

SPATIOTEMPORAL PATTERNS OF MACROHABITAT USE BY FEMALE BLACK BEARS DURING FALL

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Abstract: We compared habitat use and movements of 82 radio-collared female black bears (*Ursus americanus*) at 3 dissimilar study areas in Maine during fall from 1986 to 1988. We focused on the use of northern hardwood forests containing American beech (*Fagus grandifolia*). Many beech forests in the northeastern United States have been infected with beech bark disease, which may limit beechnut availability. At the Spectacle Pond and Stacyville study areas, annual variation in habitat use was pronounced and was related to abundance of beechnuts. Bears used hardwood forests more when beechnuts were abundant (1986 and 1988) than when beechnuts were scarce (1987). At the Bradford study area, where habitat was more diverse and beech trees were less common, habitat use did not vary annually, and use of hardwoods and softwoods was proportional to availability. Maximum fall movements by bears, away from summer ranges, did not vary annually within areas. Fall movements were greater for bears at Stacyville (median = 7.3 km, $n = 19$ bear-years) than at Spectacle Pond (median = 1.3 km, $n = 52$) or at Bradford (median = 0.9 km, $n = 28$) and reflected distribution of food resources on a landscape scale. In all areas, most long movements (7.7-78.6 km) during fall were to hardwood forests when beechnuts were abundant. Bears usually denned within or near (≤ 1.0 km) their summer ranges despite long fall movements. We provide recommendations for managing northern hardwoods to maintain beechnut production.

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Reproduction and recruitment of black bears have been correlated with availability of mast (Rogers 1987, Eiler et al. 1989, Elowe and Dodge 1989). American beech is a component of the northern hardwoods forest type, and beech mast is eaten by black bears during fall (Hugie 1982, Elowe and Dodge 1989). Beech bark disease has caused extensive mortality of beech trees throughout northeastern United States (Houston 1975, Miller-Weeks 1983), with mortality exceeding 50% in some forests in Maine (Miller-Weeks 1983). In North America, beech bark disease is caused by a fungus (especially *Nectria coccinea* var. *faginata*) that infects the feeding wounds in the bark made by the beech scale (*Cryptococcus fagi*) (Houston 1975). This disease was first reported at Maine in the 1930s (Houston 1975), but another disease outbreak may be occurring now because of the age and size structures of recovering beech forests (Houston 1975, Houston and Valentine 1988). Beech bark disease can reduce beechnut production in infected forests (C.M. Costello, Adirondack Ecol. Cent., pers. commun.).

Habitat use by black bears has been examined in the Northeast (Hugie 1982, Lamb 1983, Elowe 1984, Meddleton 1989), but these studies did not test relationships between availability of mast and habitat use by bears during fall. Previous studies focused on spring and summer (Meddleton 1989), combined data

for all seasons (Hugie 1982, Lamb 1983), or combined data from several years in which abundance of mast differed (Hugie 1982, Elowe 1984). Seasonal movements by black bears are mainly governed by distribution, phenology, and abundance of preferred foods (Garshelis and Pelton 1981, Pelchat and Ruff 1986, Rogers 1987). Comparing fall movements of bears from different environments should provide insight into foraging behavior and importance of forest types. Except for Hugie (1982), previous studies in northeastern United States were conducted at only 1 area.

We investigated macrohabitat use and movements of 82 female black bears during fall at 3 areas in Maine during 1986-88. Our objectives were to compare habitat use by bears among areas with different topography, land use, and distribution of northern hardwoods; to ascertain whether annual variation in habitat use was related to the abundance of beechnuts; and to determine the maximum distances that bears traveled to northern hardwood forests. This descriptive study also provides information useful for interpreting results from concurrent research on population dynamics of bears in our 3 study areas.

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STUDY AREAS

Each of the 3 study areas was about 370 km². Spectacle Pond study area was in northern Maine about 27 km southwest of Ashland, Maine. Spectacle Pond was >95% forested and elevations ranged from 226 to 692 m. Northern hardwoods (sugar maple [*Acer saccharum*], American beech, and yellow birch [*Betula alleghaniensis*]) were common on ridges and other well-drained sites, whereas spruce (*Picea* spp.)-fir (*Abies balsamea*) associations and northern white-cedar (*Thuja occidentalis*) were common along drainages and valleys. The land was privately owned, and the primary land use was commercial logging of softwoods for pulp. Clearcutting was common in the 1980s to salvage softwood stands infested with spruce budworm (*Choristoneura fumiferana*). The area had no paved roads, permanent residents, or agriculture.

Stacyville study area was in north-central Maine about 88 km south of Spectacle Pond. Stacyville was about 80% forested (Hugie 1982), and elevations ranged from 98 to 594 m. The east branch of the Penobscot River drained south through the area. West of the Penobscot River, terrain and vegetation were similar to Spectacle Pond. East of the Penobscot River, the terrain was flatter and several small towns and agricultural fields were present. Cultivated crops included oats, corn, potatoes, apples, and barley (Hugie 1982). Red oak (*Quercus rubra*) was present along the Penobscot River and nearby hills.

Bradford study area was in central Maine about 90 km south of Stacyville. Bradford was 92% forested, but the terrain was relatively flat, with elevations

ranging from 37 to 171 m. Although spruce-fir was the predominant softwood association, bogs and wooded swamps were more common than in the other 2 areas. These bogs often were associated with black spruce (*P. mariana*) and tamarack (*Larix laricina*). Northern hardwoods were less common than at Spectacle Pond and Stacyville, but several other hardwood species were more common, including red maple (*A. rubrum*), aspen (*Populus tremuloides*, *P. grandidentata*), and ash (*Fraxinus* spp.). Red oak was present, especially along the Penobscot River, which bordered the study area on the east. The area included several towns, active farms, and abandoned apple orchards. For all 3 study areas, the mean maximum daily temperatures for July ranged from 25°C to 26°C, and mean minimum daily temperatures for January ranged from -22°C to -17°C (Natl. Oceanic Atmos. Adm. 1987).

METHODS

Capture, Telemetry, and Habitat Use

We livetrapped black bears from May to August in 1986-88 with Aldrich foot snares and occasionally with culvert traps. We immobilized captured bears (≥ 4 months old) with an intramuscular injection of a 2:1 mixture of ketamine hydrochloride and xylazine hydrochloride (Addison and Kolenosky 1979). For each 45 kg of estimated body mass, we used 400 mg of ketamine and 200 mg of xylazine. Bears were weighed, measured, sexed, marked with numbered ear tags and lip tattoos, and their age estimated by counting cementum annuli on an extracted premolar (Willey 1974, McLaughlin et al. 1990). We fitted captured females (≥ 1 yr old) with motion-sensitive radio collars (Telonics, Inc., Mesa, Ariz.; use of manufacturer's name does not imply U.S. Government endorsement).

We located radio-collared bears from small aircraft equipped with side-facing H antennas mounted to each wing strut (Mech 1983:54-72). We located bears at least once per week from den emergence (usually April) to den entry (usually October or November) if weather permitted, and we considered locations for individuals >24 hours apart as independent (e.g., Garshelis and Pelton 1981, Pelchat and Ruff 1986). All locations were collected during daylight hours. Activity of black bears in Maine (Hugie 1982:71) and elsewhere (Amstrup and Beecham 1976, Lindzey and Meslow 1977, Elowe 1984:59-67) typically is diurnal and crepuscular, although nocturnal activity may increase during fall (Garshelis and Pelton 1980). Tests with stationary transmitters indicated error in locating radio

collars was usually ≤ 40 m, but additional error occurred from plotting locations on black-and-white aerial photographs (1:80,000 scale) and then obtaining Universal Transverse Mercator coordinates from orthophotoquads (1:24,000 scale). This additional error was not quantified but may have been ≤ 200 m. However, this error only affected the accuracy of locations used for our analysis of movements, because habitat use was determined from aerial classification (Schooley and McLaughlin 1993).

We classified habitat from aircraft within a 200-m radius of each location. We classified forest type by visually estimating percent canopy closure of overstory and proportion of hardwood and softwood species present (Table 1). We recorded presence of the following habitat edges within 200 m of each location: rivers or streams, lakes or ponds, clearcuts, and agriculture. We also recorded the presence of beech as a dominant species at Spectacle Pond during 1988. Dominant species were the 3 most common overstory species, based on percent canopy closure, within 200 m of locations. Tests with stationary transmitters indicated these habitat variables could be classified by our 2 observers with little bias (Schooley and McLaughlin 1993).

Habitat Availability and Selection

At Spectacle Pond and Bradford, we estimated habitat available to bears during 1986-88 within a core area defined by a composite of annual home ranges of bears with contiguous ranges. We did not measure habitat availability for Stacyville because we did not have complete coverage with low-altitude aerial photographs, cover-type maps, or satellite data. We divided the Spectacle Pond area into 2 sections (North and South) because we believed that habitat differed due to logging history. At Spectacle Pond North (147 km²) and South (168 km²), we estimated availability of habitats by plotting 500 random points (Marcum and Loftsgaarden 1980) in each area on cover-type maps (1:15,840 scale) provided by 2 companies that owned or managed the land. Forest types on the cover-type maps were classified from aerial photos according to the same criteria used for bear locations (Table 1). We updated cover-type maps for 1986-88 with data on timber harvests provided by the landowners. We used random points to estimate available habitat because we also could record habitat edges within 200 m of random points (Marcum and Loftsgaarden 1980). For Spectacle Pond South, we compared availability of forest types estimated with random points versus availability measured with a digitizing area-line meter, and these

Table 1. Classification of habitats for 3 study areas in Maine, 1986-88.

Study area	Habitat	% Canopy cover ^a	Overstory characteristics
Spectacle Pond	Hardwood	> 25	> 50% hardwood species
	Softwood	> 25	$\geq 50\%$ softwood species
	Open forest	≤ 25	Clearcuts and heavy partial cuts
Stacyville and Bradford	Hardwood	> 15	> 50% hardwood species
	Softwood	> 15	$\geq 50\%$ softwood species
	Open forest	≤ 15	Clearcuts
	Bog	≤ 15	Sparse tamarack or black spruce

^a Classification of habitats differed among areas because 1 observer classified habitat at Spectacle Pond and a different observer classified habitat at Stacyville and Bradford.

methods yielded similar data (Schooley 1990:33-34).

Cover-type maps or low-altitude aerial photographs were not available for the Bradford core area (238 km²), so we quantified available habitat using Landsat Thematic Mapper (TM) data from June 1987. Thirty-two training sites were identified from black-and-white aerial photographs (1:80,000 scale) and then investigated by small aircraft and field verified. We identified training sites on the computer display screen by creating a false-color infrared simulation (TM3 = blue, TM4 = red, TM5 = green), which highlighted characteristics of broad forest classes. We then used a supervised classification (Jensen 1986:178-214, Sader 1989) to classify habitat in the core area based on training sites. We compared known locations of habitats, other than training sites, with habitats classified on the satellite image until we were confident that the supervised classification was correctly identifying our broad habitat classes. We did not have the capabilities to quantitatively evaluate accuracy on a pixel-level scale (e.g., $> 90\%$ pixels correctly classified), but we believe that there was no systematic bias in the classification that could have strongly influenced our analysis. Image processing was performed with the personal computer version of Earth Resources Laboratory Application Software (ELAS; Graham *et al.* 1980). We calculated the area of each habitat within the core area with a module in ELAS that sums the number of pixels (900-m² squares) of each habitat.

We defined seasons as summer (den emergence-31

Aug) and fall (1 Sep-den entry) based on plant phenology and diet of black bears in Maine (Hugie 1982:90-95, MDIFW unpubl. data). We compared habitat use versus availability during fall, within core areas, by combining habitat-use data across individuals (Design 2 of Thomas and Taylor 1990). We attempted to locate all individuals on each flight, so our results were not biased by unequal monitoring of individuals. We constructed Bonferroni simultaneous confidence intervals (Spectacle Pond North and South: Marcum and Loftsgaarden 1980; Bradford: Neu et al. 1974, Byers et al. 1984), which maintained experiment-wise error rates of 0.10. We excluded from analysis uncommon nonforested habitats (<3% of area), which were used infrequently (≤ 1 location/year), to increase power to detect selection (Allredge and Ratti 1986). Excluded habitats were bogs and open water at Spectacle Pond North and South; and agriculture, urban areas, and open water at Bradford. We used Chi-square tests for homogeneity to compare other frequency distributions, and Bonferroni intervals to compare >2 proportions (Marcum and Loftsgaarden 1980).

During fall at Spectacle Pond, we conducted qualitative mast surveys to compare relative abundances of beechnut crops among years. Beechnut crops were different enough among years that ocular estimates were sufficient for classifying crops as scarce or abundant (e.g., Rogers 1976).

Movements

For female bears ≥ 2 years old, we delineated summer ranges with the minimum convex polygon model (Hayne 1949). We did not model movements of yearlings because normally they are not independent of their mothers until mid-summer (Rogers 1987). Observation-area curves (Odum and Kuenzler 1955) indicated ≥ 18 locations were usually sufficient to delineate summer ranges (Schooley 1990:98-102). As an index to fall movements for each bear, we measured the greatest distance between a fall location and a boundary of the summer range. Bears killed during the fall hunting season before mid-October were excluded from analyses. We considered several long movements by bears that began in late August as fall locations. We compared maximum distances moved by bears among study areas, years, and age classes with analysis of variance (ANOVA) and Tukey multiple comparisons on rank-transformed data (Conover and Iman 1981, Zar 1984:199-201). For analysis of age classes, we classified bears ≥ 7 years old as adults and bears ≤ 3 years old as subadults. We classified bears 4 to 6 years

old based on known reproductive histories (i.e., adults had previously produced a litter).

Pooling data for all bears, we plotted the distribution of maximum distance moved during fall and then defined any movement greater than the seventy-fifth percentile as a long movement. We examined the direction, destination, and timing of long movements by bears to determine whether they provided insight into importance of food resources. We also compared the den locations of bears relative to boundaries of summer ranges to determine whether fall movements influenced location of den sites.

RESULTS

During fall from 1986 to 1988, we monitored 49 female bears at Spectacle Pond, 9 at Stacyville, and 24 at Bradford. At Spectacle Pond, we monitored 47% of the bears for 1 year, 16% for 2 years, and 37% for 3 years. At Bradford, we monitored 46% of the bears for 1 year, 17% for 2 years, and 37% for 3 years. At Stacyville, 6 of 9 bears were monitored for all 3 years.

At Spectacle Pond, beechnuts were relatively abundant in 1986 and 1988, but scarce in 1987. Even when nut crops were abundant, production was not consistent among stands, so availability varied spatially.

Habitat Use

Spectacle Pond.—We examined use of 3 forest types (Table 1), which had different availabilities in Spectacle Pond North and South (1986: $\chi^2 = 35.2$, 2 df, $P < 0.001$; 1987: $\chi^2 = 27.4$, 2 df, $P < 0.001$; 1988: $\chi^2 = 26.3$, 2 df, $P < 0.001$), so separate analyses for these areas were justified. Habitat use during fall differed among years at Spectacle Pond North ($\chi^2 = 35.8$, 4 df, $P < 0.001$) and South ($\chi^2 = 67.5$, 4 df, $P < 0.001$), so we examined habitat selection separately for each year (Table 2). In both areas, female black bears used hardwood stands more than expected in 1986 and 1988, but not in 1987. Bears used softwoods more than expected in 1987, but not in other years. Open forest was used less than expected, or as expected, in both areas during all years. Beech was a dominant species in 1988 at 84% of bear locations within hardwoods at Spectacle Pond North ($n = 187$) and at 90% of bear locations within hardwoods at Spectacle Pond South ($n = 137$).

The proportion of bear locations ≤ 200 m from rivers or streams was greater during 1987 than other years at Spectacle Pond North (1986: 19%, $n = 51$; 1987: 65%, $n = 72$; 1988: 16%, $n = 261$) and Spectacle Pond South (1986: 13%, $n = 169$; 1987:

Table 2. Availability and use (%) of habitats by female black bears (≥ 1 yr old) during fall (1 Sep-den entry) in Maine, 1986-88.

Study area	Year	<i>n</i>		Hardwood		Softwood		Open forest		Bog	
		Bears	Locations	Use ^a	Available	Use	Available	Use	Available	Use	Available
Spectacle Pond	1986	10	51	76.5 ⁺	62.6	23.5	30.7	0.0	6.7		
North	1987	9	72	36.1 ⁻	62.6	56.9 ⁺	30.3	6.9	7.1		
	1988	17	261	71.7 ⁺	61.2	25.7	29.9	2.7	8.9		
Spectacle Pond	1986	22	169	87.0 ⁺	51.4	12.4 ⁻	46.7	0.6	1.8		
South	1987	13	80	38.8	50.8	61.3 ⁺	45.7	0.0 ⁻	3.5		
	1988	16	182	75.3 ⁺	50.8	24.2 ⁻	44.7	0.6 ⁻	4.5		
Stacyville	1986	7	71	63.4		35.2		1.4		0.0	
	1987	8	96	33.3		62.5		1.0		3.1	
	1988	8	85	73.3		24.4		1.2		1.2	
Bradford	1986-1988	22	288	38.2	38.3	54.5	51.3	2.8 ⁻	6.3	4.5	4.2

^a Habitat selection based on Bonferroni simultaneous confidence intervals where + indicates use > availability, and - indicates use < availability ($P < 0.10$). Selection was not investigated in Stacyville.

44%, $n = 80$; 1988: 16%, $n = 182$). However, bears also used softwoods more in 1987 than other years (Table 2), and softwoods were common along drainages. To determine if habitat selection by bears in 1987 reflected use of riparian areas or simply use of softwoods, we separated habitat use of forest types into riparian and nonriparian (Table 3). In both areas, bears used softwood-riparian habitat more than expected but used softwood-nonriparian as expected. Bears also used hardwood-riparian as expected but used hardwood-nonriparian less than expected. Bears may have been foraging on beaked hazelnuts (*Corylus cornuta*), which grew along rivers and streams, or possibly on herbaceous plants, which we often observed in feces during September in other years when mast crops failed.

Stacyville.—Annual patterns of habitat use for bears at Stacyville were similar to patterns for bears at Spectacle Pond North and South (Table 2). Bears at Stacyville were located in hardwood stands more in 1986 and 1988 than during 1987 ($P < 0.05$). In contrast to Spectacle Pond, bears were not located ≤ 200 m from rivers or streams more during 1987 than other years (1986: 11%, $n = 71$; 1987: 6%, $n = 96$; 1988: 4%, $n = 86$). However, bears were located ≤ 200 m from agricultural fields more ($P < 0.05$)

during 1987 (25%) than 1986 (10%) and 1988 (4%). This pattern suggests that bears probably were eating crops at night more in 1987 than other years. Increased use of agricultural crops by bears during years of mast failure has been reported elsewhere (Rogers 1976, Elowe and Dodge 1989, Kane 1989:14).

Bradford.—We examined habitat selection of 3 forest

Table 3. Availability and use (%) of riparian habitat by female black bears (≥ 1 yr old) during fall (1 Sep-den entry) in Spectacle Pond study areas, Maine, 1987. Riparian indicates that locations were ≤ 200 m from a river or stream.

Habitat	Spectacle Pond North ^a		Spectacle Pond South ^b	
	Use ^c	Available	Use	Available
Softwood-riparian	43.1 ⁺	17.7	30.0 ⁺	17.0
Softwood	13.9	12.6	31.0	28.7
Hardwood-riparian	22.2	13.8	13.8	6.1
Hardwood	13.9 ⁻	48.8	25.0 ⁻	44.7

^a Use = 72 bear locations; available = 492 random locations.

^b Use = 80 bear locations; available = 488 random locations.

^c Selection based on Bonferroni simultaneous confidence intervals where + indicates use > availability, and - indicates use < availability ($P < 0.10$).

Open forest was not used for analysis.

types and open bogs at Bradford (Table 2). Use of these habitats by bears did not differ among years ($\chi^2 = 6.2$, 6 df, $P = 0.402$), so we pooled years to increase power to detect selection. Open forest was used less than expected and other habitats were used as expected (Table 2). Although hardwoods and softwoods were used as expected, habitat selection likely occurred, but on a finer scale than the broad habitats that we measured. Also, 3 females in 1988 responded to abundant beechnuts outside of the Bradford study area by moving long distances to the resource. These 3 bears were excluded from analysis of habitat selection.

Fall Movements

Sample sizes were sufficient only at Spectacle Pond to compare maximum fall movements between subadults and adults. The distance moved by bears was not affected by age class or year, and there was no age class-year interaction (Table 4). Although differences between age classes were not significant, movements by subadults (median = 1.60 km, $n = 29$ bear-years) were longer than movements by adults (median = 0.98 km, $n = 23$).

We pooled data for age classes and compared maximum distances moved among study areas and years. Movements differed among study areas, but there was no year effect or study area-year interaction (Table 4). Female bears at Stacyville traveled farther than bears in other areas (Table 5), but only differences

Table 4. Results of 2 ANOVA's on rank-transformed data that tested for factors affecting the maximum movements of female black bears (≥ 2 yrs old) away from summer ranges^a during fall (1 Sep-den entry) in Maine, 1986-88. We used data for the Spectacle Pond Study area in the first model, and data for all 3 study areas in the second model.

Source of variation	Sum of squares	df	F	P
Age class	773.3	1	3.42	0.07
Year	487.5	2	1.08	0.35
Age class x year	11.1	2	0.02	0.98
Error	10388.8	46		
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Area	6684.7	2	4.26	0.02
Year	2622.5	2	1.67	0.19
Area x year	1305.6	4	0.42	0.80
Error	70630.4	90		

^a Den emergence-31 Aug using the minimum convex polygon model.

between Stacyville and Bradford were significant ($P < 0.05$). Fewer subadults were sampled at Stacyville (21.1%) than at Spectacle Pond (55.8%) and Bradford (32.1%). Therefore, greater distances traveled by bears at Stacyville reflected an effect of location and not a sample biased towards subadults.

The seventy-fifth percentile of maximum distance moved for all bears was 7.2 km (Table 5). Bears at Stacyville made long movements (> 7.2 km) more than bears in other areas, although we did not test this because of small sample sizes within years. At Stacyville, 53% of fall movements were > 7.2 km (range 7.7-55.1 km), compared to 21% at Spectacle Pond (range 15.3-41.3 km), and 14% at Bradford (range 13.5-78.6 km). Combining data for all bears, 5 (25%) of 20 movements by adults with cubs were > 7.2 km, compared with 6 (19%) of 31 movements by adults without cubs.

At Spectacle Pond, bears in all years traveled primarily to areas dominated by northern hardwoods. With the exception of 1 bear in 1987 that was infrequently located in hardwoods, 53 (76%) of 69 locations of bears were in hardwoods during long movements. At Stacyville, long movements in 1986 and 1988 ($n = 8$) were northwest or southwest to areas of higher elevation, and 37 (77%) of 48 locations were in hardwoods. In contrast, no bears in 1987 made long movements west, but 2 bears moved long distances northeast near agricultural fields. At Spectacle Pond and Stacyville, long movements in 1987 occurred primarily during September, whereas long movements in 1986 and 1988 extended into October and November. At Bradford, 3 adults made extremely long movements in 1988 (50.2-78.6 km) out of the study area to a mountainous area where beechnuts were abundant. Eighty percent of the locations ($n = 44$) of these 3 bears were in hardwood stands during these movements, which lasted from late August into

Table 5. Maximum movements of female black bears (≥ 2 yrs old) away from summer ranges^a during fall (1 Sep-den entry) at 3 study areas in Maine, 1986-88.

Study area	No. bear-years	Maximum movement (km)	
		Median	Upper and lower quartiles
Spectacle Pond	52	1.3	(0.5- 5.0)
Stacyville	19	7.3	(0.7-19.4)
Bradford	28	0.9	(0.4- 2.4)
All bears	99	1.3	(0.5- 7.2)

^a Den emergence-31 Aug using the minimum convex polygon model.

November.

Despite extensive movements by some females during fall, 84 (93%) of 90 winter dens of bears were within or near (≤ 1.0 km) their summer range (Table 6). Bears that made long movements were no more likely to den outside of summer ranges than other bears ($\chi^2 = 0.85$, 1 df, $P = 0.358$). For the 6 dens > 1.0 km outside the boundaries of summer ranges, distances from dens to boundaries ranged from 1.5 to 8.0 km.

DISCUSSION

Our study demonstrated pronounced annual variation in habitat use by black bears during fall at 2 of our 3 study areas. Patterns of habitat selection at the Spectacle Pond study areas also varied among years during spring and summer (Schooley 1990:109-110). Annual variation in resource use by black bears might be expected in many areas. Black bears are omnivores with diets that generally include fruits, especially during summer and fall (Landers et al. 1979, Pelton 1982, Eagle and Pelton 1983). Fruit-producing plants may exhibit mast seeding, which is the periodic synchronous production of large seed crops (Nilsson and Wastljung 1987). In most studies of habitat selection by black bears, however, researchers have combined data from several years (e.g., Lindzey and Meslow 1977, Hugie 1982, Novick and Stewart 1982, Elowe 1984, Young and Beecham 1986, Unsworth et al. 1989, Hellgren et al. 1991). Pooling data across years may mask important patterns and potentially provide an inaccurate picture of resource use by bears.

Although we conducted mast surveys only at Spectacle Pond, patterns of habitat use indicated bears at Spectacle Pond and Stacyville responded to annual variation in beechnut abundance. These responses were not surprising because beech was the primary mast producer in both areas, and Hugie (1982:91) reported beechnuts were the most common food remains in feces

of bears during fall at Spectacle Pond. Beechnuts contain more fat than herbaceous plants typically available to bears during fall (Elowe and Dodge 1989), and beechnuts are comparable to acorns (*Quercus* spp.) in metabolizable energy, higher in crude protein, and lower in total phenols (Servello and Kirkpatrick 1987). Compared to the 2 northern study areas, bears at Bradford used habitat more consistently among years. Beech trees were less common at Bradford, and other fall foods, such as feral apples and acorns, were available to some bears.

Differences in movement patterns among study areas reflected distribution of available food (Amstrup and Beecham 1976, Garshelis and Pelton 1981, Pelchat and Ruff 1986). At Spectacle Pond, northern hardwoods were most common on ridges, which were distributed relatively evenly throughout the area, at least compared with Stacyville. During years when beechnuts were abundant, most bears probably could exploit nut-producing stands without moving long distances. It is not clear why fall movements at Spectacle Pond did not increase when mast seemed scarce in 1987. Beech masting may be synchronized over such a large area that bears can recognize widespread mast failures by assessing conditions within or near their summer ranges. At Spectacle Pond, there was no other concentrated food source during late fall to induce bears to leave their ranges. The proportion of black bears traveling outside ranges in northeastern Minnesota also did not differ among years when mast was abundant or scarce (Rogers 1987), whereas Garshelis and Pelton (1981) suggested availability of acorns may affect the frequency of home range shifts during fall by bears in the Great Smoky Mountains National Park.

At Stacyville, northern hardwoods were most common in the western section of the study area, but summer ranges of monitored bears were located in the eastern section. This dichotomy caused some bears to move relatively long distances to exploit the beechnut resource in 1986 and 1988. There probably were bears that we did not monitor with summer ranges in the western section of Stacyville. It is unknown whether these individuals moved long distances during fall. Our inferences apply only to the bears that we sampled. Forty percent of female bears in northeastern Minnesota traveled > 7 km outside of their usual range during late summer and fall (Rogers 1987), which is most similar to frequencies at Stacyville in our study. Food resources in Rogers' (1987) study area also were unevenly distributed, and most bears traveled to an area where fruit and nuts were abundant.

Fall movements by bears at Bradford were relatively

Table 6. Proportion of winter dens of female black bears (≥ 2 yrs old) within and outside boundaries of summer ranges^a, Maine, 1986-88.

Study area	No. bear-years	Within boundaries	Outside boundaries	
			≤ 1.0 km	> 1.0 km
Spectacle Pond	48	0.79	0.10	0.10
Stacyville	17	0.41	0.53	0.06
Bradford	25	0.84	0.16	0.00

^a Den emergence-31 Aug using minimum convex polygon model.

short with the exception of 3 adults in 1988. It is unclear what prompted these bears to move such great distances in 1988, and how they were able to locate the same productive mast area. Klenner (1987) observed few extra-range excursions by female black bears in an agriculture-forest ecotone in Manitoba and suggested bears were able to obtain required resources without foraging far from their home ranges.

Although distribution of food resources probably had the greatest effect on fall movements by female bears, other factors may affect movements. Garshelis and Pelton (1981) suggested dominant males may exclude other bears from preferred feeding areas during fall. Because males were not radiotracked in our study, we could not determine whether intersexual competition influenced movements of females. Age or reproductive status potentially could influence movements, but we detected no significant differences between subadults and adults, and evidently movements of adult females with cubs are not restricted during fall (Rogers 1987). Amstrup and Beecham (1976) and Meddleton (1989:32) reported bears sometimes leave areas with available food and suggested such exploratory movements might provide information about future food sources. That hypothesis seems plausible for short excursions, but it seems unlikely that bears would move long distances if food was available near their range. Elowe (1984:80) indicated much individual variation occurred in behavior of bears, and some individuals may make long movements independent of physiological needs.

Bears may learn of productive mast areas as cubs when they accompany their mothers during foraging movements (Garshelis and Pelton 1981, Rogers 1987). In 1986, an adult female (F319) from Stacyville left her summer range during fall and foraged 27 km northwest in an area dominated by northern hardwoods. F319 was accompanied by a female cub (F740). In 1987, neither F319 nor F740 made a long movement during fall. In 1988, F319 and F740 (then 2 yrs old) separately traveled long distances (>19.5 km) northwest to hardwood-dominated ridges. Movements by these 2 bears were in the same direction but not to the same forest stand, as was reported for mother-offspring pairs by Garshelis and Pelton (1981) and Rogers (1987). Summer ranges of F319 and F740 overlapped considerably. However, F740 left her summer range several weeks before her mother (F319) in 1988, suggesting F740 was not simply following her mother but was relying upon knowledge gained as a cub.

Most bears returned to their summer ranges to den regardless of fall movements. Similar behavior by

female black bears has been reported elsewhere (Fuller and Keith 1980, Tietje and Ruff 1980, Lecount 1983, Kolenosky and Strathearn 1987, Rogers 1987, Klenner and Kroeker 1990). It probably is beneficial for females to den in familiar areas so they can efficiently exploit resources after emerging from dens in spring. This behavior may be especially important for pregnant females whose movements may be restricted near den areas in spring (Lindzey and Meslow 1976, Kolenosky and Strathearn 1987).

MANAGEMENT IMPLICATIONS

Foraging behavior of black bears is flexible in response to distribution of food resources. Short-term studies from 1 area will likely produce inferences applicable only to a subset of habitat conditions that black bears may experience in a region. Such studies may underestimate spatial needs of bears and provide a limited view of habitat selection, which may vary spatially and temporally.

In this study, annual patterns of habitat use suggested beechnuts were an important food resource for bears during fall. This conclusion is supported by the long movements that bears made to northern hardwood forests, and by their delayed den entry during years with abundant beechnuts (Schooley et al. 1994). However, information on habitat selection can not be used by itself to identify habitat requirements. Habitat use may not reflect habitat quality in some situations (Van Horne 1983, Hobbs and Hanley 1990). Although the mechanisms relating resource use to population dynamics (Hobbs and Hanley 1990) are not completely understood for black bears, previous studies have correlated reproduction and cub survival of black bears with availability of berries and nuts (Rogers 1976, 1987; Eiler et al. 1989; Elowe and Dodge 1989). At Spectacle Pond, reproductive synchrony of females is greater than has been reported for other populations of black bears. From 1982 to 1991, females ≥ 4 years old produced 73 (94.8%) of 77 litters after falls when beechnuts were abundant (MDIFW, unpubl. data). Therefore, our current understanding of the importance of beechnuts to bears is restricted to correlations of mast availability with bear behavior and reproductive success. Managers often must make decisions when many questions remain unanswered, however, so we provide the following recommendations for habitat management.

It is essential to retain mature beech trees to maintain mast production in northern hardwood forests. Beech usually does not produce seed until 40 years old, and

may not produce large quantities until 60 years old (Fowells 1965:173). If northern hardwood stands are to be harvested, we recommend uneven-age management and retention of beech trees that are resistant to beech bark disease. Mature susceptible trees also should be retained if they have vigorous crowns, because they may continue to produce mast (D.R. Houston, U.S. For. Serv., pers. commun.). Northern hardwood stands may be used by female bears with summer ranges ≤ 78 km away, and the value of an individual stand depends on the distribution and quality of other hardwood stands in a region. Thus, a stand containing beech should be managed within the context of the surrounding landscape and not as an isolated, local resource. Habitat management on a landscape scale will be a challenge in Maine because 96% of the timberland is privately owned, with 47% owned by the forest industry (Brooks et al. 1986:15).

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