range size and daily movement differences between ONF and Lynne would be needed to more clearly define the differences between the two sites.

Previous studies on black bears have indicated that home range sizes may be different between females with cubs and females without cubs (Lindzey and Meslow 1977; Alt et al. 1980; Hellgren and Vaughan 1990; Smith and Pelton 1990). More specifically, these studies have documented smaller home range sizes for females with cubs during summer when cub mobility is restricted, and larger home ranges for females with cubs during fall (Lindzey and Meslow 1977; Alt et al. 1980; Smith and Pelton 1990). In this study, when annual home ranges are averaged across years, females with cubs used larger home ranges than females without cubs (Table 2.1). This trend was most pronounced during the mast failure of 2000. Total nutritional requirements of females with cubs are greater than females alone, which may explain the dramatic increase in home range size. An alternative explanation is that females with cubs during the mast failure were forced to use larger areas in order to avoid males (Jonkel and Cowan 1971; Reynolds and Beecham 1980; Schoen 1990), whereas the females without cubs did not need to make as extreme adjustments. My data also suggest a seasonal effect such that females with cubs have smaller home ranges in the summer and larger home ranges in the fall. However, this interaction was not significant in the GLM analyses.

Until recently many studies reporting home range size estimates for black bears have used the minimum convex polygon method (Reynolds and Beecham 1980; Young and Ruff 1982; Hellgren and Vaughan 1990; Smith and Pelton 1990). The MCP home range connects the outermost location points, and is convenient due to its simplicity, flexibility of shape, and comparability to older studies. Its accuracy is questionable, however, in that it is boundary oriented, sensitive to sample size and outlying locations, and assumes a uniform distribution of animal locations within it (White and Garrot 1990; Millspaugh and Marzluff 2001). The kernel density estimator, on the other hand, provides more accurate estimates of space use in that the density of locations is prioritized over the outermost locations (Millspaugh and Marzluff 2001). This method has been recommended over MCP by many authors (Seaman and Powell 1996; Powell et al. 1997; Seaman et al. 1999).

Factors influencing home range size did not differ based on the home range estimation method. The final GLM models for annual and seasonal home ranges generally had the same significant main and interaction effects regardless of the home range estimation method used, although exact *p*-values were somewhat different. Differences were found, however, in cases where significant interaction effects were further analyzed using LSMEANS. These differences may be partially due to small sample sizes and methodological differences. Home ranges estimated using MCP might contain large areas that are not used by the individual (Fig. 2.2), while the corresponding home ranges estimated using the kernel method might consist of several discontinuous polygons that more precisely estimate total area used (Fig. 2.3). The fact that both models identified the same factors to be significant influences on home range size reinforces the validity of my results.

Conclusions and Management Implications

Most previous studies that have investigated the influence of multiple factors on home range size have examined these factors individually using a t-test, ANOVA, or equivalent non-parametric tests (Alt et al. 1980; Reynolds and Beecham 1980; Garshelis and Pelton 1981; Hellgren and Vaughan 1990). This methodology might reveal the effect of that single variable on home range size; however, important interaction effects would likely be missed when variables act to produce a synergistic effect. In this study, the interaction between season and study area would have been overlooked had factors been analyzed separately, and the misleading conclusion that there is no difference between study sites would have been made. Additionally, the interaction between year and reproductive status would also have been missed. It appears from the actual home range sizes that females with cubs consistently had larger annual home ranges, but this was in fact not the case when effects of all factors were evaluated simultaneously. I recommend performing home range analyses within the GLM framework so that multiple main effects, as well as interaction effects, can be considered simultaneously (Slade et al. 1997).

Year, season, study area, and reproductive status all influenced home range size to some degree. The larger home ranges during 2000 emphasized the fact that resource availability is a major factor in determining home range size. This is useful from a management perspective to capture the potential variation in home range size and movements exhibited in times of poor resource availability. Female black bears in Lynne used much larger home ranges during fall than females in ONF, indicating that these bears use space differently and may require a different management protocol based on the degree of habitat fragmentation. Because they move over a large area during fall, further loss and fragmentation of habitat, and other anthropogenic development, may negatively impact the persistence of these bears. Further research on daily movements of black bears in Lynne would provide a more detailed interpretation of space use in a highly fragmented landscape. In summary, environmental factors and individual factors contributed to variation in female black bear spatial ecology and simultaneous analysis of these factors provided a more comprehensive understanding of the Ocala black bear population.

Table 2.1. Annual home range sizes for female black bears in north central Florida, USA. The average annual home range size of female Florida black bears estimated using the 95% fixed kernel density estimator (Kernel) and the 95% minimum convex polygon (MCP) methods. Average home range size (±SE) is presented by year (2000-2003), by study area (ONF and Lynne), and by reproductive status of the female (with or without cubs). "N" is the number of home ranges used to estimate average home range size and the number in parentheses is the number of different females included when averages spanned multiple years. "Locations" is the average number of locations (±SE) used to estimate each home range.

Variable	**N**	**Locations**	**Mean Home Range Size (km^2)**	
Year			Kernel	MCP
2000	14	35.57 ± 1.51	42.58 ± 9.96	34.96 ± 15.42
2001	11	39.09 ± 1.69	22.54 ± 3.04	17.56 ± 4.44
2002	15	62.13 ± 2.10	15.52 ± 2.90	18.32 ± 7.27
2003	8	79.25 ± 3.75	10.62 ± 1.76	15.69 ± 3.97
Study area				
ONF	37 (24)	49.38 ± 2.88	25.89 ± 4.44	22.75 ± 6.17
Lynne	11 (7)	60.64 ± 5.59	18.54 ± 3.86	21.92 ± 9.43
Reproductive status				
Female with cub	21 (18)	54.71 ± 4.06	32.07 ± 7.49	30.19 ± 11.39
Female no cub	27 (21)	49.81 ± 3.44	18.09 ± 1.88	16.62 ± 2.34
Combined	48 (30)	51.96 ± 2.62	24.20 ± 3.55	22.60 ± 5.18

Table 2.2. Seasonal home range sizes for female black bears in north central Florida, USA. The average seasonal home range sizes of female Florida black bears estimated using the 95% fixed kernel density estimator (Kernel) and the 95% minimum convex polygon (MCP) method. Average summer (S) and fall (F) home range sizes are presented by year (2002-2003), by study area (ONF and Lynne), and by reproductive status of the female (with or without cubs). "N" is the number of home ranges used to estimate average home range size and the number in parentheses is the number of different females included when averages spanned multiple years. "Locations" is the average number of locations (±SE) used to estimate home ranges.

Variable		**Season**	**N**	**Locations**	**Mean Home Range Size (km^2)**	
Year					Kernel	MCP
	2002	S	15	32.27 ± 0.95	9.53 ± 1.50	7.10 ± 1.87
		F	19	33.00 ± 0.423	21.47 ± 6.39	16.54 ± 5.73
	2003	S	14	43.21 ± 1.42	6.90 ± 1.22	4.41 ± 0.74
		F	8	40.25 ± 2.67	16.23 ± 3.36	15.68 ± 4.09
Study area						
	ONF	S	19 (15)	38.21 ± 1.66	9.82 ± 1.29	7.05 ± 1.50
		F	19 (16)	36.37 ± 1.30	13.24 ± 1.80	11.56 ± 2.05
	Lynne	S	10 (7)	36.30 ± 2.27	5.30 ± 1.01	3.41 ± 0.60
		F	8 (5)	32.25 ± 1.26	35.76 ± 13.91	27.49 ± 12.90
Reproductive status						
	Female with cub	S	14 (14)	39.79 ± 1.76	6.55 ± 1.04	4.36 ± 0.54
		F	11 (11)	34.18 ± 1.54	22.93 ± 10.04	19.17 ± 9.80
	Female no cub	S	15 (14)	35.47 ± 1.86	9.86 ± 1.58	7.14 ± 1.92
		F	16 (15)	35.81 ± 1.41	17.85 ± 3.83	14.30 ± 2.47
Combined						
		S	29 (22)	37.55 ± 1.32	8.26 ± 0.99	5.80 ± 1.04
		F	27 (21)	35.15 ± 1.04	19.92 ± 4.59	16.28 ± 4.17

Table 2.3. Factors influencing annual home ranges estimated using 95% fixed kernel density estimator (Kernel) and 95% minimum convex polygon (MCP). Results of final general linear models (GLM) by home range estimation method, including all main effects and significant interaction effects, are presented. Degrees of freedom (*df*), value of *F* statistic (*F*), and observed significance level (*P*) are given for each effect.

Home Range	**Source**	***df***	***F***	***P***
Kernel				
	Year	3	1.12	0.3529
	Study Area	1	1.33	0.2557
	Reproductive status	1	0.97	0.3311
	Year X Reproductive status	1	3.55	0.0230
MCP				
	Year	3	0.81	0.4950
	Study area	1	1.99	0.1663
	Reproductive status	1	0.12	0.7299
	Year X reproductive status	1	3.90	0.0158

Table 2.4. Factors influencing seasonal home ranges estimated using 95% fixed kernel density estimator (Kernel) and 95% minimum convex polygon (MCP). Results of final general linear models (GLM) for each home range estimation method including all main effects and significant interaction effects, are presented. Degrees of freedom (*df*), value of *F* statistic (*F*), and observed significance level (*P*) are given for each effect.

Home Range	**Source**	***df***	***F***	***P***
Kernel				
	Year	1	0.75	0.3906
	Season	1	15.58	0.0003
	Study area	1	0.05	0.8274
	Reproductive status	1	2.71	0.1064
	Year X Reproductive Status	1	6.07	0.0173
	Season X study Area	1	10.58	0.0021
MCP				
	Year	1	0.18	0.6739
	Season	1	19.91	<0.0001
	Study area	1	0.0	0.9951
	Reproductive status	1	1.99	0.1642
	Year X reproductive status	1	5.88	0.0190
	Season X study area	1	7.32	0.0094

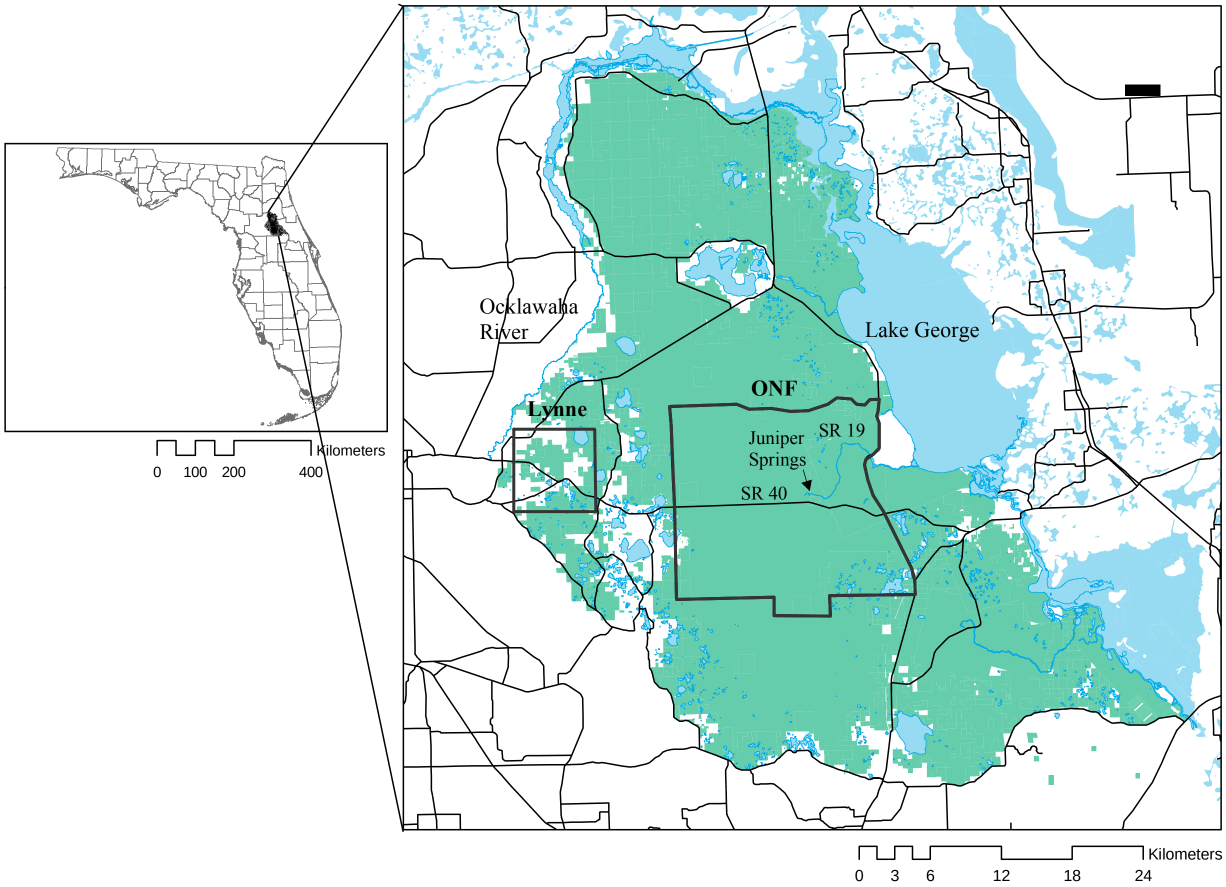

Figure 2.1. The location of Ocala National Forest in north central Florida. ONF and Lynne are the two study sites within Ocala. ONF is located in the center of the forest, north and south of State Road 40 and bounded on the east by State Road 19. Lynne is located to the west of ONF and consists of a matrix of public (green) and private (white) lands. Black lines represent roads and water bodies are blue.

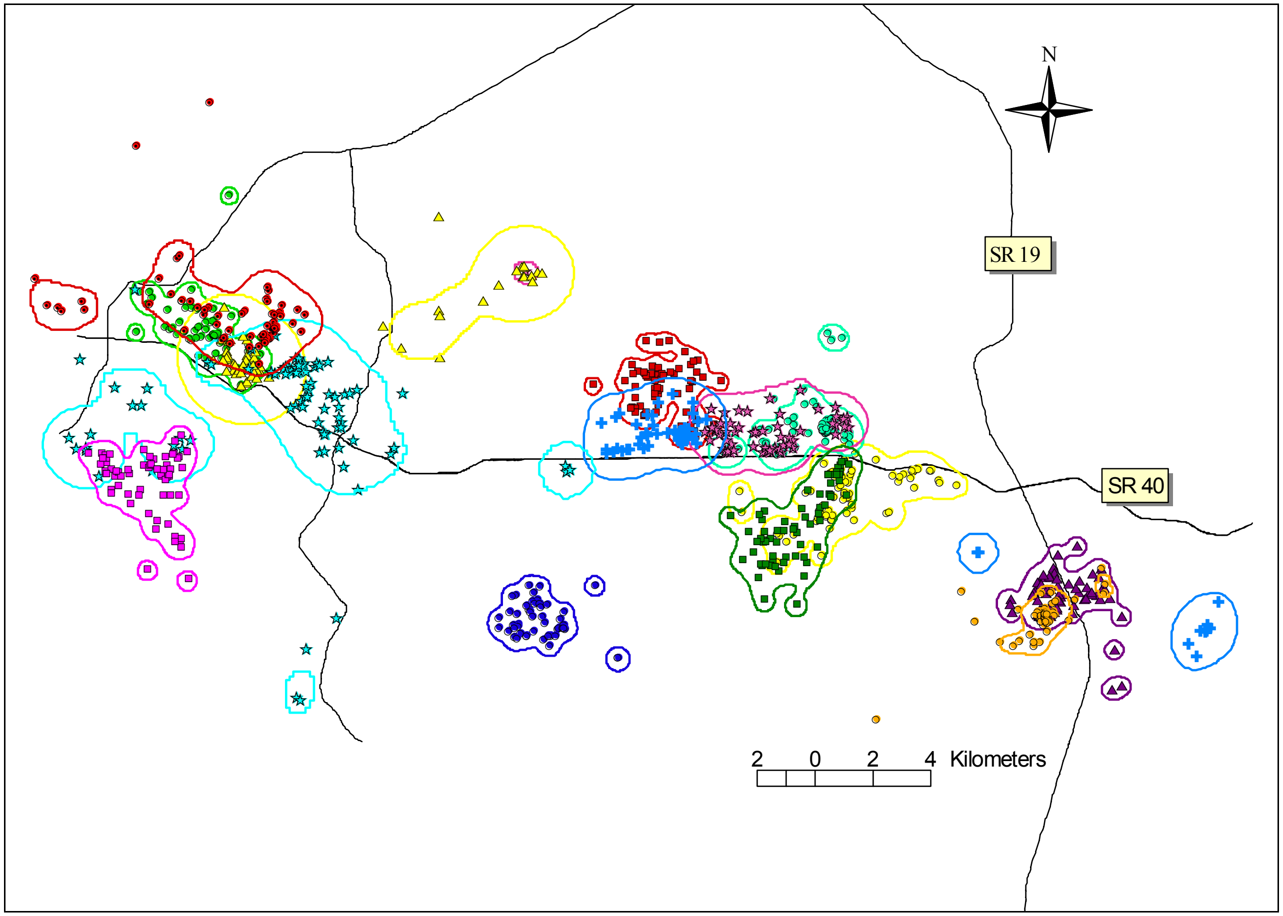

Figure 2.2. Annual home ranges for 14 female black bears in 2002 estimated using the 95% fixed kernel density estimation method. Colored lines represent home range boundaries. Line and point colors distinguish individual females. Major roads are the black lines drawn in the background for orientation (see Fig. 2.1).

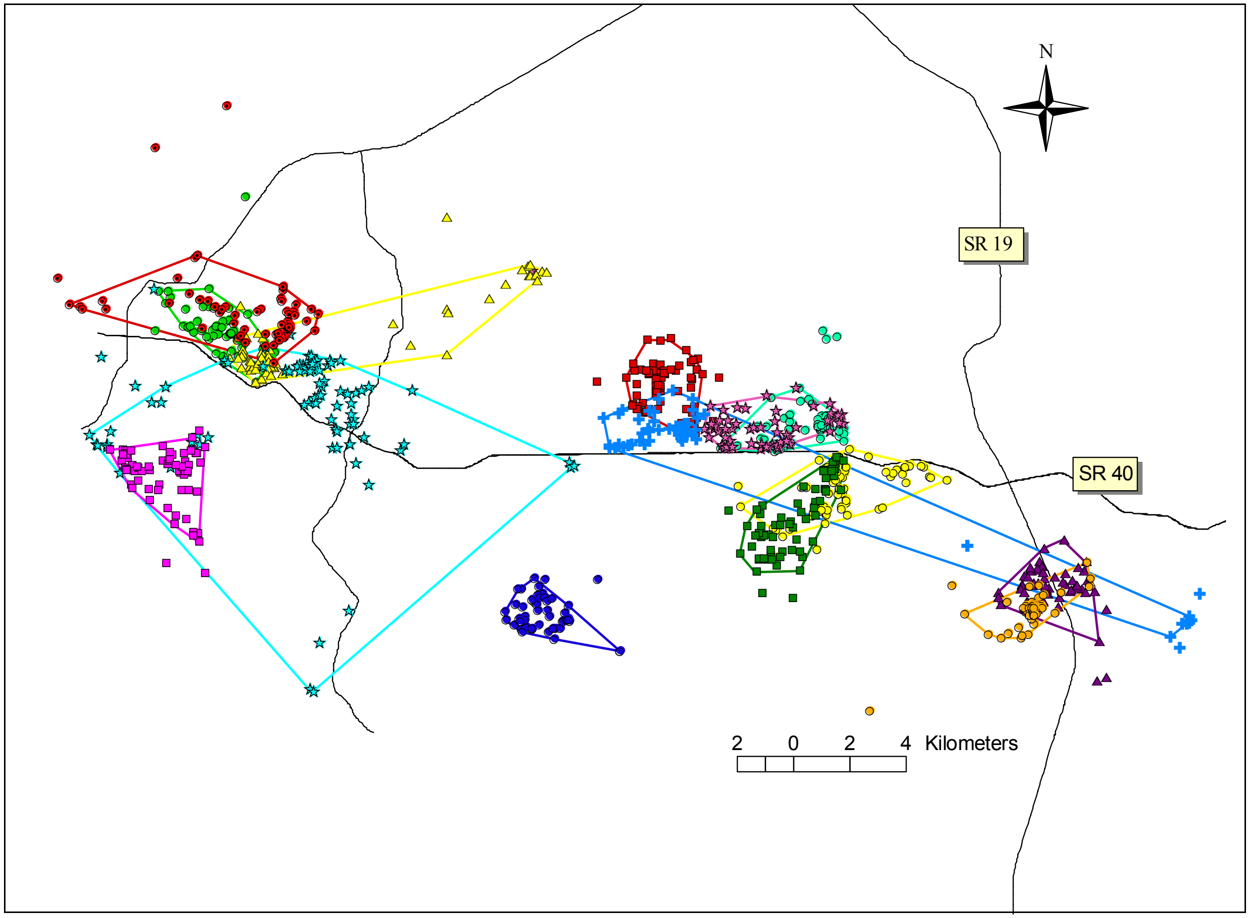

Figure 2.3. Annual home ranges for 14 female black bears in 2002 estimated using the 95% minimum convex polygon method. Colored lines represent home range boundaries. Line and point colors distinguish individual females. Major roads are the black lines in the background for orientation (see Fig. 2.1).

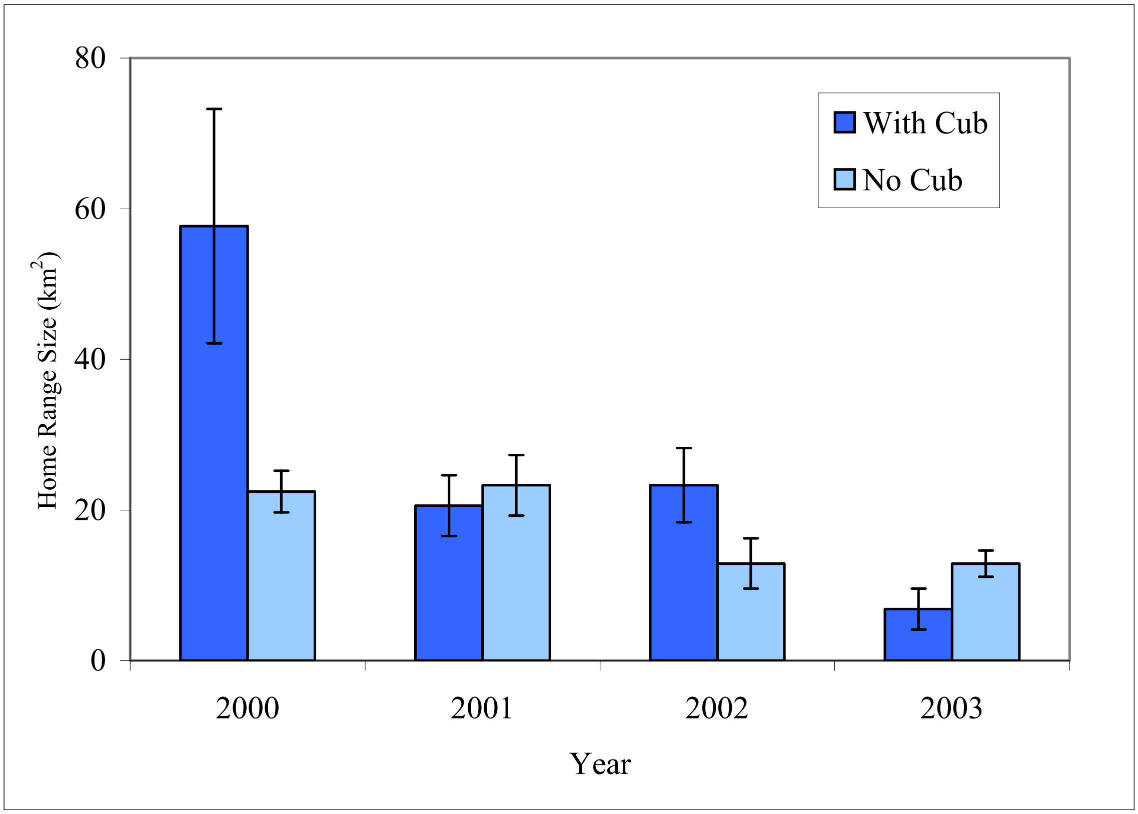

Figure 2.4. Average annual home range size (± SE) for all females with and without cubs during 2000-2003 estimated using the 95% kernel density estimator. A similar pattern was seen when least squares means comparisons were evaluated and when home range sizes were estimated using the 95% minimum convex polygon.

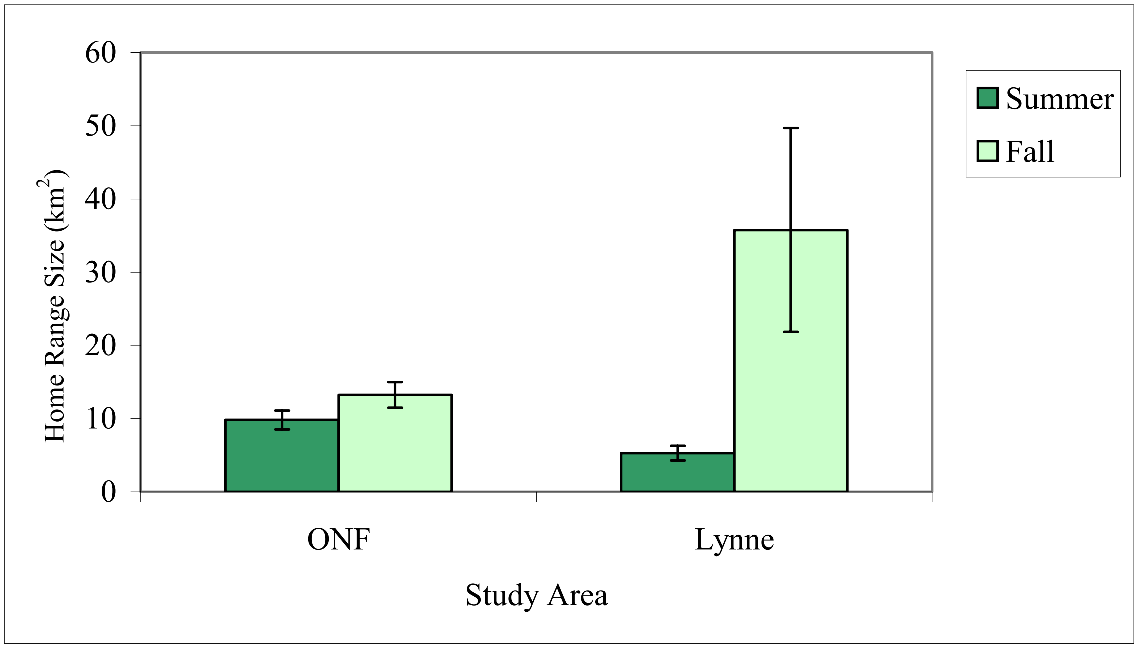

Figure 2.5. Average seasonal home ranges sizes (± SE) for females in ONF and Lynne estimated using the 95% kernel density estimator. A similar pattern was seen when least squares means were evaluated and when home range sizes were estimated using the 95% minimum convex polygon.

CHAPTER 3
HIERARCHICAL HABITAT SELECTION BY FEMALE FLORIDA BLACK BEARS IN OCALA NATIONAL FOREST, FLORIDA

Introduction

Understanding why animals occur where they do is a cornerstone of the field of ecology (Krebs 1978). Animals do not use all of the available land within their geographic range, nor do they use different features of the landscape with equal intensity. Species-habitat associations are the product of both evolutionary and ecological processes; however, the distribution of animals within their geographic range is often influenced by an individual's behavior when selecting habitat (Krebs 1978; Morrison et al. 1992). It is presumed that wildlife species select habitat to enhance their fitness, and will choose high quality habitat over low quality habitat when available (Manly et al. 1993).

These selection behaviors often occur across multiple scales and result in a hierarchical nature of habitat selection (Johnson 1980; Orians and Wittenberger 1991). An individual will select a home range from the population range or study area, and will also select patches of habitat to use within that home range. Different habitat attributes may be selected for at different spatial scales. Rettie and Messier (2000) suggest that the most important, or most limiting, factors affecting individual fitness should be selected for at the coarsest scales. Finer scale habitat selection, therefore, is based on less critical factors. Formal testing of habitat and resource selection at multiple scales has emerged as one focus within the field of ecology to address the relationship between animals and their environments (Johnson 1980; Alldredge and Ratti 1992; Morrison et al. 1992; Aebischer et al. 1993; Manly et al. 1993). Evaluation of habitat use without considering hierarchical effects may produce incomplete or misleading results that would provide an inadequate understanding of habitat requirements (Orians and Wittenberger 1991). In this study, I considered habitat selection of the Florida black bear (*Ursus americanus floridanus*), a subspecies of the North American black bear, at multiple spatial scales.

The North American black bear historically occupied a wide variety of forested habitats throughout the United States and Canada (Hall 1981). Although their geographic range has been contracted, black bears have retained their affinity to forested areas; as habitat generalists they have adapted to many different habitat types (Maehr and Brady 1984; Schoen 1990; Smith and Pelton 1990; Wooding and Hardisky 1994). The black bear is also considered to be a landscape species in that it utilizes a large home range and many different habitats within that home range (Schoen 1990). These habitats must contain all the requirements for the bears' survival and reproduction, including habitat types with adequate food resources and cover for concealment (Burt 1943).

The pattern of habitat selection has been studied extensively throughout the black bears' geographic range. Almost all studies have found that black bears use habitat types disproportionately to their availabilities, indicating that they show preferences for some habitats over others (Jonkel and Cowan 1971; Lindzey and Meslow 1977; Unsworth et al. 1989; Hellgren et al. 1991; Wooding and Hardisky 1994; Heyden and Meslow 1999; Hirsch et al. 1999). Preferred habitats, however, vary widely depending on geographic region and diversity of available habitats, and may vary seasonally depending on vegetation structure and plant phenology (Powell 1987; Rogers 1987; Unsworth et al.

1989; Smith and Pelton 1990; Powell et al. 1997; Samson and Huot 1998; Stratman et al. 2001; Fecske et al. 2002; Lyons et al. 2003).

The Florida black bear is listed by the state of Florida as a threatened species. It is currently restricted to 17% of its former range in Florida due to habitat loss and fragmentation (Wooding 1993). Conservation of the remaining black bears in Florida requires knowledge of this subspecies' habitat utilization at multiple spatial scales as well as how selection changes with temporal variation; however, this subspecies of the North American black bear has been less thoroughly studied than other subspecies. Near the southern tip of their geographic range, Florida black bears have access to different habitat types and persist in isolated populations within a human dominated landscape.

My objective was to investigate the spatial and temporal pattern of habitat selection by female Florida black bears in Ocala National Forest in north central Florida. Using radio-telemetry data for 35 female bears (2000-2003) and a distance-based habitat selection method (Conner and Plowman 2001; Conner et al. 2003), I tested the null hypothesis that female black bears used habitat types in proportion to their availability when selecting a home range within the study area in Ocala National Forest, and when utilizing habitat types within that home range (corresponding to Johnson's (1980) second and third orders of selection, respectively). This null hypothesis was tested using data collected during the entire study period, as well as separately for fall and summer. At each spatial scale, if the null hypothesis of no selection was rejected, I identified habitats that were selected more or less than expected and ranked all habitat types in order of preference.

Methods

Study Site and Land Cover Map

The study was conducted in the Ocala National Forest in north central Florida, which is located along a ridge of ancient sand dunes and is bisected by State Road 40. The forest slopes downward toward the St. Johns and Ocklawaha Rivers to the east and west. The lower elevations closer to the rivers correspond with the increase in mesic forest cover types. Human disturbance, due to selective logging, clear-cutting, prescribed burning, and road building practices within the forest, provide much of the heterogeneity in the forest cover type and stand age. Only bears within the ONF study area (the study area in the center of Ocala National Forest) were considered in this analysis (see Chap. 2 and Fig. 2.1).

Seven habitat types were defined within the study area based on the forest cover types presented in the Florida Vegetation and Land Cover map (FVLC) (Table 3.1) (Florida Fish and Wildlife Conservation Commission 2003). The original FVLC map was refined by merging cover types that were similar in plant species or structure. Two forest cover types were not considered because they were present in discrete patches at the periphery of the study area, comprised less than 1% of the total area, and were potentially available to only a few individual bears. The resulting habitat types were sand pine forest, xeric oak scrub, pine flatwoods, swamp forests, marshes/open water, disturbed areas, and high impact urban areas.

The most prominent forest cover type within ONF was sand pine forest (Figure 3.1). The overstory of this cover type is predominantly sand pine (*Pinus clausa*), while the shrub layer consists of six species in approximately the following order of abundance: myrtle oak or scrub oak (*Quercus myrtifolia*, *Q. inopina*), saw palmetto (*Serenoa repens*), sand live oak (*Q. geminata*), Chapman's oak (*Q. chapmanii*), rusty lyonia (*Lyonia ferruginea*), and Florida rosemary (*Ceratiola ericoides*) (Myers 1990). The density of sand pine in the overstory can vary greatly from dense stands to widely scattered and is inversely related to the density of the scrub oak below. The xeric oak scrub classification is similar to sand pine forest, though it lacks the overstory of sand pine, and constitutes the second largest portion of the study area. This forest is intensively managed for timber and stands of 50-100 ha are regularly clearcut. I classified these clearcuts and other open disturbed areas, such as roadsides and forest logging roads, as disturbed. These three cover types, clear cuts, xeric oak scrub, and sand pine scrub, represented three successional stages within ONF and their distribution created a mosaic of stand ages.

The remaining land cover classifications are found more frequently at lower elevations as the forest slopes towards the Ocklawaha and St. Johns Rivers, and are mesic or hydric in nature. Pine flatwoods have an overstory composed of slash pine (*Pinus elliottii*) or pond pine (*P. serotina*) while saw palmetto, gallberry (*Ilex glabra*), and fetterbush (*Lyonia lucida*) are frequent understory species. Land cover types merged to define swamp forests included hardwood swamp, bay swamp, cypress swamp, and mixed wetland forest. Swamp forests have standing water or saturated soils for at least part of the year as well as a hardwood component (Ewel 1990). Major tree species include cypress (*Taxodium distichum*), sabal palm (*Sabal palmetto*), loblolly bay (*Gordonia lasianthus*), and sweet bay (*Magnolia grandiflora*). Within the study area swamps are found near Juniper Springs and also east of State Road 19.

Open water and freshwater marshes were combined into a single habitat type because of the tendency for one to grade into the other with variation in annual and seasonal rainfall. High impact urban areas included major paved roads such as State Road 40 and developed areas. Although the proportion of this cover type within the forest was low it was readily available to most females throughout the study area and thus was retained as a separate cover classification so that its effect on black bear habitat use could be evaluated.

Field Methods

Black bears were captured from 1999 through 2002 using spring activated Aldrich foot snares disguised in natural vegetation and baited with donuts or a combination of corn and donuts. Although bears were trapped from May through December, the most intensive trapping occurred during summer months. Bears were anesthetized with Telazol® delivered through a CO_2 charged low-impact dart delivery system. Once sedated, bears were ear tagged and lip-tattooed for individual identification. Hair and blood samples were collected for genetic analyses, and a pre-molar tooth was extracted to estimate age (Willey 1974). Morphometric measurements and body mass as well as physical and reproductive condition scores also were recorded. Most females, and some males, were fitted with a motion-sensitive radio-collar (150-151 MHz; Telonics, Mesa, Arizona). Radio-collars included a leather connector, which would allow the collar to fall off within two to three years. Reproductive females or those $\geq$ 3 years of age were considered adults and included in analyses (Garrison 2004).

Adult female bears were located on average once per week during 1999-2001, twice per week in 2002, and three times per week in 2003. The majority of locations were obtained from the ground during daylight hours (0900-1800) using a 4-element hand held antenna and a Telonics® receiver, but bears were also tracked 1-4 times per month from a fixed wing aircraft. For each bear, $\geq$ 3 compass bearings were obtained within 30 minutes to minimize location error due to movements. Point locations from ground telemetry were estimated using the program Locate II (Pacer 1990). Telemetry error was estimated by comparing estimated locations of dropped collars and female natal dens to their actual locations. The average ground telemetry error was 157 m, based on 303 locations on 19 dens and 7 test collars. In these cases observer distances varied from 0.25-1 mile from the actual location. The average aerial telemetry error was 251 m, based on 25 dropped and deployed collar locations.

Data Analysis

Female locations over the duration of the study were used to define the 620 km^2 ONF study area (Fig. 3.1) by using the composite minimum convex polygon (MCP) of these female locations, excluding distant outliers. For each bear, I used the program CALHOME (Kie et al. 1994) to estimate the 95% MCP for three categories of home ranges: a) overall home ranges b) summer home ranges and c) fall home ranges. Overall (or multi-annual) home ranges were estimated for each bear from locations collected from May-December over the four years of the study. Summer home ranges were estimated for each bear from locations collected between May and August combined over the four years of the study. Fall home ranges were estimated for each bear from locations collected between September and December during the course of the study. I used MCP home range estimates, which always consist of one polygon, instead of kernel home range estimates, which may be represented by many polygons, so that all intervening habitat among telemetry locations would be included in the home range and thus considered available. The beginning of September was chosen as the transition between summer and fall based on the start of the availability of acorns at this time, the end of the breeding season, and to distribute sampling effort evenly across seasons.

I used a distance-based method to compare habitat use to availability within ONF (Conner and Plowman 2001; Conner et al. 2003). This method compares actual distances from telemetry locations to each habitat type to expected distances to each habitat type in order to test the null hypothesis that different habitat types are used proportionately to their availabilities (Conner et al. 2003). Locations closer to a given habitat type than expected indicate preference of that habitat type. When compared to a classification-based method (e.g. compositional analysis, Aebischer et al. 1993), the distance-based analysis generates more accurate results from data that include telemetry error because in the distance-based analysis telemetry locations are not assigned to a habitat type wherein misclassifications could occur (Conner et al. 2003; Bingham and Brennan 2004).

The coarse scale of habitat analysis was the selection of the home range from the study area (second order selection of Johnson (1980)). In order to evaluate habitat use at this level, I generated random points with a uniform distribution at the density of 300 points per km^2 using the Animal Movement extension of ArcView 3.2 (Hooge et al. 1999). This density of points was selected because it was where the variance of the average distance to a given habitat type began to stabilize (Fig. 3.2). Habitat availability was estimated using the random points within the study area. Habitat use was estimated using the random points within each bear’s home range. I measured the distance from each random point in the study area to the nearest patch of each habitat type. I created a vector from the average distances to each habitat type (**r**). Entries in **r** represented expected values of distances under the null hypothesis of no habitat selection (Conner et al. 2003). I also created a vector from the average distances of random points within each home range to each habitat type (**u**). A different vector **u** was created for each bear and entries in **u** represented habitat use. Each element in **u** was divided by the corresponding element in **r** for each bear. A ratio of 1.0 indicated that use equaled availability for a given habitat type. These ratios were then averaged over all bears to produce a vector $\boldsymbol{\rho}$. The null hypothesis that $\boldsymbol{\rho}$ is not significantly different from a vector of 1's was tested using multivariate analysis of variance (MANOVA) (SAS procedure GLM; SAS Institute Inc. 1999). Rejection of the null hypothesis of no habitat selection ($p < 0.05$) would indicate that use differed from availability for at least one habitat.

If the null hypothesis was rejected, I used a paired t-test to compare each element in $\boldsymbol{\rho}$ to 1.0 to determine which habitat types were used differently than expected. When an element in $\boldsymbol{\rho} < 1$, points were closer than expected, and when an element in $\boldsymbol{\rho} > 1$ points were further away than expected. The elements in $\boldsymbol{\rho}$ were then used to rank the habitat types in order of preference and significant differences between habitat types were determined using a paired t-test. These analyses were performed using the SAS code adapted from Conner and Plowman (2001).

I also evaluated habitat use at a finer scale, the selection of habitat types within the individual home range (third order selection of Johnson (1980)). In this case, habitat availability was defined using the random points within each home range, while habitat use was defined by the telemetry locations for each bear within the home range. A vector of the ratio of mean distances for each bear ($\boldsymbol{\rho}$) was generated as described above. The null hypothesis that $\boldsymbol{\rho}$ equaled a vector of 1's was tested using MANOVA. Again, each habitat type was evaluated independently and a matrix of rankings was generated if the null hypothesis of no habitat selection was rejected.

Results

The average number of locations (±SE) used to estimate home ranges was 83 ± 11 for overall (multi-annual), 61 ± 6 for summer, and 56 ± 6 for fall. The average home range size was 25.74 ± 7.99 km^2 for overall home ranges, 11.09 ± 2.48 km^2 for summer home ranges, and 35.17 ± 11.14 km^2 for fall home ranges.

At the scale of home range selection within the study area, the mean vector of distance ratios ($\boldsymbol{\rho}$) did not differ from a vector of 1's for the overall or the fall home ranges, indicating that habitat selection did not occur (Table 3.2). However, habitat selection did occur as females selected a summer home range from the study area (p = 0.026). In particular, the elements representing xeric oak scrub and sand pine forest in $\boldsymbol{\rho}$ were significantly less than 1.0 ($p < 0.001$, $p = 0.014$, respectively). The order of preference was: xeric oak scrub > sand pine forest > disturbed > pine flatwoods > swamp forest > marsh/open water > high impact urban. Pairwise comparisons suggested that xeric oak scrub was preferred over disturbed, pine flatwoods, and high impact urban patches (Table 3.3).

Analysis of habitat selection within the home range indicated that $\boldsymbol{\rho}$ for overall and fall home ranges was not significantly different from a vector of 1's (Table 3.2), indicating that habitat selection did not occur. During summer, however, habitat selection was detected ($p = 0.026$). For summer home ranges, individual comparisons of each element in $\boldsymbol{\rho}$ to 1.0 indicated that bears were located significantly farther away from xeric oak scrub than the random points within the home range ($p = 0.005$). The order of habitat preference at this scale was: high impact urban > pine flatwoods > swamp forest >

marsh/open water > disturbed > xeric oak scrub > sand pine forest. Telemetry locations were significantly closer to high impact urban and pine flatwoods than to xeric oak scrub and disturbed cover types (Table 3.4).

Discussion

In ONF, black bears used habitat types in proportion to their availability when selecting overall and fall home ranges as well as in utilization of habitat within those home ranges. However, during summer bears used some habitat types disproportionately to their availabilities, both when selecting a home range from the study area and within the individual home range.

At the level of home range selection (second order selection), summer home ranges included more xeric oak scrub and sand pine forest than expected, while other habitat types were included in expected proportions. These scrub oak habitats frequently have a very dense understory, which provides excellent cover, and are dominated by acorn producing species. Although primarily a fall food source, acorns remaining after the winter may be an important early summer food source after den emergence as well.

Black bears did not select fall or overall home ranges to include proportionately more acorn producing habitat types than available. Sand pine forest and xeric oak scrub combined comprise over 65% of the available habitat in the study area (Table 3.1). Even though selection did not occur, scrub habitats composed a large portion of the home range and were thus heavily used. This non-significant result also may be due to how the study area and thus available habitat at this scale was defined. I used the bear locations themselves to define the study area and thus the study area predominantly included sand pine scrub and xeric oak scrub. If the study area had been defined as the entire range of the Ocala black bear population, significant home range selection at this scale may have been detected, particularly if a larger amount of the habitat near the Ocklawaha and St. Johns Rivers had been included. Had the study area been defined this way, a strong affinity for sand pine forest and xeric oak scrub most likely would have been the major trend.

While sand pine forest and xeric oak scrub were the most preferred habitats for summer home ranges at the coarse scale of analysis, these same habitats were the least preferred when utilizing the habitat within the home range. Within summer home ranges, black bears were more closely associated with pine flatwoods and swamp forests than expected. The scrub habitats may have been least preferred during summer because they primarily produce hard masts available during fall. Pine flatwoods and swamp forests have a higher vegetative diversity as well as more abundant berry producing species and saw palmetto shoots which are the largest components in the summer diet (Roof 1997). Surprisingly, the high impact urban habitat type was the most preferred habitat type during summer, but this may be due to the proximity of paved roads to pine flatwoods and swamp forest. Within the study area, these two habitat types are most abundant near SR 40 and Juniper Springs and south of SR 40 along SR 19. Areas near roads also may have contained edge habitat that provided more food. Regardless of the ultimate cause for habitat use near paved roads, it is important to note that black bears did not avoid roads at this scale of selection.

No habitat selection was detected within the home range (third order selection) for fall or overall home ranges, indicating that habitat types were used in proportion to their availabilities. When contrasted to habitat use within summer home ranges, sand pine forest and xeric oak scrub were more heavily utilized for fall and on an annual basis.

During fall, the primary food sources are the acorns of various scrub oak species (Roof 1997). Because sand pine forest and xeric oak scrub comprise a large portion of the forest, the fact that there was no selection is evidence that black bears heavily use these habitats for the substantial fall food that they supply. However, while scrub oaks may provide the most abundant fall food source, utilization of other habitat types and alternative food sources also was observed. Habitat selection also was not detected for overall home ranges, suggesting that on a year round basis habitat types were used in proportion to their availability.

The results of this study suggest parallels between habitat use in ONF and in other black bear populations, although the unique habitat composition of ONF makes direct comparison difficult. Other bear populations in the southeastern United States utilize riparian and wetland habitats for both food and cover (Hellgren et al. 1991; Wooding and Hardisky 1994; Stratman et al. 2001), especially upon den emergence, because wetlands provide one of the first available sources of food (Fecske et al. 2002). Other studies also have confirmed that black bears rely heavily on acorns in hardwood stands during fall (Garshelis and Pelton 1981; Smith and Pelton 1990; Powell et al. 1997). Study areas that have a conifer component to the landscape often report avoidance of this cover type because of a lack of food (Stratman et al. 2001), although in some cases conifer forests can be utilized as escape cover (Fecske et al. 2002).

The utilization of more mesic cover types during summer in ONF, especially the swamp forests, reflects what has been found in other black bear populations. However, Ocala National Forest is different from most of the southeastern forests in that hardwood forests dominated by red oak (*Quercus rubra*) and white oak trees (*Q. alba*) are not common. Instead, abundant fall mast is available in the sand pine forest and xeric oak scrub from the scrub oak species, especially myrtle oak (*Q. myrtifolia*) and scrub oak (*Q. inopina*). Although sand pine forest and xeric oak scrub are not considered preferred habitat types, they are a highly utilized fall food source.

Subtle trends in habitat use within the forest may be difficult to detect due to the degree of individual variation in home range placement and habitat use. Some females established home ranges in the central portion of the scrub habitats and did not utilize other habitat types, while others had home ranges that encompassed swamp and pine flatwoods in addition to sand pine and xeric oak scrub. Another confounding factor may be the spatial and temporal variation in the distribution of food resources. Within one habitat type, the diversity and abundance of food may vary between years and seasons. Black bears are highly adaptable and are able to exploit a wide variety of food resources (Rogers 1987; Smith and Pelton 1990). Their adjustments to seasonal fluctuations make trends in resource utilization more difficult to detect.

Responses to the human modified habitat types (disturbed and high impact urban areas) were mixed. Random points within the home range were closer to sand pine and xeric oak scrub than to both disturbed and urban features of the landscape, indicating that when selecting a home range the bears appear to avoid both paved roads and clearcut openings. At the finer scale, however, the disturbed habitat was still one of the least preferred habitat types, but the high impact urban habitat was the most preferred relative to its availability. Females most likely select against clearcuts within their home ranges because they do not provide the necessary cover. The bears do appear to be somewhat tolerant to human disturbance though, as long as they have adequate escape cover such as the very dense roadside vegetation of ONF.

The pattern of habitat selection in this study for the summer home ranges of females is different at different spatial scales. Rettie and Messier (2000) suggest that the most important, or most limiting, factors affecting individual fitness should be selected for at the coarsest scales. At the coarse scale, other studies have found that habitats were selected for predator avoidance in woodland caribou (Rettie and Messier 2000), den site availability in wolves (McLoughlin et al. 2004), and prey availability in barren-ground grizzly bears (McLoughlin et al. 2002), while habitat types with higher food availability were selected at the finer scale in each of these cases. Lyons et al. (2003) suggested that black bears in Washington selected home ranges from the study area to include sufficient food; however, they utilized habitat types within the home range for both food and escape cover. In this study, the major differences between the habitat selection of black bears at two spatial scales during summer were that at the coarser scale, densely forested habitat types were primarily selected for and human impacted habitat types were generally avoided, while within the home range this order was reversed. The strong selection for forested habitat types used for food and cover may indicate that these factors are most limiting. Specific food resources may be less limiting and only selected for at a finer scale.

In ONF, a primary goal of habitat managers should be to maintain a diversity of habitats. This is critically important as bears utilize food resources from different habitats on both a seasonal and annual basis. Reduced diversity may increase the likelihood that mast failure of one species will have a dire impact on the population as a whole. At the scale of a stand within the forest, females selected against open clearcut areas. However, these clearcut areas may regenerate to xeric oak scrub over time, which provides both food and cover. A balance of stand ages should be maintained so that the overall abundance of acorn producing species in the forest will remain high.

Table 3.1. Description of habitat types used for habitat selection analysis. Seven habitat types were defined in the ONF study area within Ocala National Forest from the original forest cover types in the Florida Vegetation and Land Cover Map (Florida Fish and Wildlife Conservation Commission 2003). The percentage of occurrence in the final map indicates the contribution of each habitat type to the overall habitat composition of the ONF study area (see Fig. 3.1).

Habitat type	% of final map	Original FVLC cover types
Xeric Oak Scrub	23.90	Xeric Oak Scrub
Sand Pine Forest	44.34	Sand Pine Scrub
Pine Flatwoods	3.15	Pinelands
Marsh/Open Water	6.99	Fresh Water Marsh and Wet Prairie Sawgrass Marsh Cattail Marsh Open Water
Swamp Forest	8.59	Shrub Swamp Bay Swamp Cypress Swamp Mixed Wetland Forest Hardwood Swamp
Disturbed	10.00	Shrub and brushland Grassland Bare Soil/Clearcut Agriculture Low Impact Urban
High Impact Urban	1.42	High Impact Urban Mining (Extractive)

Table 3.2. Results of the distance-based analysis of habitat selection at two spatial scales in Ocala National Forest: the selection of the home range from the study area (home range selection) and selection of habitat types within the home range (habitat selection within the home range), for overall (multi-annual), summer and fall home ranges. The *F* value and significance level (*p*) are the results of separate multivariate analysis of variance tests comparing the ratio of mean distances from "used" points to each habitat type and mean distances of "available" points to each habitat type to a vector of 1's. A significant *p* value indicates that habitat use differed from availability. The number of females represents the number of home ranges included in each analysis.

Test	**Number of Females**	***df***	***F***	***p***
Home range selection				
Overall	22	7,15	0.9	0.530
Summer	20	7,13	3.46	0.026
Fall	19	7,12	0.7	0.674
Habitat selection within the home range				
Overall	22	7,15	1.6	0.210
Summer	20	7,12	3.46	0.026
Fall	19	7,12	1.85	0.166

Table 3.3. Ranking matrix of habitat types used by female black bears when selecting a home range in Ocala National Forest. The habitat types are listed in order of preference and *t* statistics (*p*-value) are given for each pair of habitat types. A negative *t* statistic indicates that the column cover type was used more relative to its availability than the row cover type.

Cover Type	Xeric Oak Scrub	Sand Pine Forest	Disturbed	Pine Flatwoods	Swamp Forest	Marsh/Open Water	High Impact Urban
Xeric Oak Scrub		0.05 (0.961)	3.89 (0.001)	3.10 (0.006)	1.66 (0.114)	2.07 (0.053)	2.65 (0.016)
Sand Pine Forest	-0.05 (0.961)		1.57 (0.132)	1.86 (0.078)	1.30 (0.208)	1.66 (0.113)	2.66 (0.015)
Disturbed	-3.89 (0.001)	-1.57 (0.132)		0.78 (0.443)	0.49 (0.632)	0.85 (0.406)	1.41 (0.175)
Pine Flatwoods	-3.10 (0.006)	-1.86 (0.078)	-0.78 (0.443)		0.15 (0.880)	0.65 (0.523)	1.10 (0.287)
Swamp Forest	-1.66 (0.114)	-1.30 (0.208)	-0.49 (0.632)	-0.15 (0.880)		0.75 (0.463)	0.89 (0.386)
Marsh/Open Water	-2.07 (0.053)	-1.66 (0.113)	-0.85 (0.406)	-0.65 (0.523)	-0.75 (0.463)		0.41 (0.683)
High Impact Urban	-2.65 (0.016)	-2.66 (0.015)	-1.41 (0.175)	-1.10 (0.287)	-0.89 (0.386)	-0.41 (0.683)	

Table 3.4. Ranking matrix of habitat types used by female black bears when selecting habitat within a home range in Ocala National Forest. The habitat types are listed in order of preference and *t* statistics (*p*-value) are given for each pair of habitat types. A negative *t* statistic indicates that the column cover type was used more relative to its availability than the row cover type.

Cover Type	High Impact Urban	Pine Flatwoods	Swamp Forests	Marsh/Open Water	Disturbed	Xeric Oak Scrub	Sand Pine Forest
High Impact Urban		1.10 (0.286)	1.06 (0.301)	1.16 (0.260)	2.86 (0.010)	2.62 (0.017)	1.16 (0.259)
Pine Flatwoods	-1.10 (0.286)		0.38 (0.708)	0.57 (0.576)	2.97 (0.008)	2.76 (0.012)	1.04 (0.310)
Swamp Forests	-1.06 (0.301)	-0.38 (0.708)		0.22 (0.825)	2.06 (0.053)	1.97 (0.063)	0.98 (0.342)
Marsh/Open Water	-1.16 (0.260)	-0.57 (0.576)	-0.22 (0.825)		2.03 (0.056)	2.14 (0.046)	0.97 (0.346)
Disturbed	-2.86 (0.010)	-2.97 (0.008)	-2.06 (0.053)	-2.03 (0.056)		0.68 (0.504)	0.70 (0.493)
Xeric Oak Scrub	-2.62 (0.017)	-2.76 (0.012)	-1.97 (0.063)	-2.14 (0.046)	-0.68 (0.504)		0.64 (0.533)
Sand Pine Forest	-1.16 (0.259)	-1.04 (0.310)	-0.98 (0.342)	-0.97 (0.346)	-0.70 (0.493)	-0.64 (0.533)	

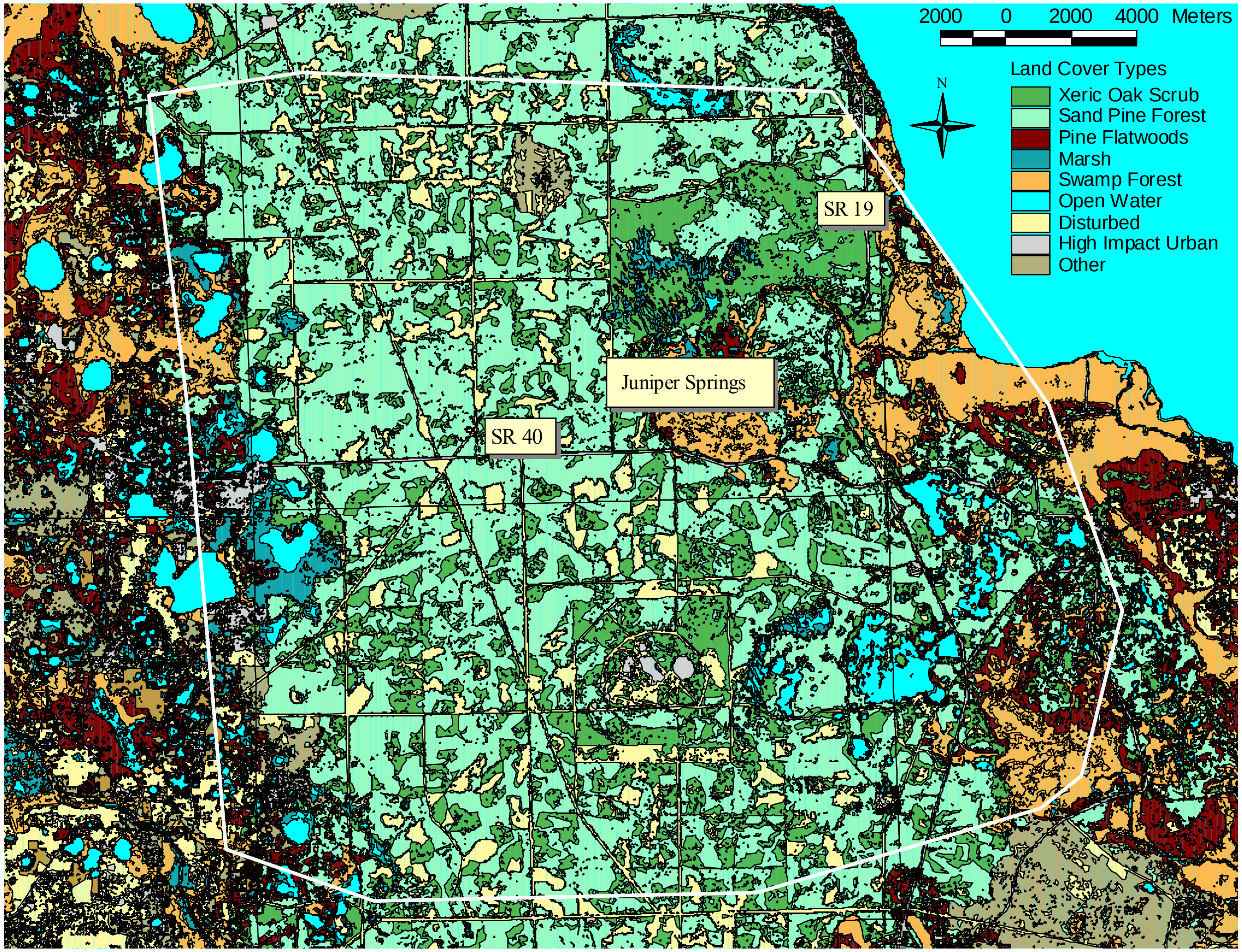

Figure 3.1. Map of habitat types in Ocala National Forest, north central Florida, USA. Forest cover types of the Florida Vegetation and Land Cover Map were merged to form seven habitat types in the ONF study area (represented by the white line). State road 40 (SR 40) bisects the study area and state road 19 (SR 19) is near the eastern edge. Much of the swamp forest in the center of ONF is associated with Juniper Springs, which flows toward Lake George shown in the upper right corner.

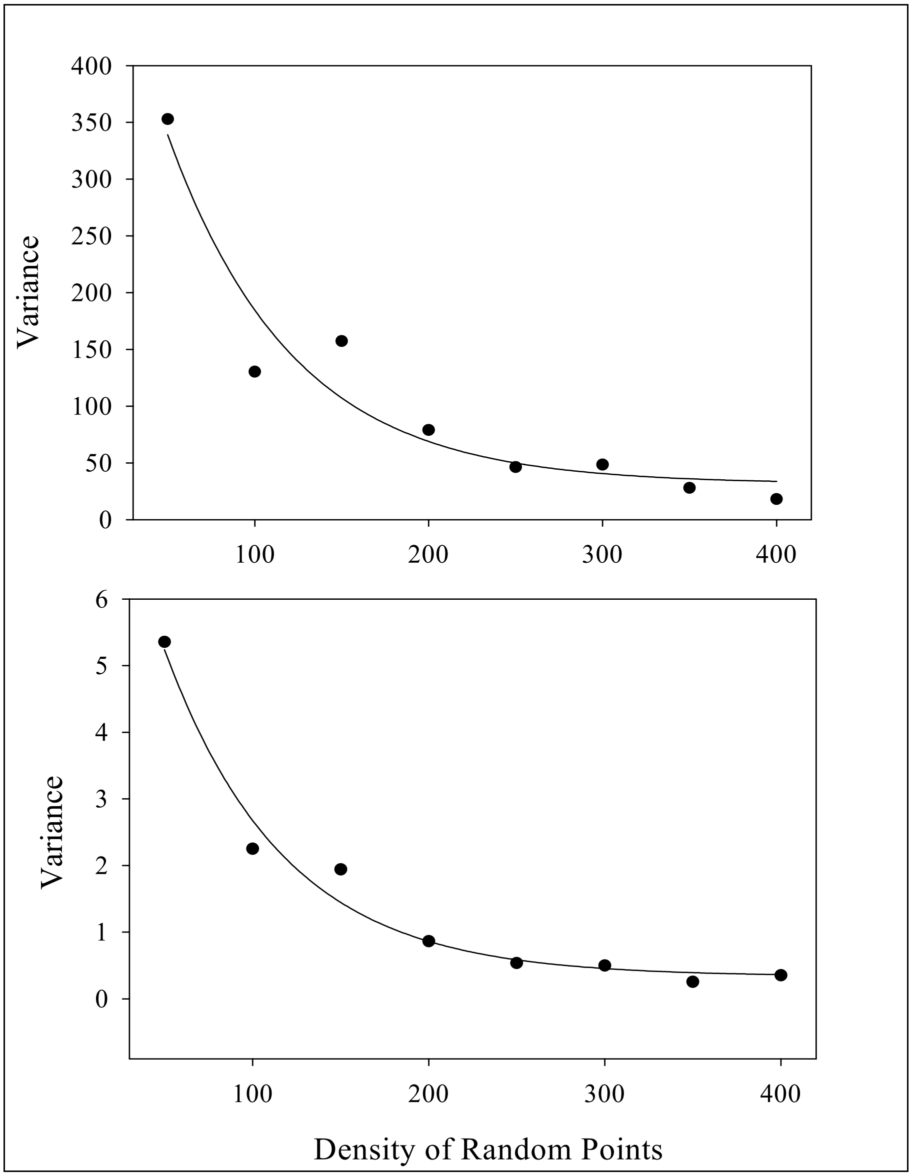

Figure 3.2. The relationship between the density of random points per km^2 and the variance of the average distance to individual habitat types. Curves for the remaining 5 habitat types are similar to those for the swamp forest (top) and xeric oaks scrub (bottom) presented here.

CHAPTER 4
DOES GENETIC RELATEDNESS INFLUENCE SPACE USE PATTERN? A TEST ON FLORIDA BLACK BEARS

Introduction

Social interactions between individuals in mammalian species may influence home range placement and access to resources (Carpenter and MacMillen 1976; McLoughlin et al. 2000). Interest in the familial relationships between interacting individuals as an explanation for these social behaviors has been a recurring theme in recent ecological literature (Gompper and Wayne 1996). With the advent of genetic techniques that allow reliable estimates of relatedness, relationships between genetic relatedness and behavioral patterns are now being tested with some surprising results.

Close spatial association between related individuals has been demonstrated for many mammalian species including the California ground squirrel *Otospermophilus beecheyi* (Boellstorff and Owings 1995), the gray mouse lemur *Microcebus murinus* (Wimmer et al. 2002), the banner-tailed kangaroo rat *Dipodomys spectabilis* (Winters and Waser 2003), the raccoon *Procyon lotor* (Ratnayeke et al. 2002), and the lion *Panthera leo* (Van Orsdol et al. 1985). However, the hypothesis that genetic relatedness explains spatial association has been contradicted in other species including the harbour seal *Phoca vitulina* (Schaeff et al. 1999), the snowshoe hare *Lepus americanus* (Burton and Krebs 2003), and the wild chimpanzee *Pan troglodytes schweinfurthii* (Goldberg and Wrangham 1997).

In solitary carnivores, females are predicted to be natal philopatric and to establish home ranges close to their place of birth (Waser and Jones 1983); however, the influence of relatedness on space use pattern has been less frequently evaluated in large solitary carnivores than in small and/or social mammals. Where spatial association between related females has been documented, long-term studies and intimate knowledge of individuals was required (e.g. Bengal tiger *Panthera tigris* (Smith et al. 1987); black bear *Ursus americanus* (Rogers 1987)). Subsequent studies of large carnivores have considered these observations as evidence of widespread natal philopatry and have interpreted territorial, foraging, and mating behaviors accordingly. However, the influence of genetic relatedness on spatial organization is largely untested in large carnivore species. If natal philopatry is a dominant space use trend in large carnivores, clusters of related females should develop over time across the landscape.

Intensive studies and opportunistic observations have provided evidence of female natal philopatry by means of home range establishment of female offspring and by observations of tolerance of adult females toward female offspring in the black bear (Rogers 1987; Schenk et al. 1998). Based on these limited observations, genetic relatedness is frequently invoked to explain space sharing and home range overlap in many black bear populations. However, Schenk et al. (1998) found that the spatial distribution and pattern of home range overlap was independent of the genetic relatedness of the females involved. Furthermore, Powell (1987) documented cases of female offspring establishing a home range separated from that of the mother, and noted that the degree of overlap in his study area was extensive enough that it was unlikely that home range overlap occurred exclusively among related individuals. Conflicting results on this subject necessitate rigorous tests of the hypothesis that genetic relatedness influences spatial organization.

My objective was to test the hypothesis that genetic relatedness influenced the space use pattern of female Florida black bears (*U. a. floridanus*) in Ocala National Forest. I used microsatellite DNA to estimate relatedness among females and radio-telemetry data to estimate home ranges. If the spatial organization of female black bears is dictated by genetic relatedness, the distance between home ranges of females should be negatively correlated with genetic relatedness. Furthermore, females that share a substantial proportion of their home ranges should be more closely related to each other than those that have spatially segregated home ranges.

Study Area and Methods

Study Site

The study was conducted in the Ocala National Forest of north central Florida. Ocala National Forest is the largest public land holding in central Florida and supports one of the nine subpopulations of black bears in Florida (Dixon 2004). Black bears from two study areas within the Ocala population were examined simultaneously. The ONF study area was located within the central Ocala National Forest and the Lynne study area was located in a residential community located on the western edge of the Ocala National Forest (Fig. 2.1). ONF ranges in elevation from 15 m to 53 m above sea level and largely is vegetated by sand pine scrub and xeric oak scrub (for a more thorough description of vegetation see Chapter 2 of this thesis and Myers and Ewel (1990)). Human disturbance due to selective logging, clear-cutting, prescribed burning and road building practices within the forest, provides much of the heterogeneity in the forest cover type and stand age. The Lynne study area encompasses both U.S. Forest Service land as well as privately owned land, and elevations range from 0 m to 12 m above sea level. Predominant vegetation types are patches of pine flatwoods, mixed wetland forest, and hardwood swamps interspersed with roads and housing developments.

Field Methods

Black bears were captured from 1999 through 2002 using spring activated Aldrich foot snares disguised in natural vegetation and baited with donuts or a combination of corn and donuts. Although bears were trapped from May through December, the most intensive trapping occurred during summer months. Bears were anesthetized with Telazol® delivered through a CO_2 charged low-impact dart delivery system. Once sedated, bears were ear tagged and lip-tattooed for individual identification. Hair and blood samples were collected for genetic analyses, and a pre-molar tooth was extracted to estimate age (Willey 1974). Morphometric measurements and body mass as well as physical and reproductive condition scores also were recorded. Most females were fitted with a motion-sensitive radio-collar (150-151 MHz; Telonics, Mesa, Arizona). Radio-collars included a leather connector, which would allow the collar to fall off within two to three years. Reproductive females or those ≥ 3 years of age were considered adults and included in analyses (Garrison 2004).

Adult female bears were located on average once per week during 1999-2001, twice per week in 2002, and 3 times per week in 2003. The majority of locations were obtained from the ground during daylight hours (0900-1800) using a 4-element hand held antenna and a Telonics® receiver, but bears were also tracked 1-4 times per month from a fixed wing aircraft. For each bear, ≥ 3 compass bearings were collected within 30 minutes to minimize location error due to movements. Point locations from ground telemetry were estimated using the program Locate II (Pacer 1990). Telemetry error was estimated by comparing estimated locations of dropped collars and female natal dens to their actual locations. The average ground telemetry error was 157 m, based on 303 locations on 19 dens and 7 test collars. In these cases, observer distances varied from 0.25-1 mile from the actual location. The average aerial telemetry error was 251 m, based on 25 dropped and deployed collar locations.

Hair samples from 40 radio-collared females and 19 cubs of 9 of these females were sent to Wildlife Genetics International (www.wildlifegenetics.ca/) for microsatellite analyses. DNA was extracted from each hair sample and 12 independent microsatellite loci were amplified using PCR primers G1A, G10B, G10C, G1D, G10H, G10J, G10L, G10M, G10P, G10X, MU50, and MU59 as described in Paetkau and Strobeck (1994), and Paetkau et al. (1995). Microsatellites are preferred genetic markers for black bears because they allow sufficient differentiation to identify individuals and do not require calibration from known individuals in the population (Paetkau and Strobeck 1994).

Data Analysis

I estimated annual and seasonal home ranges (95% contour) and core home ranges (50% contour) using the fixed kernel density estimator with least squares cross validation (LSCV) (Seaman and Powell 1996) in the Animal Movement extension of ArcView 3.2 (Hooge et al. 1999). While the 95% contour provides an estimate of the home range boundary, the 50% contour corresponds to the part of the home range that receives more concentrated use. Annual home ranges were estimated using locations collected from May-December within a given year, summer home ranges were estimated from locations collected during May-August, and fall home ranges were estimated from locations collected during September-December. For these analyses the number of home ranges was more important in order to establish a pattern than the precision of home range estimation, so I reduced the number of required locations in this chapter from 25 to 19. I estimated annual or seasonal home ranges of a bear if it had a minimum of 19 locations to more accurately reflect the relationships between known individuals and so that seasonal home ranges for 2000 and 2001 could be estimated. I analyzed the data by year due to the fact that not all bears were collared simultaneously, and because pooling data across years can mask annual variation in home range size (Schooley 1994). I included seasonal as well as annual home ranges in analyses so that differences between seasons or years could be discerned.

I calculated the distance between the centroids of each pair of core home ranges by year and season using the Nearest Features extension in ArcView 3.2 (Jenness 2004). Pairwise distances between home range centroids were compiled in a distance matrix for each year and season. I also placed these pairs into categories based on the degree of overlap between home ranges. Pairs of females whose home ranges did not overlap were designated as no overlap (NO). Females that overlapped the 95% utilization contour, but did not overlap core home ranges were designated to have low overlap (LO). Females that overlapped core home ranges were considered to have high overlap (HO).

For individuals included in my sample, I used the program Genepop (Raymond and Rousset 1995) to calculate the observed heterozygosity (H_o), expected heterozygosity (H_e), and number of alleles (A) for each locus. I also used Genepop to test for any deviations from Hardy-Weinberg equilibrium for each locus and the population as a whole using the Hardy-Weinberg probability test.

I analyzed the microsatellite data using the program Kinship (Goodnight et al. 2004) to estimate the relatedness between pairs of female Florida black bears in the Ocala population. Relatedness values were then compiled into a matrix of relatedness. The program Kinship provides an unbiased estimate of the true relatedness between individuals using a non-parametric method described in detail by Queller and Goodnight (1989). This method uses the allele frequencies of the population to weight the relationship based on the population allele frequency (Blouin et al. 1996). Because of the variability associated with relatedness estimates, two unrelated individuals should have a relatedness value within a distribution around zero. Likewise, though the expected relatedness value for a pair of fully related individuals (mother-offspring, full sibling) is 0.5, the actual value will fall within a distribution around the mean of 0.5. Potential relatedness values ranged from -1 to 1. Both the number of independent microsatellite loci analyzed and the heterozygosity of the population can influence the variance around the mean (Blouin et al. 1996). I ran 10,000 simulations using the program Kinship to estimate the distribution of relatedness values for a fully related pair of individuals and an unrelated pair, based on the allele frequencies of my data. Additionally, the average relatedness value was calculated from known mother-offspring pairs using a bootstrap technique with 50,000 simulations and the 90% confidence interval (CI) compared to 0.5 to assess deviation from this theoretical value (Manly 1991).

I examined the association between genetic relatedness and spatial pattern in two ways. First, I compared each matrix of geographic distance to the corresponding matrix of relatedness using the nonparametric Mantel test (Mantel 1967) using PC-ORD for Windows (McCune and Mefford 1999). The p-values were estimated using the randomization (Monte Carlo) method with 9999 permutations. Secondly, I evaluated the differences between mean relatedness of pairs of females in each of my three overlap categories (NO, LO, and HO). Because each female was involved in more than one pair in the analysis, the data were not independent, so traditional methods of mean comparisons were not appropriate. To avoid the assumption of an underlying distribution, the mean and 90% confidence interval for each category were calculated using a bootstrap technique with 50,000 simulations (Manly 1991). To improve statistical power, tests were considered significant at $\alpha = 0.1$ due to the relatively small sample sizes in the study and the variable, yet conservative, nature of the relatedness estimates.

Results

Annual home ranges of female Florida black bears averaged (± SE) 25.68 ± 3.71 km^2. Fall home ranges averaged 27.67 ± 5.09 km^2, while summer home ranges averaged 11.79 ± 1.31 km^2. Core home range size averaged 3.94 ± 0.60 km^2 for annual home ranges, 4.50 ± 1.32 km^2 during fall, and 1.96 ± 0.33 km^2 during summer. These data differ slightly from those presented in Chapter 2 due to the different number of minimum locations. Pooling data across years, annual home ranges of each bear overlapped with 3.87 ± 0.38 other bears, and core home ranges overlapped with those of 1.11 ± 0.14 other bears (see Fig. 2.2 for a graphical representation of the 95% contour overlap for female annual home ranges for 2002). During fall, home ranges of each bear overlapped with 4.02 ± 0.42 other female bears, and core home ranges overlapped with those of 1.31 ± 0.18 other bears. During summer, home ranges of each female overlapped with 2.54 ± 0.26 other bears, and core home ranges overlapped with those of 0.72 ± 0.095 other females. These estimates likely reflect the minimum level of home range overlap within the population, as not all bears in my study area were radio-collared.

The average observed heterozygosity (H_o) (mean ± SE) was 0.365 ± 0.029, average expected heterozygosity (H_e) was 0.376 ± 0.031, and mean number of alleles (A) was 4.83 ± 0.27 (Table 4.1). The population did not deviate from Hardy-Weinberg equilibrium ($p = 0.51$), and all but one of the individual microsatellite loci were in equilibrium (Table 4.1).

The distributions of simulated relatedness values, for fully related and unrelated pairs of bears, are presented in Figure 4.1. If the cut-off value for discrimination between related (0.5) and unrelated (0.0) is 0.25, then 10% of the time a relationship that should be classified as unrelated will be misclassified as related and vice versa.

The average value of relatedness for known mother-offspring pairs was 0.424 (90% CI 0.381 - 0.468). The upper confidence limit of this value is lower than the theoretically expected value of 0.5. This suggests that relatedness may be slightly underestimated in this population and thus somewhat conservative. However, underestimates of relatedness should not substantially influence my results because I tried to detect broad scale trends and not explain individual relationships.

The Mantel tests indicated a significantly negative relationship ($p < 0.1$) between the relatedness of pairs of female black bears and the distance between their core home ranges; fall of 2000 was the only season for which a significant relationship was not observed (Table 4.2). The negative values of the Mantel statistic (r) indicate that female relatedness decreased with geographic distance such that related females were more likely to have home ranges close together than farther apart.

Mean relatedness values and the 90% confidence intervals for each of the three categories of overlap are presented in Table 4.3. Mean relatedness values ranged from -0.106 to 0.054 for non-overlapping (NO) bears, -0.033 to 0.156 for bears overlapping home ranges (LO), and 0.090 to 0.619 for bears overlapping core home ranges (HO). The sample size of female pairs in the HO category was smaller than that of LO and NO. This led to a CI for the HO females that was consistently larger than that for NO or LO. Therefore, the mean relatedness of HO was compared to the CI of the means of female pairs in the NO and LO categories. I focused on examining the differences in genetic relatedness between the NO and HO pairs of females because of the high variability of relatedness within each overlap category and of the relatedness value itself. In every case, the mean relatedness of the HO group was greater than the upper confidence limit of the NO group, suggesting that females with overlapping core home ranges were more closely related than those with non-overlapping home ranges (see Fig. 4.2 for a graphical representation of home ranges from summer 2001).

Discussion

Home range overlap between individuals within a species has been documented for a wide array of taxa (Carpenter and MacMillen 1976; Sandell 1989; Boellstorff and Owings 1995; Bull and Baghurst 1998; Gehrt and Fritzell 1998; Bixler and Gittleman 2000; Nielsen and Woolf 2001; Bonaccorso et al. 2002; Admasu et al. 2004). Natal philopatry, where offspring establish home ranges near that of the mother, is a leading hypothesis to explain this pattern. Natal philopatry would result in a pattern such that individuals with overlapping home ranges are genetically related (Waser and Jones 1983). Tests of this hypothesis require the ability to estimate the relatedness among individuals, but assessing relatedness based on observations in wild populations is difficult, particularly in long-lived and elusive species. Genetics techniques, such as microsatellite analysis (Paetkau and Strobeck 1994; Blouin et al. 1996), can provide rigorous estimates of relatedness in a short period of time.

Home range overlap is an inherent part of the spatial organization of many populations of black bears as documented by researchers throughout the species' geographic range (Lindzey and Meslow 1977; Reynolds and Beecham 1980; Klenner 1987; Pacas and Paquet 1994; Samson and Huot 2001; Lyons et al. 2003). In many black bear populations in the southeastern United States the overlap is reported to be extensive (Garshelis and Pelton 1981; Powell 1987; Hellgren and Vaughan 1990; Horner and Powell 1990; Smith and Pelton 1990; Powell et al. 1997; Oli et al. 2002). The detailed study in Minnesota by Rogers (1987) provided evidence of yearling female black bears establishing a home range within the home range of the mother. This pattern has been subsequently observed in other black bear populations (Garshelis and Pelton 1981; Clevenger and Pelton 1987; Schwartz and Franzmann 1992). These observations led to the hypothesis that genetic relatedness drives female spatial organization and explains home range overlap. Schenk et al. (1998) tested this hypothesis in one population of black bears in northern Ontario, but no relationship between spatial proximity and genetic relatedness was detected.

In this study, I found a negative correlation between the geographic distance between home range centroids and relatedness among females for all years and seasons except fall 2000. The distribution of home ranges in relation to genetic relatedness was consistent among years and between seasons. These findings corroborate the hypothesis that natal philopatry structures female spatial organization in the Ocala black bear populations, and that the pattern of space use by female black bears is strongly influenced by relatedness among them. The lack of a relationship between relatedness and space use pattern during fall 2000 is most likely due to the concurrent acorn mast failure in the forest. During this time, female black bears, particularly females with cubs, used larger home ranges and shifted and enlarged their core home ranges. These abnormal movements may have disrupted the spatial organization as bears covered large areas in search of food.

The average relatedness between females with varying degrees of home range overlap also is consistent with the prediction that genetic relatedness influences the spatial pattern of female Florida black bears. For each season and year, the mean relatedness of females with overlapping core home ranges was greater than the upper confidence limit of the mean relatedness of females with non-overlapping home ranges. This suggests that females with a high degree of home range overlap were more closely related than females whose home ranges were geographically separated.

Circumstantial evidence for natal philopatric tendencies of female black bears in Ocala includes the average heterozygosity and the relatedness estimates between known mother-offspring pairs. My estimates of H_o, and H_e were slightly lower than those reported by Dixon (2004), whose sample of Ocala black bears was collected over a larger area and also included adult male bears. The difference in estimates of heterozygosity between my study and that of Dixon (2004) suggests that there may be a higher degree of background relatedness among female black bears than between male and female black bears in Ocala. Furthermore, the lower than expected genetic relatedness between known mother-offspring pairs also may reflect the low heterozygosity of the loci used, as has been previously documented (Kays et al. 2000).

One potential pitfall with these conclusions concerns the age structure of the population. If yearling or subadult females had been included in the analyses while they were still utilizing a home range within the maternal home range, then this could have given the impression of a significant overall relationship. This situation would have allowed the possibility that had only adults been included the same pattern might not have been found. However, all females included in this study were ≥ 3 years of age and/or were reproductively active. Additionally, no female dispersal events were ever documented and home ranges were stable for bears that were monitored over multiple years. Pairs of females with overlapping home ranges maintained this pattern even when both individuals were well into their adult years.

Although the general pattern of space use by female Florida black bears in Ocala was consistent with predictions of the relatedness-based hypothesis, there were notable exceptions. For example, individuals R080 and R086, aged 7 and 6 in 2003, had overlapping core home ranges throughout the study, yet they had a relatedness value of - 0.24. Given this relatedness value, there is only a 0.01% chance that they were fully related (Fig. 3.1). These females could have been only partially related, such as cousins, but my data did not allow for this determination. Not only did the core home ranges of this pair overlap, they were also consistently radio-tracked within close proximity to one another and even selected denning sites in 2003 within 200 m of each other. These observations suggest that, although influential, relatedness alone cannot fully explain the pattern of space use by female bears.

Spatial arrangement and overlap of black bear home ranges can also be influenced by the distribution and availability of resources (Powell 1987; Schenk et al. 1998). Studies conducted in northern climates, such as the boreal forest where there is seasonally low food abundance, report home ranges that are non-overlapping between most female bears (Jonkel and Cowan 1971; Young and Ruff 1982; Rogers 1987). A yearling bear establishing a home range within the maternal home range is an exception to this trend (Clevenger and Pelton 1987; Rogers 1987). On the other hand, black bear populations in the southeastern region of the United States, where food abundance is much higher, frequently exhibit extensive home range overlap with little documented aggression between the individuals sharing space (Powell 1987; Horner and Powell 1990; Oli et al. 2002). Even when no association was found between spatial proximity and genetic relatedness in one population of black bears, home range overlap was still extensive, suggesting that relatedness is not the only factor governing spatial pattern (Schenk et al. 1998).

Several studies also suggest that areas of overlap are larger, and tolerance towards conspecifics greater, in seasons when the distribution of food resources is patchy (Pacas and Paquet 1994; Samson and Huot 2001). My study indicates more extensive core home range overlap during fall than during summer because females overlapping core home ranges tend to be more closely related during summer than fall (Table 4.3). Drought and associated food scarcity may also generate a patchy resource distribution leading to increased home range overlap (Jonkel and Cowan 1971; Powell 1987; Hellgren and Vaughan 1990). During the scrub oak mast failure of fall 2000, patches of acorns were sparsely distributed in the ONF study area. The spatial arrangement of female home ranges during this time ceased to reflect genetic relatedness, and there was no difference in relatedness between females that shared low home range overlap and females that shared high home range overlap.

In summary, closely related female Florida black bears had home ranges closer together than those that were unrelated or distantly related. Moreover, my data suggest that females that shared core home ranges tended to be more closely related to each other than those with non-overlapping home ranges. These observations are consistent with the hypothesis that genetic relatedness influences the space use pattern. Exceptions to this trend, however, are also noted, indicating that the influence of relatedness on space use pattern may be modulated by the abundance and distribution of food resources.

Table 4.1. The observed heterozygosity (H_o), expected heterozygosity (H_e) and number of alleles (A) for each of 12 microsatellite loci and their average values for 59 Florida black bears in Ocala. Results of the Hardy-Weinberg equilibrium tests are also given (p).

Locus	H_o	H_e	A	p
G1A	0.453	0.44	6	0.139
G10B	0.380	0.39	5	0.574
G10C	0.233	0.25	4	1.000
G1D	0.471	0.50	6	0.566
G10H	0.446	0.49	5	0.548
G10J	0.267	0.28	4	0.762
G10L	0.153	0.14	4	0.389
G10M	0.396	0.41	4	0.460
G10P	0.339	0.34	4	0.031
G10X	0.411	0.41	4	0.425
Mu50	0.374	0.37	6	0.663
Mu59	0.457	0.49	6	0.308
Average (± SE)	0.365 ± 0.029	0.376 ± 0.031	4.83 ± 0.27	0.507

Table 4.2. Results of the Mantel test comparing genetic relatedness and geographic distance between pairs of female Florida black bears in Ocala National Forest, Florida. The number of bears in each sample (N), the Mantel statistic (*r*), and the observed significance level (*p*) are provided for each Mantel test by year and season.

Season	**N**	***r***	***p***
2000			
Annual	16	-0.194	0.058
Fall	13	0.047	0.415
2001			
Annual	14	-0.177	0.093
Summer	13	-0.252	0.035
Fall	8	-0.329	0.078
2002			
Annual	15	-0.166	0.061
Summer	17	-0.123	0.095
Fall	20	-0.231	0.013
2003			
Annual	8	-0.444	0.042
Summer	16	-0.264	0.016
Fall	8	-0.444	0.042

Table 4.3. Mean genetic relatedness and degree of home range overlap for female Florida black bears in Ocala National Forest, Florida. The mean genetic relatedness and the 90% confidence interval around the mean estimated using the bootstrap technique (50,000 bootstrap samples) for 3 categories of home range overlap. Category NO indicates non-overlapping pairs, category LO indicates pairs with home range overlap, and category HO indicates pairs of individuals that overlap core home ranges.

	NO bears	**LO bears**	**HO bears**
Annual			
2000	-0.052 (-0.093 - 0.010)	-0.033 (-0.088 - 0.022)	0.138 (0.002 - 0.279)
2001	0.007 (-0.036 - 0.049)	0.073 (0.002 - 0.142)	0.119 (-0.138 - 0.405)
2002	0.054 (0.018 - 0.091)	0.156 (0.055 - 0.266)	0.099 (-0.016 - 0.223)
2003	-0.086 (-0.145 - -0.027)	------------	0.158 (-0.076 - 0.452)
Summer			
2001[a]	0.017 (-0.027 - 0.061)	0.057 (0.002 - 0.112)	0.273 (0.072 - 0.473)
2002	0.036 (0.005 - 0.067)	0.123 (0.044 - 0.204)	0.206 (0.012 - 0.405)
2003	-0.005 (-0.038 - 0.029)	0.120 (0.054 - 0.194)	0.307 (-0.023 - 0.635)
Fall			
2000	-0.106 (-0.160 - -0.053)	0.040 (-0.011 - 0.093)	0.049 (-0.070 - 0.173)
2001	0.043 (-0.024 - 0.108)	0.120 (-0.040 - 0.284)	0.619 (0.619 - 0.619)
2002	0.029 (0.002 - 0.057)	0.109 (0.047 - 0.171)	0.153 (0.043 - 0.271)
2003	-0.094 (-0.156 - -0.032)	0.005 (-0.157 - 0.167)	0.159 (-0.076 - 0.452)

----No data

[a] See Fig. 4.2 for graphical representation comparing relatedness of NO and HO bears.

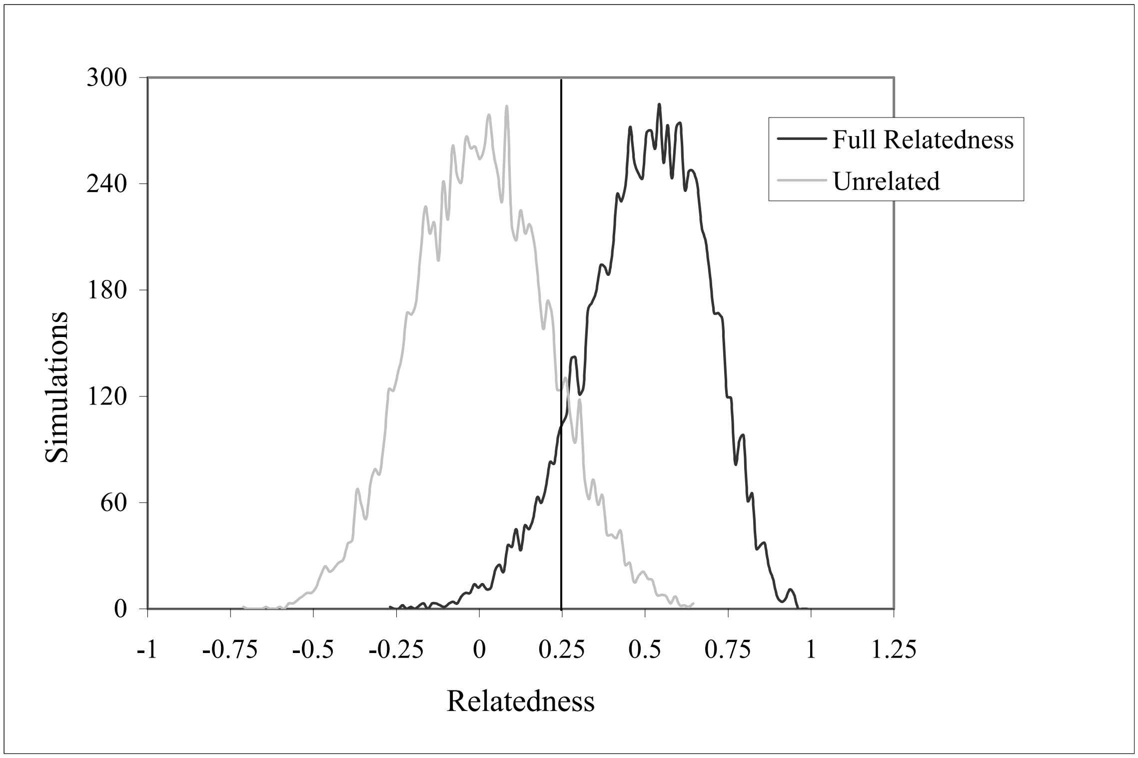

Figure 4.1. Simulation of the distribution of the relatedness values for fully related and unrelated black bears in Ocala National Forest, Florida. The two curves represent the distribution of expected relatedness values given an initial hypothesis as to the relationship between a pair of bears. Data were simulated with the allele frequencies of the Ocala data set using the program Kinship. “A” indicates the type I error that would occur when classifying a pair with a value larger than 0.25 as related when they in fact are unrelated.

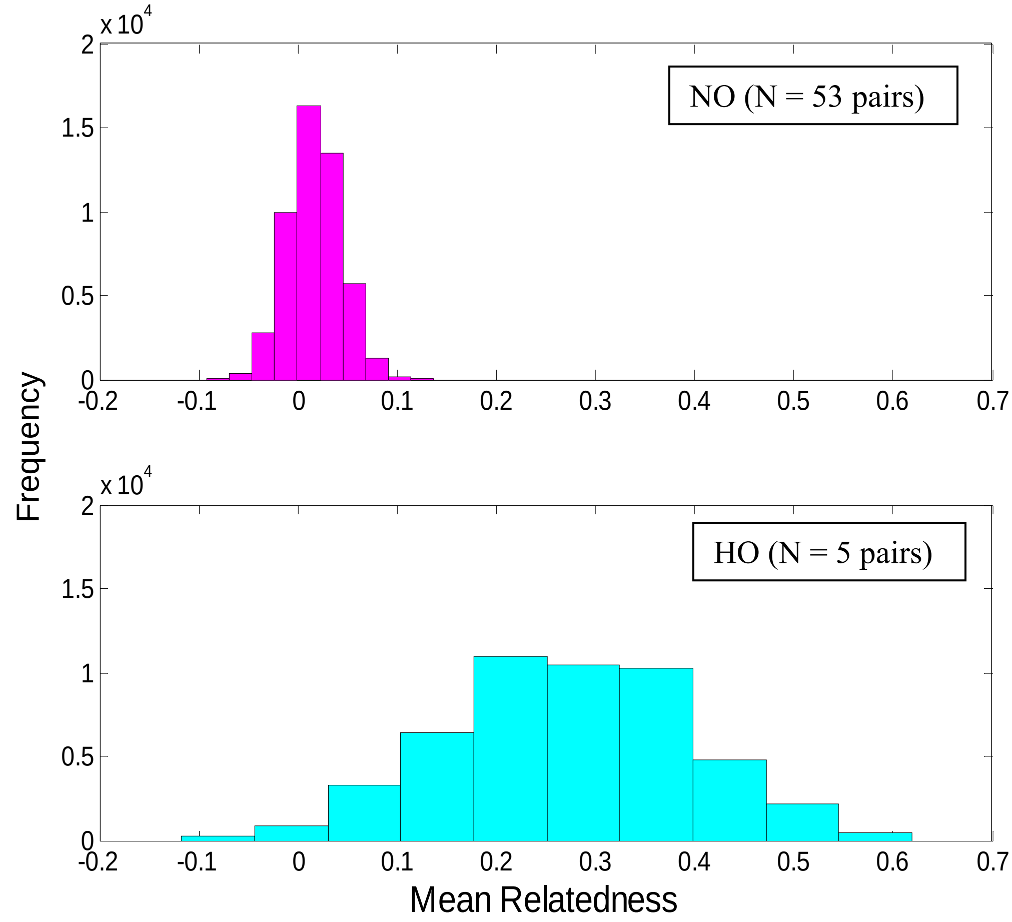

Figure 4.2. Distribution of estimated mean relatedness values for female black bears with no home range overlap (NO) and for females with high home range overlap (HO) for summer home ranges 2001. The mean genetic relatedness and the 90% confidence interval around the mean were estimated using the bootstrap technique (50,000 bootstrap samples). The larger 90% CI corresponds to the smaller sample size of pairs of bears in the HO category.

CHAPTER 5
CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS

In this thesis, I examined several aspects of the spatial ecology of female Florida black bears in Ocala National Forest. I estimated annual and seasonal home ranges, evaluated the factors influencing the annual and seasonal variation in home range size, and tested for differences in home range size between two study sites and between females with and without cubs. Resource availability is one of the primary indicators of home range size, and the connection between home range use and available habitat types was further explored through a multi-scale analysis of habitat use. I also evaluated the space use pattern from a social interaction perspective, and tested the hypothesis that genetic relatedness influences home range distribution and home range overlap.

Conclusions

Average annual home range size within ONF was slightly larger than previously reported in the southeast, perhaps due to a lower overall productivity within ONF compared to other southeastern bear habitats. I documented significant seasonal variation in home range size, with fall home ranges larger than summer home ranges. Annual home ranges appeared to be selected by females in order to provide access to habitat types that provide food and escape cover. The habitat composition of annual home ranges reflected the habitat composition of the study area as a whole. During summer, however, home ranges were smaller and females were located closer than expected to pine flatwoods and swamp forests. The early spring growth within these mesic habitat types may make them preferable to the dry scrub habitats. During fall, however, the home ranges were larger and the composition mirrored that of the larger study area, which indicated that bears were not only utilizing the sand pine and xeric oak scrub forest for the abundant acorns, but also sought other food sources. While some females stayed within the oak forest and foraged on acorns, other females traveled to the swamp forests and riparian areas to diversify their fall diets.

Bears in Lynne displayed a greater seasonal variation in home range size than those in ONF. Summer home ranges were very small, while fall home ranges included a much larger area. Although a formal test of habitat selection by these individuals was not possible, the seasonal movements away from the summer home range, both east towards the sand pine/scrub oak of ONF and west towards the Ocklawaha River, suggest that summer home ranges may provide adequate resources but that bears must roam more widely to access resources during fall.

My data also suggest that female black bears in Ocala National Forest do exhibit natal philopatry and establish home ranges near their place of birth. This trend culminates in a forest-wide space use pattern such that black bears within close proximity are more likely to be related than females whose home ranges are farther apart. Home range placement within the study area, therefore, is not exclusively determined by active selection of the habitat composition or resource availability, although both of these factors are important and undoubtedly modify space use pattern. The observation that core home ranges of unrelated females also may overlap further suggests that resource availability can occasionally have a greater influence on space use pattern than genetic relatedness alone.

Management Recommendations

This research highlights several important aspects of black bear spatial ecology that could have important implications for management practices. Conservation of vegetative and structural diversity within the forest is highly recommended. Bears rely on a variety of food sources available within multiple habitat types. Swamp forests and pine flatwoods, in particular, should be conserved to provide a variety of food sources and prevent human-bear conflict in the event of an acorn mast failure. Timber management within sand pine forest and xeric oak scrub should be aware of the effects of logging and stand age on acorn production in order to keep acorn production high.

Management of black bears in Lynne should address the additional challenges of significant fragmentation of habitat from both commercial and residential development as well as the high mortality rate of adult females due to anthropogenic causes. While many of these females utilize small areas during the summer months, their movements increase substantially during fall. Black bears in Lynne would benefit from reliable forested access routes to both the Ocklawaha River and the scrub habitats of ONF. A program is currently in place to foster education for Lynne residents about black bears. Community outreach to increase awareness of black bears and reduce human-bear conflicts should be continued and strengthened.

Although this study did not directly address survival of black bears in Ocala National Forest, the adult mortality of black bears due to vehicle collisions is substantial (McCown et al. 2004). Because females forage in habitats close to roads, and traffic on these roads will likely increase in coming years, wildlife underpasses or other mitigation options should be considered.

Recommendations for Further Research

A study explicitly designed to assess home range and both macro- and micro-habitat use within Lynne would be beneficial, as the available cover types and degree of fragmentation are different from ONF. Detailed studies of movements and habitat requirements could help reduce the high mortality rate of female black bears in this area.

Additional studies are needed to test for differences in habitat use based on age class and reproductive status. A female with cubs may have different needs than a female foraging alone, and better understanding of habitat requirements could enhance reproductive success. More detailed analyses of micro-habitat use and how forest management practices influence the distribution of resources also should be pursued.

At the population level, genetic relatedness did influence the distribution of home ranges; however, instances of unrelated females sharing space were also documented. The interaction between genetic relatedness and resource availability in the temporal partitioning of space may also be important. This type of study would provide a more complete picture of tolerance toward conspecifics under different environmental conditions and may help estimate a biological carrying capacity of the forest.

Finally, in order to conserve Florida black bears within Ocala National Forest the interaction between spatial ecology and population dynamics must be considered. Linking home range dynamics and habitat use to reproductive success and survival of adult females in a comprehensive demographic study would indicate how spatial ecology ultimately influences long-term persistence of the black bear in Ocala. An understanding of black bear spatial and behavioral responses to natural and human modified environments in the face of habitat loss and fragmentation may greatly assist conservation efforts in the future.

LIST OF REFERENCES

Admasu, E., S. J. Thirgood, A. Bekele, and M. K. Laurenson. 2004. Spatial ecology of golden jackal in farmland in the Ethiopian Highlands. African Journal of Ecology 42:144-152.

Aebischer, N. J., P. A. Robertson, and R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74:1313-1325.

Alldredge, J. R., and J. T. Ratti. 1992. Further comparison of some statistical techniques for analysis of resource selection. Journal of Wildlife Management 56:1-9.

Alt, G. L., G. J. Matula, F. W. Alt, and J. S. Lindzey. 1980. Dynamics of home range and movements of adult black bears in northeastern Pennsylvania. International Conference on Bear Research and Management 4:131-136.

Beckmann, J. P., and J. Berger. 2003. Rapid ecological and behavioural changes in carnivores: the responses of black bears (*Ursus americanus*) to altered food. Journal of Zoology 261:207-212.

Belant, J. L., and E. H. Follmann. 2002. Sampling considerations for American black and brown bear home range and habitat use. Ursus 13:299-315.

Biedermann, R. 2003. Body size and area-incidence relationships: is there a general pattern? Global Ecology and Biogeography 12:381-387.

Bingham, R. L., and L. A. Brennan. 2004. Comparison of type I error rates for statistical analyses of resource selection. Journal of Wildlife Management 68:206-212.

Bixler, A., and J. L. Gittleman. 2000. Variation in home range and use of habitat in the striped skunk (*Mephitis mephitis*). Journal of Zoology 251:525-533.

Blouin, M. S., M. Parsons, V. Lacaille, and S. Lotz. 1996. Use of microsatellite loci to classify individuals by relatedness. Molecular Ecology 5:393-401.

Boellstorff, D. E., and D. H. Owings. 1995. Home range, population structure, and spatial organization of the California ground squirrel. Journal of Mammalogy 76:551-561.

Bonaccorso, F. J., F. R. Winkelmann, E. R. Dumont, and K. Thibault. 2002. Home range of *Dobsonia minor* (Pteropodidae): a solitary foliage-roosting fruit bat in Papua New Guinea. Biotropica 34:127-135.

Boydston, E. E., K. M. Kapheim, M. Szykman, and K. E. Holekamp. 2003. Individual variation in space use by female spotted hyenas. Journal of Mammalogy 84:1006-1018.

Bull, C. M., and B. C. Baghurst. 1998. Home range overlap of mothers and their offspring in the sleepy lizard, *Tiliqua rugosa*. Behavioral Ecology and Sociobiology 42:357-362.

Burt, W. H. 1943. Territoriality and home range concepts as applied to mammals. Journal of Mammalogy 24:346-352.

Burton, C., and C. J. Krebs. 2003. Influence of relatedness on snowshoe hare spacing behavior. Journal of Mammalogy 84:1100-1111.

Carpenter, F. L., and R. E. MacMillen. 1976. Threshold model of feeding territoriality and test with a Hawaiian honeycreeper. Science 194:639-642.

Clevenger, A. P., and M. R. Pelton. 1987, Pre and post breakup movements and space use of black bear family groups in Cherokee National Forest, Tennessee. International Conference on Bear Research and Management 7:289-295.

Clutton-Brock, T. H. 1989. Mammalian mating systems. Proceedings of the Royal Society of London B 236:339-372.

Conner, L. M., and B. W. Plowman. 2001. Using Euclidean distances to assess nonrandom habitat use, Pages 275-290 *in* J. J. Millspaugh, and J. M. Marzluff, eds. Radio tracking and animal populations. Academic Press, San Diego, CA.

Conner, L. M., M. D. Smith, and L. W. Burger. 2003. A comparison of distance-based and classification based analyses of habitat use. Ecology 84:526-531.

Crooks, K. R. 2002. Relative sensitivities of mammalian carnivores to habitat fragmentation. Conservation Biology 16:488-502.

Dixon, J. D. 2004. The conservation genetics of the Florida black bear, M.S. Thesis. University of Florida, Gainesville, FL.

Ewel, K. C. 1990. Swamps, Pages 281-323 *in* R. L. Myers, and J. J. Ewel, eds. Ecosystems of Florida. University of Central Florida Press, Orlando, FL.

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

Florida Fish and Wildlife Conservation Commission. 2003. Florida vegetation and land cover data derived from 2003 Landsat ETM+ imagery, Tallahassee, FL.

Ford, R. G. 1983. Home range in a patchy environment: optimal foraging predictions. American Zoologist 23:315-326.

Garrison, E. P. 2004. Reproductive ecology, cub survival and denning ecology of the Florida black bear, MS Thesis. University of Florida, Gainesville, FL.

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

Gehring, T. M., and R. K. Swihart. 2004. Home range and movements of long-tailed weasels in a landscape fragmented by agriculture. Journal of Mammalogy 85:79-86.

Gehrt, S. D., and E. K. Fritzell. 1998. Resource distribution, female home range dispersion and male spatial interactions: group structure in a solitary carnivore. Animal Behaviour 55:1211-1227.

Goldberg, T. L., and R. W. Wrangham. 1997. Genetic correlates of social behaviour in wild chimpanzees: evidence from mitochondrial DNA. Animal Behaviour 54:559-570.

Gompper, M. E., and J. L. Gittleman. 1991. Home range scaling–intraspecific and comparative trends. Oecologia 87:343-348.

Gompper, M. E., and R. K. Wayne. 1996. Genetic relatedness among individuals within carnivore societies, Pages 429-452 *in* J. L. Gittleman, ed. Carnivore behavior, ecology, and evolution. Cornell University Press, Ithaca, NY.

Goodnight, K. F., D. C. Queller, and T. Poznansky. 2004. Kinship 1.3.1.Goodnight Software, Dallas, TX.

Grigione, M. M., P. Beier, R. A. Hopkins, D. Neal, W. D. Padley, C. M. Schonewald, and M. L. Johnson. 2002. Ecological and allometric determinants of home-range size for mountain lions (*Puma concolor*). Animal Conservation 5:317-324.

Hall, E. R. 1981. The mammals of North America. 2nd edition. John Wiley and Sons, New York.

Hellgren, E. C., and M. R. Vaughan. 1990. Range dynamics of black bears in great dismal swamp, Virginia-North Carolina. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 44:268-278.

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

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

Hirsch, J. G., L. C. Bender, and J. B. Haufler. 1999. Black bear, *Ursus americanus*, movements and home ranges on Drummond Island, Michigan. Canadian Field Naturalist 113:221-225.

Hooge, P. N., W. Eichenlaub, and E. Solomon. 1999. The animal movement program. USGS Alaska Biological Science Center, Gustavus, AK.

Horner, M. A., and R. A. Powell. 1990. Internal structure of home ranges of black bears and analyses of home range overlap. Journal of Mammalogy 71:402-410.

Jenness, J. 2004. Nearest features, version 3.7a. Jenness Enterprises, Flagstaff, AZ.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65-71.

Jonkel, C. J., and I. M. Cowan. 1971. The black bear in the spruce-fir forest. Wildlife Monographs 27:1-57.

Kays, R. W., J. L. Gittleman, and R. K. Wayne. 2000. Microsatellite analysis of kinkajou social organization. Molecular Ecology 9:743-751.

Kie, J. G., J. A. Baldwin, and C. J. Evans. 1994. CALHOME: home range analysis program electronic user's manual. U.S. Forest Service.

Kjellander, P., A. J. M. Hewison, O. Liberg, J. M. Angibault, E. Bideau, and B. Cargnelutti. 2004. Experimental evidence for density-dependence of home-range size in roe deer (*Capreolus capreolus L.*): a comparison of two long term studies. Oecologia 139:478-485.

Klenner, W. 1987. Seasonal movements and home range utilization patterns of the black bear, *Ursus americanus*, in western Manitoba. Canadian Field Naturalist 101:558-568.

Koehler, G. M., and D. J. Pierce. 2003. Black bear home range sizes in Washington: climatic, vegetative and social influences. Journal of Mammalogy 84:81-91.

Krebs, C. J. 1978. Ecology: the experimental analysis of distribution and abundance. Harper and Row, Publishers, Inc., New York.

Lariviere, S., and F. Messier. 2001. Space-use patterns by female striped skunks exposed to aggregations of simulated duck nests. Canadian Journal of Zoology 79:1604-1608.

Lindzey, F. G., K. R. Barber, R. D. Peters, and E. C. Meslow. 1986. Responses of a black bear population to a changing environment. International Conference on Bear Research and Management 6:57-63.

Lindzey, F. G., and E. C. Meslow. 1977. Home range and habitat use by black bears in southwestern Washington. Journal of Wildlife Management 41:413-425.

Lyons, A. L., W. L. Gaines, and C. Servheen. 2003. Black bear resource selection in the northeast Cascades, Washington. Biological Conservation 113:55-62.

Macdonald, D. W. 1983. The ecology of carnivore social behavior. Nature 301:379-384.

Maehr, D. S. 1984. Distribution of black bears in eastern North America. Eastern Workshop on Black Bear Management and Research 7:74.

Maehr, D. S., and J. R. Brady. 1984. Food habits of Florida black bears. Journal of Wildlife Management 48:230-235.

Maehr, D. S., T. S. Hoctor, L. J. Quinn, and J. S. Smith. 2001. Black bear habitat management guidelines for Florida: Technical Report No. 17, Pages 1-83. Florida Fish and Wildlife Conservation Commission, Tallahassee.

Maehr, D. S., and J. B. Wooding. 1992. Florida black bear, Pages 265-275 *in* S. R. Humphrey, ed. Rare and endangered biota of Florida. University Press of Florida, Gainesville, FL.

Manly, B. F. J. 1991. Randomization and monte carlo methods in biology. Chapman and Hall, London.

Manly, T. L., L. L. McDonald, and D. L. Thomas. 1993. Resource selection by animals: statistical design and analysis for field studies. Chapman & Hall, London.

Mantel, N. 1967. The detection of disease clustering and generalized regression approach. Cancer Research 27:209-220.

Mares, M., T. Lacher, M. Willig, N. Bitar, R. Adams, A. Klinger, and D. Tazik. 1982. An experimental analysis of social spacing in *Tamias striatus*. Ecology 63:267-273.

McCown, J. W., P. Kubilis, T. H. Eason, and B. Scheick. 2004. Black bear movements and habitat use relative to roads in Ocala National Forest, Pages 1-134. Florida Fish and Wildlife Conservation Commission, Tallahassee, FL.

McCune, B., and M. J. Mefford. 1999. Multivariate analysis of ecological data, version 4.20. MjM Software, Gleneden Beach, CA.

McLoughlin, P. D., R. L. Case, R. J. Gau, H. D. Cluff, R. Mulders, and F. Messier. 2002. Hierarchical habitat selection by barren-ground grizzly bears in the central Canadian Arctic. Oecologia 132:102-108.

McLoughlin, P. D., S. H. Ferguson, and F. Messier. 2000. Intraspecific variation in home range overlap with habitat quality: a comparison among brown bear populations. Evolutionary Ecology 14:39-60.

McLoughlin, P. D., L. R. Walton, H. D. Cluff, P. C. Paquet, and M. A. Ramsay. 2004. Hierarchical habitat selection by tundra wolves. Journal of Mammalogy 85:576-580.

Millspaugh, J. J., and J. M. Marzluff. 2001. Radio tracking and animal populations. Academic Press, Inc., San Diego,CA.

Morrison, M. L., B. G. Marcot, and R. W. Mannan. 1992. Wildlife-habitat relationships: concepts and applications. The University of Wisconsin Press, Madison, WI.

Myers, R. L. 1990. Scrub and high pine, Pages 150-193 *in* R. L. Myers, and J. J. Ewel, eds. Ecosystems of Florida. University of Central Florida Press, Orlando, FL.

Myers, R. L., and J. J. Ewel. 1990. Ecosystems of Florida. University of Central Florida Press, Orlando, FL.

Nielsen, C. K., and A. Woolf. 2001. Spatial organization of bobcats (*Lynx rufus*) in southern Illinois. American Midland Naturalist 146:43-52.

Oehler, M. W., R. T. Bowyer, and V. C. Bleich. 2003. Home ranges of female mountain sheep, *Ovis canadensis nelsoni*: effects of precipitation in a desert ecosystem. Mammalia 67:385-401.

Oli, M. K., H. A. Jacobson, and B. D. Leopold. 2002. Pattern of space use by female black bears in the White River National Wildlife Refuge, Arkansas, USA. Journal for Nature Conservation 10:87-93.

Orians, G. H., and J. F. Wittenberger. 1991. Spatial and temporal scales in habitat selection. The American Naturalist 137:S29-S49.

Pacas, C. J., and P. C. Paquet. 1994. Analysis of black bear home range using a geographic information system. International Conference on Bear Research and Management 9:419-425.

Pacer. 1990. Locate II, version 1.3. Pacer Software, Truro, Nova Scotia, Canada.

Paetkau, D., W. Calvert, I. Stirling, and C. Strobeck. 1995. Microsatellite analysis of population structure in Canadian polar pears. Molecular Ecology 4:347-354.

Paetkau, D., and C. Strobeck. 1994. Microsatellite analysis of genetic variation in black bear populations. Molecular Ecology 3:489-495.

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

Powell, R. A., J. W. Zimmerman, and D. E. Seaman. 1997. Ecology and behaviour of North American black bears: home ranges habitat and social organization: Chapman and Hall Wildlife Ecology and Behaviour Series, v. 4. Chapman and Hall, London.

Queller, D. C., and K. F. Goodnight. 1989. Estimating relatedness using genetic markers. Evolution 43:258-275.

Ratnayeke, S., G. A. Tuskan, and M. R. Pelton. 2002. Genetic relatedness and female spatial organization in a solitary carnivore, the raccoon, *Procyon lotor*. Molecular Ecology 11:1115-1124.

Raymond, M., and F. Rousset. 1995. Genepop (Version-1.2) Population genetics software for exact tests and ecumenicism. Journal of Heredity 86:248-249.

Rettie, W. J., and F. Messier. 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. Ecography 23:466-478.

Reynolds, H. V., and J. J. Beecham. 1980. Home range activities and reproduction of black bears in west-central Idaho. International Conference on Bear Research and Management 4:181-190.

Riley, S. P. D., R. M. Sauvajot, T. K. Fuller, E. C. York, D. A. Kamradt, C. Bromley, and R. K. Wayne. 2003. Effects of urbanization and habitat fragmentation on bobcats and coyotes in southern California. Conservation Biology 17:566-576.

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

Roof, J. C. 1997. Black bear food habits in the lower Wekiva River basin of central Florida. Florida Field Naturalist 25:92-97.

Samson, C., and J. Huot. 1998. Movements of female black bears in relation to landscape vegetation type in southern Quebec. Journal of Wildlife Management 62:718-727.

—. 2001. Spatial and temporal interactions between female American black bears in mixed forests of eastern Canada. Canadian Journal of Zoology 79:633-641.

Sandell, M. 1989. The mating tactics and spacing patterns of solitary carnivores, Pages 164-182 *in* J. L. Gittleman, ed. Carnivore behavior, ecology, and evolution. Cornell University Press, Ithaca, NY.

SAS Institute Inc. 1999. SAS/STAT® user's guide, version 8. SAS Institute Inc., Cary, NC.

Schaeff, C. M., D. J. Boness, and W. D. Bowen. 1999. Female distribution, genetic relatedness, and fostering behaviour in harbour seals, *Phoca vitulina*. Animal Behaviour 57:427-434.

Schenk, A., M. E. Obbard, and K. M. Kovacs. 1998. Genetic relatedness and home-range overlap among female black bears (*Ursus americanus*) in northern Ontario, Canada. Canadian Journal of Zoology 76:1511-1519.

Schoen, J. W. 1990. Bear habitat management: a review and future perspective. International Conference on Bear Research and Management 8:143-154.

Schooley, R. L. 1994. Annual variation in habitat selection - patterns concealed by pooled data. Journal of Wildlife Management 58:367-374.

Schwartz, C. C., and A. W. Franzmann. 1992. Dispersal and survival of subadult black bears from the Kenai Penninsula, Alaska. Journal of Wildlife Management 56:426-431.

Seaman, D. E., J. J. Millspaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke, and R. A. Gitzen. 1999. Effects of sample size on kernel home range estimates. Journal of Wildlife Management 63:739-747.

Seaman, D. E., and R. A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology 77:2075-2085.

Slade, N. A., L. A. Russell, and T. J. Doonan. 1997. The impact of supplemental food on movements of prairie voles (*Microtus ochrogaster*). Journal of Mammalogy 78:1149-1155.

Smith, J. L. D., C. W. McDougal, and M. E. Sunquist. 1987. Female land tenure system in tigers, Pages 97-109 *in* R. L. Tilson, and U. S. Seal, eds. Tigers of the world. Noyes Publications, Park Ridge, NJ.

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

South, A. 1999. Extrapolating from individual movement behaviour to population spacing patterns in a ranging mammal. Ecological Modelling 117:343-360.

Southeast Regional Climate Center. 2004. Drought and agriculture information. Southeast Regional Climate Center (http://www.dnr.state.sc.us/climate/sercc/climateinfo/drought/html). Last accessed 6/15/04.

Stratman, M. R., C. D. Alden, M. R. Pelton, and M. E. Sunquist. 2001. Habitat use by American black bears in the sandhills of Florida. Ursus 12:109-114.

Unsworth, J. W., J. J. Beecham, and L. R. Irby. 1989. Female black bear habitat use in west-central Idaho. Journal of Wildlife Management 53:668-673.

Van Orsdol, K. G., J. P. Hanby, and J. D. Bygott. 1985. Ecological correlates of lion social organization (*Panthera leo*). Journal of the Zoological Society of London 206:97-112.

Waser, P. M., and W. T. Jones. 1983. Natal philopatry among solitary animals. The Quarterly Review of Biology 58:355-382.

White, G. C., and R. A. Garrot. 1990. Analysis of wildlife radio-tracking data. Academic Press, Inc., New York.

Willey, C. H. 1974. Aging black bears from first premolar tooth sections. Journal of Wildlife Management 38:97-100.

Wimmer, B., D. Tautz, and P. M. Kappeler. 2002. The genetic population structure of the gray mouse lemur (*Microcebus murinus*), a basal primate from Madagascar. Behavioral Ecology and Sociobiology 52:166-175.

Winters, J. B., and P. M. Waser. 2003. Gene dispersal and outbreeding in a philopatric mammal. Molecular Ecology 12:2251-2259.

Wooding, J. B. 1993. Management of the black bear in Florida. Staff report to the commissioners. Florida Game and Fresh Water Fish Commission, Tallahassee.

Wooding, J. B., and T. S. Hardisky. 1994. Home range, habitat use and mortality of black bears in north-central Florida. International Conference on Bear Research and Management 9:349-356.

Young, B. F., and R. L. Ruff. 1982. Population dynamics and movements of black bear in east central Alberta. Journal of Wildlife Management 46:845-860.

BIOGRAPHICAL SKETCH

Melissa Ann Moyer was born in Nashville, Tennessee, on March 7, 1976. She moved to Gainesville, Florida, when she was 10 years old so that her parents, both microbiologists, could join the faculty of the University of Florida College of Medicine. After graduating from the International Baccalaureate Program at Eastside High School in 1994, she attended Yale University in New Haven, Connecticut, and graduated magna cum laude, with a double Bachelor of Science degree in biology and organismal biology in 1998. She spent the next several years traveling the country and working with a large variety of wildlife species in seasonal field biologist positions. She moved back to Gainesville and enrolled in the Department of Wildlife Ecology and Conservation in January 2002. She received her Master of Science degree in December 2004.