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

Melissa A. Moyer, J. Walter McCown, Thomas H. Eason, and Madan K. Oli*

Department of Wildlife Ecology and Conservation, 110 Newins–Ziegler Hall, University of Florida, Gainesville, FL 32611, USA (MAM, MKO)
Florida Fish and Wildlife Conservation Commission, 4005 S Main Street, Gainesville, FL 32601, USA (JWM)
Florida Fish and Wildlife Conservation Commission, Bryant Building, 620 S Meridian Street, Tallahassee, FL 32399-1600, USA (THE)

It has been hypothesized that, in species exhibiting natal philopatry, genetically related individuals would have home ranges closer to each other than those of unrelated individuals. Using radiotelemetry (2001–2003) and genetic data from 35 female Florida black bears (*Ursus americanus floridanus*), we tested the hypothesis that genetic relatedness among individuals influenced the spatial organization of home ranges. Genetic relatedness was negatively correlated with geographic distance between home ranges for each year and season (except autumn 2000), suggesting that genetically related individuals established home ranges closer to each other, whereas home ranges of unrelated females were geographically separated. Additionally, females that had overlapping core home ranges were more closely related than females whose home ranges did not overlap. These results are consistent with the hypothesis that genetic relatedness influences spatial organization of home ranges.

Key words: Florida black bear, genetic relatedness, home range, natal philopatry, space use, *Ursus americanus floridanus*

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 among 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 space use 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 (*Spermophilus beecheyi*—Boell-storff 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 influences spatial association has been contradicted in the harbor seal (*Phoca vitulina*—Schaeff et al. 1999), the snowshoe hare (*Lepus americanus*—Burton

and Krebs 2003), and the common 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). If so, then clusters of home ranges of related females should develop over time across the landscape. Few long-term studies have documented spatial association among related individuals of large carnivores (e.g., Bengal tigers [*Panthera tigris*—Smith et al. 1987] and American black bears [*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 rarely tested in large carnivores.

A long-term study by Rogers (1987) indicated that female black bears are natal philopatric and that adult females show tolerance toward female offspring. 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 of black bears was independent of 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 home-range overlap in his study population was extensive enough that it was

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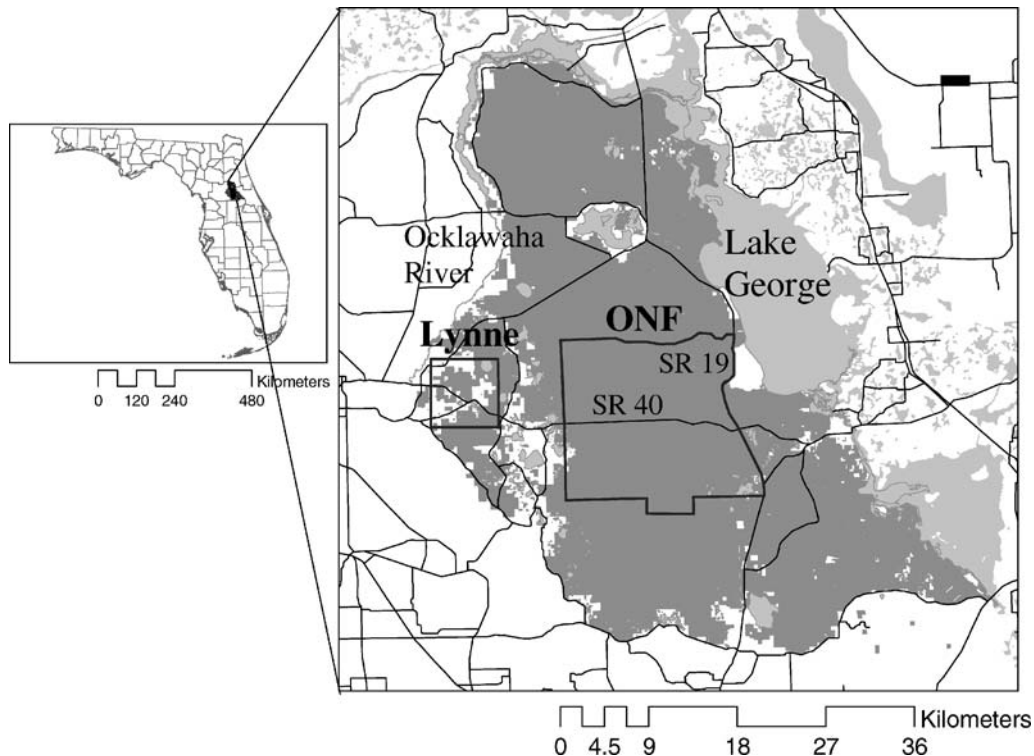* Correspondent: olimadan@wec.ufl.edu

FIG. 1.—Location of Ocala National Forest in north-central Florida. The 2 study sites within Ocala National Forest are referred to as ONF and Lynne. 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 (dark gray) and private (white) lands. Black lines represent roads and light gray areas represent bodies of water.

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.

Our 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, Florida. 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 to those that have spatially segregated home ranges.

MATERIALS AND METHODS

Study site.—The study was conducted in the Ocala National Forest, north-central Florida. Ocala National Forest is the largest public landholding in central Florida and supports 1 of the 9 subpopulations of black bears in Florida (Dixon et al. 2006). Black bears from 2 study areas within the Ocala population were examined simultaneously. One study site was located within the central Ocala National Forest and is referred to here as the ONF study area, and the other was located in the residential community of Lynne on the western edge of the Ocala National Forest and is referred to as the Lynne study area (Fig. 1). The ONF study area ranges in elevation from 15 to 53 m above sea level and largely is vegetated by sand pine scrub and xeric oak scrub. A thorough description of vegetation is given by 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 United States Forest Service land as well as privately owned land, and elevation ranges from 0 to 12 m above sea level. Predominant vegetation types included patches of pine flatwoods, mixed wetland forest, and hardwood swamps interspersed with roads and housing developments. The bear population in our study area has not been hunted since 1971 (Wooding 1993).

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 (Fort Dodge Laboratories, Fort Dodge, Iowa) 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 premolar 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 radiocollar (150–151 MHz, Telonics, Mesa, Arizona). Radiocollars included a leather connector that would allow the collar to fall off within 2–3 years. Reproductive females or those ≥ 3 years of age were considered adults and included in analyses (Garrison 2004). The procedures followed the guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists (Animal Care and Use Committee 1998).

Adult female bears were located 1–3 times per week. The majority of locations were obtained from the ground during daylight hours

(0900–1800 h) using a 4-element handheld 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 min 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, and the average aerial telemetry error was 251 m.

Hair samples from 40 radiocollared females and 19 cubs of 9 of these females were sent to Wildlife Genetics International (Nelson, British Columbia, Canada; www.wildlifegenetics.ca/) for microsatellite analyses. DNA was extracted from each hair sample, and 12 independent microsatellite loci were amplified using polymerase chain reaction primers G1A, G10B, G10C, G1D, G10H, G10J, G10L, G10M, G10P, G10X, MU50, and MU59 (Paetkau and Strobeck 1994; Paetkau et al. 1995).

Data analysis.—We 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 (Seaman and Powell 1996) using the Animal Movement extension of ArcView 3.2 (Hooge et al. 1999). The 95% contour provides an estimate of the home-range boundary, and the 50% contour corresponds to the part of the home range that receives more concentrated use. Annual home ranges were estimated using a minimum of 19 locations collected from May to December within a given year, summer home ranges were estimated from locations collected during May–August, and autumn home ranges were estimated from locations collected during September–December. Data were analyzed by year because not all bears were collared simultaneously, and also because pooling data across years can mask annual variation in home-range size (Schooley 1994). Analyses were considered by year and season so that differences between seasons or years could be discerned.

We calculated the distance between 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. We 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.'' Females whose home ranges overlapped the 95% utilization contour, but did not overlap core home ranges were designated as ''low overlap.'' Females whose core home ranges overlapped were considered to have ''high overlap.''

We used the program Genepop (Raymond and Rousset 1995) to estimate the observed heterozygosity (H_O), expected heterozygosity (H_E), and number of alleles (A) for each locus. Genepop also was used to test for deviations from Hardy–Weinberg equilibrium for each locus and the population as a whole using the Hardy–Weinberg probability test.

We analyzed microsatellite data using the program Kinship (Goodnight et al. 2004) to estimate the relatedness between pairs of female Florida black bears. 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). Because of the variability associated with relatedness estimates, 2 unrelated individuals (i.e., individuals who do not share an ancestry) should have a relatedness value within a distribution around zero. Likewise, although the expected relatedness value for a pair of fully related individuals (mother–offspring or full siblings) is 0.5, the actual value would fall within a distribution around the mean of 0.5.

Potential relatedness values ranged from −1 to 1, and in populations at Hardy–Weinberg equilibrium the relatedness value for parent–offspring or full siblings approaches 0.5 (Kays et al. 2000). 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). We ran 10,000 simulations using the program Kinship to estimate the distribution of relatedness values using data for a fully related pair of individuals and an unrelated pair. 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*) was compared to 0.5 to assess deviation from this theoretical value (Manly 1991).

We examined the association between genetic relatedness and spatial pattern in 2 ways. First, we compared each matrix of geographic distance to the corresponding matrix of genetic 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 9,999 permutations. Second, we evaluated the differences between mean relatedness of pairs of females in each of the 3 overlap categories (no overlap, low overlap, and high overlap). Because each female was involved in more than 1 pair in the analysis, the data were not independent, so traditional methods of mean comparisons were not appropriate. Thus, we estimated mean and 90% *CI* for each category using 50,000 bootstrap simulations (Manly 1991). Because of the relatively small sample size, the likelihood of failure to reject the null hypothesis when it was false was likely high. To minimize this likelihood, statistical comparisons were considered significant at $\alpha = 0.1$. Values are given as mean $\pm SE$.

RESULTS

Annual home ranges of female Florida black bears averaged 25.68 ± 3.71 km^2. Seasonal home ranges averaged 27.67 ± 5.09 km^2 during autumn and 11.79 ± 1.31 km^2 during summer. Core annual home-range size averaged 3.94 ± 0.60 km^2, but varied seasonally from 1.96 ± 0.33 km^2 during summer to 4.50 ± 1.32 km^2 during autumn. Pooling data across years, annual home ranges of each bear overlapped with those of 3.87 ± 0.38 other bears, and core home ranges overlapped with those of 1.11 ± 0.14 other bears. During autumn, home ranges of each bear overlapped with those of 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 those of 2.54 ± 0.26 other females, 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, because not all bears in the study area were radiocollared.

The average observed heterozygosity (H_O) was 0.365 ± 0.029, average expected heterozygosity (H_E) was 0.376 ± 0.031, and mean number of alleles per locus (A) was 4.83 ± 0.27. The population did not deviate from Hardy–Weinberg equilibrium ($P = 0.51$), and all but 1 of the individual microsatellite loci (G10P) were in equilibrium.

The distribution of simulated relatedness values for fully related and unrelated pairs of bears are presented in Fig. 2. If the cutoff value for discrimination between fully related (0.5) and unrelated (0.0) bears was 0.25, then, because of overlap between distributions, 10% of the time a relationship that
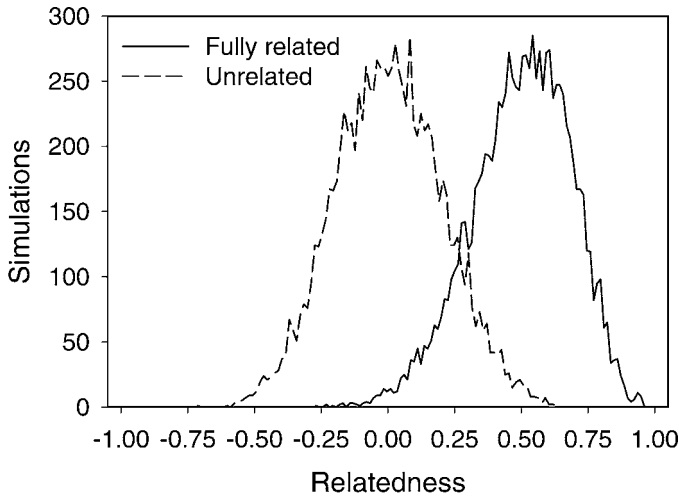
Fig. 2.—Simulation of distribution of relatedness values for fully related and unrelated black bears in Ocala National Forest, Florida. The 2 curves represent the distribution of expected relatedness values given an initial hypothesis as to the relationship between a pair of bears. Data were simulated with the allele frequencies of the Ocala bears using the program Kinship.

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). Note that the upper confidence limit of this value is lower than the theoretically expected value of 0.5, which suggests that relatedness may be slightly underestimated in this population and thus somewhat conservative.

The Mantel tests indicated a significantly negative relationship ($P < 0.1$) between relatedness of pairs of female black bears and distance between their core home ranges; autumn of 2000 was the only season for which a significant relationship

TABLE 1.—Results of the Mantel test comparing genetic relatedness and geographic distance between pairs of female Florida black bears in Ocala National Forest, Florida. The sample size (*n*; number of bears), the Mantel statistic (*r*), and the observed significance level (*P*) are provided for the Mantel test by year and season.

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

TABLE 2.—Mean genetic relatedness and degree of home-range overlap for female Florida black bears in Ocala National Forest, Florida, with mean genetic relatedness (*r*) and 90% confidence interval (90% *CI*) around the mean estimated using bootstrap technique (50,000 bootstrap samples) for 3 categories of home-range overlap. No overlap indicates pairs of bears with nonoverlapping home ranges, low overlap indicates pairs of bears with overlapping home ranges, and high overlap indicates pairs of bears with core home ranges overlapping.

	No-overlap bears		Low-overlap bears		High-overlap bears	
	r	90% *CI*	*r*	90% *CI*	*r*	90% *CI*
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	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
Autumn						
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

was not observed (Table 1). 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 ranged from −0.106 to 0.054 for bears with nonoverlapping ranges, −0.033 to 0.156 for bears overlapping home ranges, and 0.090 to 0.619 for bears overlapping core home ranges (Table 2; Fig. 3). The sample size of female pairs in the high-overlap category was smaller than that of low-overlap and no-overlap categories. This led to a confidence interval for the females with overlapping home ranges consistently larger than that for bears in no-overlap or low-overlap categories. Therefore, we focused on examining the differences in genetic relatedness between the no-overlap and high-overlap 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 females in the high-overlap group was greater than the upper confidence limit of females in the no-overlap group, suggesting that females with overlapping core home ranges were more closely related than those with nonoverlapping home ranges.

DISCUSSION

Home-range overlap between individuals within a species has been documented for many species of mammals (Admasu et al. 2004; Bixler and Gittleman 2000; Gehrt and Fritzell 1998). 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 relatedness among individuals, but estimating relatedness based on observations in wild populations is difficult, particularly in long-lived and elusive species. Genetic techniques, such as microsatellite analysis (Blouin et al. 1996; Paetkau and Strobeck 1994), can provide rigorous estimates of relatedness in a short period of time.

Home-range overlap is an important aspect of the spatial organization of black bear populations (Klenner 1987; Lyons et al. 2003; Pacas and Paquet 1994; Samson and Huot 2001). Home-range overlap is reported to be extensive in many black bear populations in the southeastern United States (Garshelis and Pelton 1981; Hellgren and Vaughan 1990; Horner and Powell 1990; Oli et al. 2002; Smith and Pelton 1990). The detailed study in Minnesota by Rogers (1987) provided evidence of yearling female black bears establishing home ranges within the home range of the mother. This pattern has been subsequently observed in other black bear populations (Clevenger and Pelton 1987; Garshelis and Pelton 1981; Schwartz and Franzmann 1992). These observations led to the hypothesis that genetic relatedness influences the spatial organization of female black bears and explains home-range overlap. Schenk et al. (1998) tested this hypothesis in 1 population of black bears in northern Ontario, but no relationship between spatial proximity and genetic relatedness was detected.

In this study, we found a negative correlation between the geographic distance between home-range centroids and relatedness among females for all years and seasons except autumn 2000. Spatial 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 Florida 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 genetic relatedness and space use pattern during autumn 2000 is perhaps due to the concurrent acorn mast failure in the forest. During this time, female black bears, particularly those with cubs, used larger home ranges and shifted and enlarged their core home ranges. These atypical 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 hypothesis that genetic relatedness influences the spatial pattern of female Florida black bears. For each season and year, mean relatedness of females with overlapping core home ranges was greater than the upper confidence limit of the mean relatedness of females with nonoverlapping 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.

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, 2 individuals, aged 7 and 6 years in 2003, had overlapping core home ranges throughout the study, yet they had a relatedness value of −0.24. Given this relatedness value,
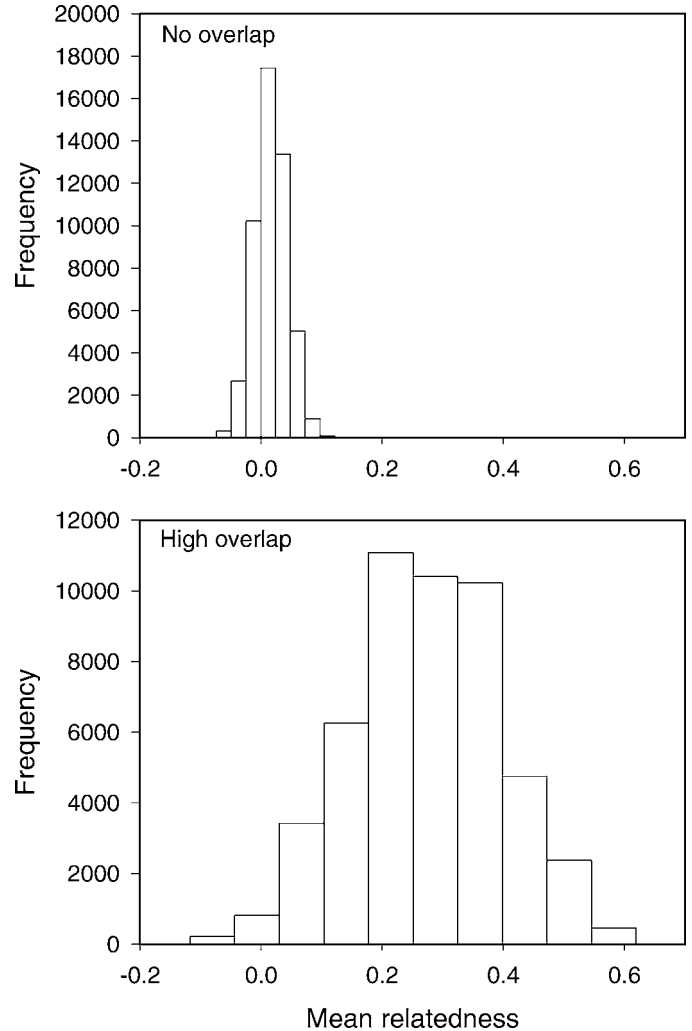

FIG. 3.—Distribution of estimated mean relatedness values for female black bears with no home-range overlap and for females with high home-range overlap for summer home ranges, 2001. The mean genetic relatedness and the 90% confidence interval around the mean were estimated using the bootstrap technique (50,000 bootstrap samples).

there is only a 0.01% probability that they were fully related (Fig. 2). Not only did the core home ranges of this pair overlap, they were also consistently radiotracked 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 also can be influenced by the distribution and availability of resources (Powell 1987; Schenk et al. 1998). Studies conducted in northern boreal forest where food abundance is generally low have reported little or no home-range overlap among female bears (Jonkel and Cowan 1971; Rogers 1987; Young and Ruff 1982). On the other hand, home-range overlap is extensive in black bear populations in the southeastern region where food abundance is much higher (Horner and Powell 1990; Oli et al. 2002; Powell 1987).

The extent of home-range overlap with, and tolerance toward, conspecifics may be greater when the distribution of food resources is patchy (Pacas and Paquet 1994; Samson and Huot 2001). Our results indicate more extensive core home-range overlap during autumn than during summer (Table 2), perhaps due to the patchy distribution of mast-producing species. Similar patterns of the influence of patchy distribution of food resources on home-range overlap have been reported for other black bear populations (Hellgren and Vaughan 1990; Jonkel and Cowan 1971; Powell 1987).

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

ACKNOWLEDGMENTS

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