Range Dynamics of Black Bears in Great Dismal Swamp, Virginia–North Carolina

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Abstract: Range size and dynamics of black bears (*Ursus americanus*) were determined in Great Dismal Swamp (GDS), an 850-km^2 forested wetland straddling the eastern border of Virginia and North Carolina. Male ranges were larger ($P < 0.05$) than female ranges annually and seasonally. Median range sizes were 21.4 km^2 for adult females ($N = 11$), 33.1 km^2 for subadult females ($N = 7$), and 79.0 km^2 for males ($N = 10$). Extensive fall movements inflated female ranges. Range shifts were maximal from late summer to early fall and early fall to late fall, averaging 4.4 ± 0.7 km ($N = 14$) and 4.4 ± 0.8 km ($N = 17$), respectively. Annual and seasonal overlap were extensive within and between sexes, with female range overlap increasing from spring to early fall. Range use and territoriality among female bears were influenced by spatial and temporal distribution of food.

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Ecology of the black bear in the Atlantic Coastal Plain has received limited study (Hamilton 1978, Landers et al. 1979, Hamilton and Marchinton 1980). Habitat use in southeastern wetlands is strongly tied to food availability and phenological development of plant foods (Smith 1985). Spatial and temporal distribution of food in turn affect range dynamics of black bears, including seasonal movements, range overlap, and range size (Garshelis and Pelton 1981). Other factors, such as age, sex, reproductive status, and social interactions also affect spatial use by black bears.

Available data on food habits (Daniel 1978) and anecdotal information are too limited to predict bear behavioral responses to management actions in GDS in particular and the region in general. Indeed, the effect of management strategies on

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bear movements and distribution and, conversely, the potential effects of bear range use and distribution shifts on management planning, are largely unknown in the Atlantic Coastal Plain. Thus, our objective was to characterize home range dynamics of black bears in the Coastal Plain black bear population of the GDS.

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Methods

Study Area

Great Dismal Swamp is a forested wetland located on the Virginia-North Carolina border in the mid-Atlantic Coastal Plain. Field work was conducted from April 1984 to August 1986 and from December 1986 to March 1987 primarily on the 440-km^2 GDS National Wildlife Refuge; the 57.5-km^2 Dismal Swamp State Park, North Carolina; and adjacent privately-owned swamp land. The entire study area was 555 km^2. A west-east gradient of about 19 cm/km characterized the generally flat Swamp (Gammon and Carter 1979). Long-term mean temperatures for January and July were 5.1 and 26.0 C, respectively (Lichtler and Walker 1979). Annual precipitation averages 120 cm, with light and irregular snowfall (Natl. Oceanic and Atmos. Admin. 1984, 1985).

The vegetation composition of GDS included a variety of herbaceous plants; evergreen and deciduous shrubs; vines; and deciduous and evergreen, broad-leaved or needle-leaved tree species (Gammon and Carter 1979). The major forest cover type is the red maple (*Acer rubrum*)-black gum (*Nyssa sylvatica*) association. Other major tree species found with this association are sweetgum (*Liquidambar styraciflua*) redbay (*Persea borbonia*), sweetbay (*Magnolia virginiana*), and yellow poplar (*Liriodendron tulipifera*). Bald cypress (*Taxodium distichum*)-gum (*Nyssa* spp.) forests occur on seasonally inundated, mineral soils. Major understory shrubs for both cypress-gum and maple-gum forests include sweet pepperbush (*Clethra alnifolia*), blueberry (*Vaccinium* spp.), fetterbush (*Lyonia lucida*), leucothoe (*Leucothoe* spp.), and hollies (*Ilex* spp.). Loblolly pine (*Pinus taeda*) occurs in pure stands or mixed with red maple or maple-gum. Remnant stands of Atlantic white cedar (*Chamaecyparis thyoides*) also occur. Dense inkberry (*I. glabra*)-dominated pocosins cover part of the study area, especially southeast of lake Drummond. Mesic stands containing oak-beech (*Quercus-Fagus* spp.) associations occur as islands within GDS and along the western periphery. They occur at higher elevations and in areas with well-drained, mineral soils. For a more complete study area description, see Hellgren and Vaughan (1988).

Trapping and Handling

Bears were captured and handled as described by Hellgren and Vaughan (1989b). Bears were equipped with radio-transmitter collars (Telonics, Inc., Mesa, Ariz.) in the 164–165 MHz range with a 5-minute delay motion sensor. Twenty-four females and 22 males were radio-collared and monitored for periods of 45 to 1,168 days. A breakaway cotton spacer was inserted in each collar (Hellgren et al. 1988) to minimize chafing and rubbing of the collar and to prevent bears from retaining the collars indefinitely.

Telemetry Data Collection and Analysis

Radioequipped bears were located 1 to 7 times each week with handheld receiving equipment by triangulation from at least 3 points on refuge or state roads. All bearings for a given location were taken within 30 minutes. Locations were made primarily (99%) between 0700 and 2100 hours. To supplement ground locations, aircraft-mounted receiving equipment was used to locate bears 2–4 times/month. Locations were plotted on USGS 1:24,000 topographic maps and assigned grid coordinates (to the nearest 50 m) based on the Universal Transverse Mercator (UTM) system. Telemetry data were processed by Telem (Koeln 1980, Coleman and Jones 1988) and ranges determined by the convex polygon method. Locations were considered independent as only 1 location/day and averages of 2.4 locations/week/female and 1.6 locations/week/male were used for analysis. Swihart and Slade (1985) state that an approximation of independence of successive observations is likely achieved in studies with long (>24-hour) interlocation intervals. The standard deviation of bearing error associated with handheld equipment averaged ±5.1° ($N = 25$). Because virtually all radiotracking was done from roads, distance to roads is essentially equal to distance to observer. Thirty-two percent of female radiolocations were collected <200 m from roads, 23% were 200–400 m from roads, and 29% were 400–800 m from roads. Error arcs were developed from average standard deviation of error estimates; 95% error arc widths of radiotelemetry bearings were 70, 145, and 290 m for these distance categories, respectively.

Females monitored for $\geq$8 months ($N = 18$) and males monitored for $\geq$6 months ($N = 10$) were used to estimate total range size. Four females monitored for >12 months provided annual range size estimates. Seasonal ranges were calculated for bears that were monitored for >50% of a given season and were relocated on average at least once/week during that season. Seasons were based on changes in plant phenology and shifts in bear food habits: spring (den emergence—15 Jun), early summer (16 Jun–31 Jul), late summer (1 Aug–15 Sep), early fall (16 Sep—15 Nov), and late fall (16 Nov–den entry or 15 Jan). Dates for the early fall season varied slightly for individual bears depending on when they moved to take advantage of mast concentrations outside their spring-summer ranges. Early fall range size estimates were based on radiolocations after bears had moved to fall feeding areas.

Mean den entry dates ranged between 15 December and 5 January for different cohorts. Den emergence ranged from 21 March to 14 April (Hellgren and Vaughan 1989*a*).

Seasonal and annual range areas were tested for differences among age and sex groups with nonparametric 1-way layout tests (Kruskal-Wallis [K-W] tests) and a protected ($P < 0.05$) LSD procedure to make median comparisons. The K-W test was used because range size data were not normally distributed. Data were pooled between years because of small sample sizes and similar movement patterns between years. Male data were not divided by age, as all collared males were >3 years of age except 2 that were 2.5 years old.

Female range shifts were evaluated in 2 ways for each seasonal range: distance between arithmetic mean centers (Garshells and Pelton 1961) and distance between harmonic mean centers (Dixon and Chapman 1980). Although the arithmetic mean center may have characteristics that make it disadvantageous as a measure of the center of animal activity (Dixon and Chapman 1980), we used it to facilitate comparisons with previously published data and because seasonal ranges generally had a unimodal distribution. Signed rank tests were used to compare arithmetic mean center and harmonic mean center range shifts. Seasonal changes in overlap of female ranges were examined by determination of the percent of each seasonal convex polygon range that was nonoverlapping in the same year with ranges of other females. Only range data from females monitored south of centrally located Lake Drummond ($N = 12–17$) were used in this analysis because of an inadequate sample north of the Lake. Paired *t*-tests were used to test for differences in percent nonoverlapping range between seasons.

Results

Range Size

Total range size differed ($P \leq 0.01$) among groups (Table 1). Male total ranges were larger than either subadult ($P \leq 0.01$) or adult ($P \leq 0.01$) female ranges. Annual range size estimates were 14.3, 32.7, 20.6, and 94.3 km^2 for solitary females (the first 2 estimates are annual ranges for a single female) and 14.5 km^2 for a female with cubs. Spring-summer and early fall ranges were commonly disjunct. When convex polygons were drawn around all locations, large unused areas between spring-summer ranges and fall feeding areas greatly inflated total home range estimates. Removing early fall locations from convex polygon analysis reduced median home range size to 10.4 km^2 for adult females ($N = 11$) and 9.7 km^2 for subadult females ($N = 7$), reductions in estimates of 51 and 71%, respectively.

During spring, solitary adult females had larger ranges than subadults ($P = 0.01$) and females with cubs ($P \leq 0.01$); in early summer, solitary adult female ranges were larger than subadults ($P \leq 0.01$). Subadult females, however, had larger ($P < 0.05$) ranges than other female groups during early fall, as well as larger ($P = 0.04$) ranges than females with cubs during late fall (Table 1). Male ranges were

Table 1. Total and seasonal range size (km^2) of solitary adult females, females with cubs, subadult females, and male black bears in Great Dismal Swamp, 1984–86.

Sample[a]	N	Median[b]	Mean	SE	Range	Locations/ bear
Spring (emergence to 15 Jun)						
Solitary adults	10	5.3B[c]	6.0	1.0	2.2–14.4	25–61
Subadult females[d]	4	2.1C	2.7	0.8	1.6–4.9	25–29
Females with cubs	5	3.4C	3.3	0.5	1.6–4.7	22–41
Males	9	22.5A	34.7	17.1	2.6–169.6	11–33
Early summer (16 Jun–31 Jul)						
Solitary adults	11	4.5B	4.9	0.6	1.1–7.2	13–21
Subadult females	4	3.0C	2.7	0.4	1.5–3.4	13–30
Females with cubs	3	5.8ABC	6.9	3.2	2.1–12.9	12–29
Males	5	6.7A	10.7	3.9	5.5–26.2	6–20
Late summer (1 Aug–15 Sep)						
Solitary adults	9	4.7B	5.8	1.1	2.6–13.3	11–24
Subadult females	4	2.7B	3.1	0.9	1.4–5.4	13–23
Females with cubs	1	4.6	4.6	—	—	22
Males	5	14.5A	16.2	3.9	5.9–30.0	7–17
Early fall (16 Sep–15 Nov)[e]						
Solitary adults	14	5.9C	7.3	1.7	1.0–24.1	7–37
Subadult females	5	11.9B	15.7	5.8	5.1–37.7	9–39
Females with cubs	3	2.7C	2.8	1.1	1.0–4.7	19–23
Males	8	52.8A	53.0	14.0	7.5–113.4	6–24
Late fall (16 Nov–15 Jan or den entry)						
Solitary adults	12	3.7BC	4.8	1.5	0.5–18.2	9–32
Subadult females	7	3.0B	3.9	1.3	0.2–9.0	8–38
Females with cubs	3	1.0C	1.0	0.0	1.0–1.1	21–33
Males	8	22.6A	42.4	15.1	3.4–130.6	10–23
Total range size (≥8 months for females and ≥6 months for males)						
Adult females	11	21.4B	27.0	8.2	8.9–105.4	48–298
Subadult females	7	33.1B	29.0	7.5	5.5–62.4	65–353
Males	10	79.0A	111.7	36.9	16.8–427.6	28–142

[a] Only bears monitored ≥50% of the season and with at least 1 location/week are included in samples.

[b] 100% convex polygon method used to calculate seasonal and total home range.

[c] Medians within the same column and season that share the same letter are not different ($P > 0.05$) according to protected LSD.

[d] <3 years old when captured.

[e] These dates varied slightly for individual bears depending on when fall shuffle occurred.

larger ($P < 0.05$) than ranges of subadult females, solitary adult females, or females with cubs during all seasons except early summer (Table 1). In this season, range sizes of males and females with cubs were similar ($P = 0.23$).

Seasonal Range Shifts

Large range shifts to areas of high mast production primarily along the swamp's periphery (Fig. 1) were common in the fall (Table 2). Shifts of >3 km for harmonic mean range centers were observed for 9 of 14 females from late summer to early fall and 10 of 17 from early fall to late fall. These shifts represented movement from spring-summer ranges to fall feeding areas, then return to spring-summer ranges for denning in late fall and winter. Shifts of similar amplitude were observed for only

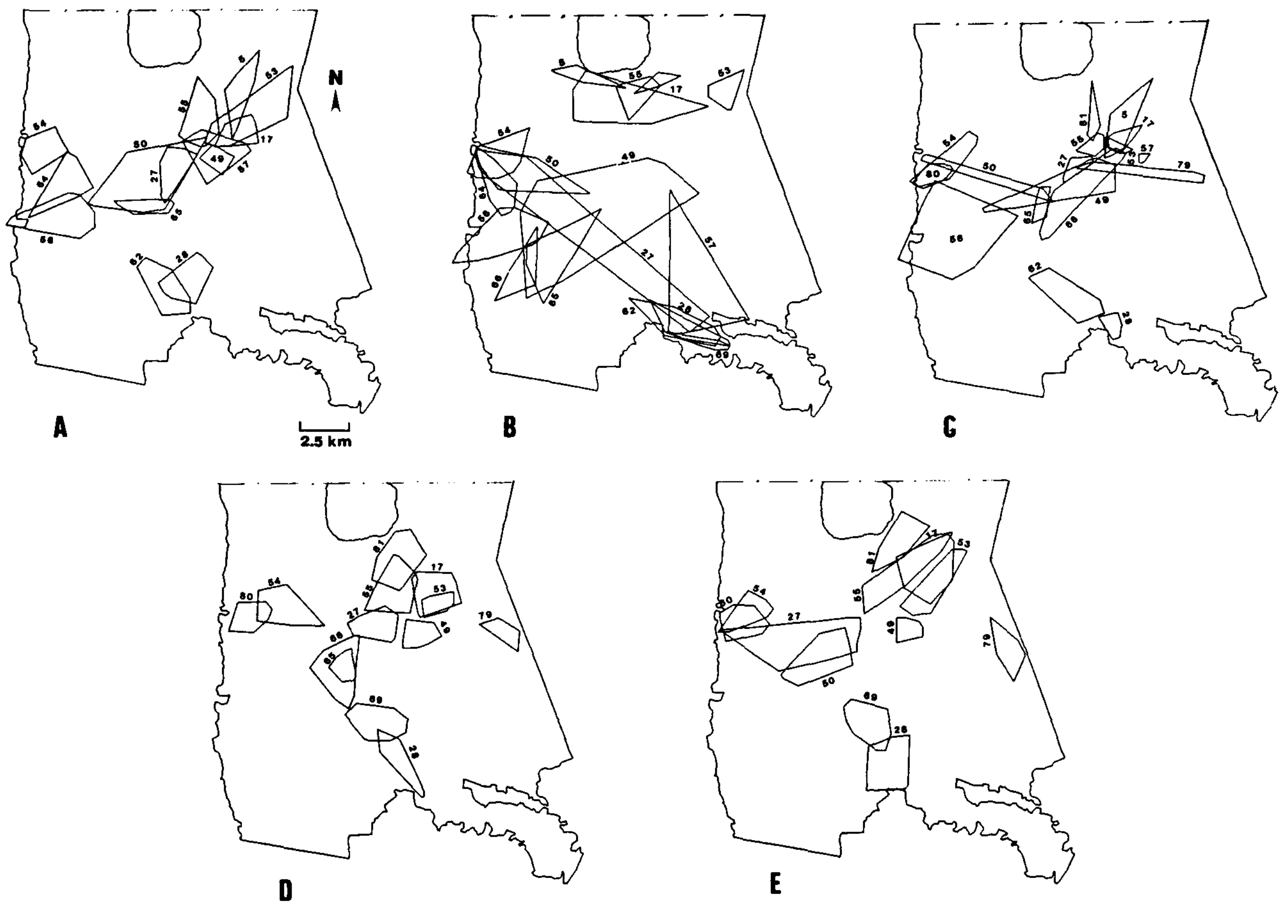

Figure 1. Seasonal convex polygon home ranges for female black bears monitored in the southern half of Great Dismal Swamp in 1985–1986. A = late summer (1 Aug–15 Sep), B = early fall (16 Sep–15 Nov), C = late fall (16 Nov–15 Jan), D = spring (emergence–15 Jun), E = early summer (16 Jun–31 Jul). Numbers represent individual bears.

Table 2. Mean distance between harmonic mean center and arithmetic mean center of seasonal ranges of telemetered female bears in Great Dismal Swamp in 1984–86.

Seasonal shift		Distance (km) between harmonic range center			Distance (km) between arithmetic range centers	
From	To	*N*	$\bar{x}$	SE	$\bar{x}$	SE
Late fall	Spring	16	1.8	0.5	1.5	0.3
Spring	Early summer	12	2.0	0.5	1.5	0.5
Early summer	Late summer	8	2.8	0.9	1.9	0.7
Late summer	Early fall	14	4.4	0.7	3.9	0.6
Early fall	Late fall	17	4.4	0.8	3.7	0.6

8 of 36 females in spring, early summer, and late summer. Range shifts from late fall to spring were for bears that returned late to their territories ($N = 3$) to den and a bear that failed to den and thus moved between late fall and spring. Bears that shifted ranges from spring to early summer and from early to late summer ($N = 4$) moved to take advantage of concentrations of early ripening fruit outside of their territories. Range shifts measured by harmonic mean centers were greater ($P < 0.05$) than measured by arithmetic mean centers for spring to early summer, late summer to early fall, and early fall to late fall shifts (Table 2).

Home Range Overlap

Total home range overlap was extensive for females and males (Hellgren 1988: 87, 94). Seasonal overlap, as estimated by percent of nonoverlapping range, did not differ ($P > 0.10$) between seasons for females (Fig. 1). Percent nonoverlapping range was highest during spring (70.3 ± 9.0%; $N = 13$) and early summer (70.8 ± 9.5%, $N = 12$) and least during late summer (54.0 ± 8.6%, $N = 14$) and early fall (48.1 ± 7.4%, $N = 17$).

Discussion

Comparisons of home range estimates among studies are difficult because methods of defining areas (Garshelis and Pelton 1981) and sampling regimes (Smith 1985) often differ. Despite these difficulties, a general pattern of bear spatial use has emerged (Smith (1985) and the GDS population appears to follow this pattern. Mean annual home range estimates in this study were comparable to convex polygon home range estimates made in other southeastern wetlands (Hardy 1974, Hamilton 1978, Abler 1985, Smith 1985).

Males occupied larger areas than females annually and seasonally. It has been hypothesized that adult males can increase their reproductive fitness by using areas that encompass the ranges of several adult females. The mating benefits of these ranges thus lead to the use of large areas that cannot be defended as territories (Amstrup and Beecham 1976, Rogers 1977).

A consequence of large areal use by male black bears is extensive overlap; for example, Smith (1985) found considerable overlap among male ranges in a bottomland hardwood forest, despite monitoring only a small percentage of resident bears. Hamilton (1978) found that males had overlapping ranges in coastal North Carolina. Both authors found that male ranges overlapped several female ranges, especially during the breeding season. Our study showed similar results.

Female ranges, on the other hand, may be directly related to habitat quality and should be large enough to supply adequate resources for successful reproduction (Armstrup and Beecham 1976). Smaller home ranges may indicate intense use of high quality habitats (Lindzey and Meslow 1977, Modafferi 1982, Garner 1986). In Arkansas, Smith (1985) found evidence of a relationship between home range size and habitat quality. Ranges were smaller for both sexes east of the White River, which bisected his study area. The eastern portion of the area was characterized by greater habitat diversity, more food production (measured qualitatively), and less human disturbance. The present study did not examine the relationship between habitat quality, range size, and reproductive fitness, but population characteristics in GDS are indicative of average quality bear habitat (Hellgren and Vaughan 1989*b*). Seasonal ranges were generally small, but annual range sizes of some bears were inflated by extensive fall movements.

Home range overlap among females has been the subject of much discussion. Some studies have reported exclusive female ranges (Rogers 1977, LeCount 1980, Young and Ruff 1982), whereas others have noted considerable spatial overlap (Amstrup and Beecham 1976, Lindzey and Meslow 1977, Reynolds and Beecham 1980, Garshelis and Pelton 1981, Garner 1986). We observed extensive annual overlap (Hallgren 1988). In coastal North Carolina, Hamilton (1978) reported that adult females showed the least overlap of any age-sex group. However, his study suffered from a common problem among bear studies examining spatial organization: namely, the monitoring of a small percentage of resident bears. In such cases, measures of overlap are minimal and must be interpreted with caution. In other wetland areas, Abler (1985) and Smith (1985) found considerable female range overlap and attributed this to utilization of aggregated food sources and kinship.

Although several studies have reported overlapping annual ranges among female black bears, rarely has extensive spring-summer overlap been noted (Garshelis and Pelton 1981, Smith 1985). Radiocollared females in GDS maintained exclusive ranges during spring and early summer (Fig. 1). An average of >70% of each of these seasonal ranges was non-overlapping with other females, compared to 48%–54% during late summer and early fall (Fig. 1). Although these differences were not significant and only a small percentage (20%–25%) of resident bears was monitored, site fidelity during spring and early summer was high, as evidenced by small shifts between seasonal range centers, and actual spatiotemporal overlap was minimal. During late summer and fall, range overlap among females appeared to increase as bears concentrated in food-rich areas. Radiocollared bears were commonly located within 100–200 m of each other in stands of black cherry (*Prunus serotina*), black gum (*Nyssa sylvatica*), or oak (*Quercus* spp.). Similarly, Landers et al. (1979) reported bears concentrated in fall to feed in hardwood swamps and on sand ridges in coastal North Carolina.

Several ideas have been proposed to explain overlapping of female ranges. Among these are kinship and social tolerance (Jonkel and Cowan 1971, Rogers 1977, Lindzey and Meslow 1977: adequately demonstrated only by Rogers 1977), spatial and temporal distribution of food (Reynolds and Beecham 1980, Garner 1986, Rogers 1987), and temporal separation of areas of common use (Lindzey and Meslow 1977, Reynolds and Beecham 1980, Garshelis and Pelton 1981).

We think that spatial and temporal distribution of food most strongly affected female range dynamics in the GDS study area, with females maintaining a territorial system as in Rogers (1987). Territory defensibility theory hypothesizes that resources are worth defending if they are economically defensible in terms of reproductive fitness (Wittenberger 1981:300). Two major factors would contribute to female bear territoriality in spring and early summer in GDS (and other bear populations—Roger 1987:13–14). First, food resources, primarily succulent leaves and stems (Hellgren and Vaughan 1988) are evenly distributed and predictable, a favorable situation for territorial behavior (Wiens 1976). Second, territoriality may increase feeding efficiency of resident females and their offspring (Rogers 1987) by intimate knowledge of food sources in a small area and may lead to increased survival of young cubs. These benefits may outweigh the costs of territorial defense. Continued territorial defense by females without cubs would be adaptive to maintain land tenure for times when tenure is necessary. A low rate of range shifts (22%, $N = 36$) between late fall and late summer supported the idea of spring–early summer range fidelity.

In late summer and early fall, bear foods in GDS become localized in small patches of productive habitat, such as pocosins and oak and gum stands (Hellgren and Vaughan 1988). Cubs are more mobile and less susceptible to predators, such as adult male bears and felids (Elowe 1987, LeCount 1987). During these seasons, the benefits of resource defense decrease and the costs increase because more competitors are likely to intrude on a productive food patch. Defensibility theory argues that as resource aggregation and unpredictability increase, territoriality eventually will break down as the resources become indefensible (Wiens 1976, Wittenberger 1981:287). The result for GDS female bears was the large observed shifts in range centers (Table 2) and extensive overlap in productive habitat patches. Factors affecting degree of overlap and how they affect efficiency of resource utilization need further study.

Management Implications

Several large tracts of public land in the Atlantic Coastal Plain harbor bear populations in areas with similar food plants and plant phenology to GDS. Although local patterns of private and public ownership vary, this study provides insight into how shifts in bear distribution can be predicted in other Coastal Plain areas. Knowledge of bear distributional shifts may affect timing of management activities such as timber harvest and hunting seasons. For example, the female bear distribution shifted significantly closer to the Swamp boundary during early fall (Hellgren 1988:108) as animals moved to feeding areas near the study area periphery. A large proportion of mesic oak stands on the edge of the Swamp are in private ownership; thus, the fall range shift concentrated female bears in vulnerable areas during October and early November. Delaying the hunting season after 15 November would allow most female bears to return to spring-summer territories within GDS National Wildlife Refuge, decreasing the proportion of females in the harvest.

Literature Cited

Abler, W. A. 1985. Bear population dynamics on a study area in southeast Georgia. Ga. Dep. Nat. Resour., Atlanta. Final Rep. W37-LII. 91pp.

Amstrup, S. C. and J. Beecham. 1976. Activity patterns of radiocollared black bears in Idaho. J. Wildl. Manage. 40:340–348.

Coleman, J. S. and A. B. Jones, III. 1988. User's guide to TELEM88: computer analysis system for radiotelemetry data. Dep. Fish. and Wildl. Sci., Va. Polytech. Inst. and State Univ., Blacksburg. Res. Ser. 1. 49pp.

Daniel, F. L. 1978. The fall and winter food habits of the black bear (*Ursus americanus*) in the Great Dismal Swamp of Virginia. M.S. Thesis, Old Dominion Univ., Norfolk, Va. 30pp.

Dixon, K. R. and J. A. Chapman. 1980. Harmonic mean measure of animal activity areas. Ecology 61: 1040–1044.

Elowe, K. D. 1987. Factors affecting reproductive success and cub survival in western Massachusetts. Ph.D. Thesis, Univ. Mass., Amherst. 82pp.

Gammon, P. T. and V. Carter. 1979. Vegetation mapping with seasonal color infrared photographs. Photogramm. Eng. Remote Sens. 45: 87–97.

Garner, N. P. 1986. Seasonal movements, habitat selection, and food habits of black bears (*Ursus americanus*) in Shenandoah National Park, Virginia. M.S. Thesis, Va. Polytech. Inst. and State Univ., Blacksburg. 104pp.

Garshelis, D. L. and M. R. Pelton. 1981. Movements of black bears in the Great Smoky Mountains National Park. J. Wildl. Manage. 45: 912–925.

Hamilton, R. J. 1978. Ecology of the black bear in southeastern North Carolina. M.S. Thesis, Univ. Ga., Athens. 214pp.

——— and R. L. Marchinton. 1980. Denning and related activities of black bears in the coastal plain of North Carolina. Intl. Conf. Bear Res. and Manage. 4:121–126.

Hardy, D. M. 1974. Habitat requirements of the black bear in Dare County, North Carolina. M.S. Thesis, Va. Polytech. Inst. and State Univ., Blacksburg. 121pp.

Hellgren, E. C. 1988. Ecology and physiology of a black bear (*Ursus americanus*) population in Great Dismal Swamp and reproductive physiology of the captive female black bear. Ph.D. Thesis, Va. Polytech. Inst. and State Univ., Blacksburg. 231pp.

———, D. W. Carney, N. P. Garner, and M. R. Vaughan. 1988. Use of breakaway cotton spacers on radiocollars. Wildl. Soc. Bull. 16:216–218.

——— and M. R. Vaughan. 1988. Seasonal food habits of black bears in Great Dismal Swamp, Virginia-North Carolina. Proc. Annu. Conf. Southeast. Assoc. Fish and Wildl. Agencies 42:295–305.

——— and ———. 1989*a*. Denning ecology of black bears in a southeastern wetland. J. Wildl. Manage. 53: 347–353.

——— and ———. 1989*b*. Demographic analysis of a black bear population in Great Dismal Swamp. J. Wildl. Manage. 53: 969–977.

Jonkel, C. J. and I. M. Cowan. 1971. The black bear in the spruce-fir forest. Wildl. Monogr. 27. 57pp.

Koeln, G. T. 1980. A computer technique for analyzing radio-telemetry data. Proc. Natl. Wild Turkey Symp. 4:262–271.

Landers, J. L., R. J. Hamilton, A. S. Johnson, and R. L. Marchinton. 1979. Foods and habitat of black bears in southeastern North Carolina. J. Wildl. Manage. 43:143–153.

LeCount, A. L. 1980. Some aspects of black bear ecology in the Arizona chaparral. Intl. Conf. Bear Res. and Manage. 4:175–179.

———. 1987. Causes of black bear cub mortality. Intl. Conf. Bear Res. and Manage. 7:75–82.

Lichtler, W. F. and P. N. Walker. 1979. Hydrology of the Dismal Swamp. Pages 140–168 *in* P. W. Kirk, ed., The Great Dismal Swamp. Univ. Press Va., Charlottesville.

Lindzey, F. G. and E. C. Meslow. 1977. Home range and habitat use by black bears in southwestern Washington. J. Wildl. Manage. 41:413–425.

Modafferi, R. D. 1982. Black bear movements and home range study. Alaska Dep. Fish and Game. Fed. Aid in Wildl. Restoration Final rep., Job 17–2R, Juneau. 73pp.

National Oceanic and Atmospheric Administration. 1984. Climatological data: Virginia, annual summary. Natl. Climatic Ctr., Asheville, N.C. 28pp.

———. 1985. Climatological data: Virginia, annual summary. Natl. Climatic Ctr., Asheville, N.C. 20pp.

Reynolds, D. G. and J. J. Beecham. 1980. Home range activities and reproduction of black bears in west-central Idaho. Intl. Conf. Bear Res. and Manage. 4:181–190.

Rogers, L. L. 1977. Social relationships, movements, and population dynamics of black bears in northeastern Minnesota. Ph.D. Thesis, Univ. Minn., Minneapolis. 194pp.

———. 1987. Effects of food supply and kinship on social behavior, movements, and population growth of black bears in northeastern Minnesota. Wildl. Monogr. 97. 72pp.

Smith, T. R. 1985. Ecology of black bears in a bottomland hardwood forest in Arkansas. Ph.D. Thesis, Univ. Tenn., Knoxville. 209pp.

Swihart, R. K. and N. A. Slade. 1985. Testing for independence of observations in animal movements. Ecology 66: 1176–1184.

Wiens, J. A. 1976. Population responses to patchy environments. Annu. Rev. Ecol. System. 7:81–120.

Wittenberger, J. F. 1981. Animal social behavior. Duxbury Press, Boston, Mass. 722pp.

Young, B. L. and R. L. Ruff. 1982. Population dynamics and movements of black bears in east-central Alberta. J. Wildl. Manage. 46:845–860.