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Ecology of black bears in a bottomland hardwood forest in Arkansas

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To the Graduate Council:

I am submitting herewith a dissertation written by Tommy Ray Smith entitled "Ecology of black bears in a bottomland hardwood forest in Arkansas." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology.

Michael R. Pelton, Major Professor

We have read this dissertation and recommend its acceptance:

Accepted for the Council:

Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

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We have read this dissertation
and recommend its acceptance:

Arthur C. Echternacht

Gary F. McCracken

Ralph W. Dimmick

Accepted for the Council:

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Vice Provost
and Dean of The Graduate School

ECOLOGY OF BLACK BEARS IN A BOTTOMLAND HARDWOOD FOREST IN ARKANSAS

A Dissertation
Presented for the
Doctor of Philosophy
Degree
The University of Tennessee, Knoxville

Tommy R. Smith
August 1985

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ABSTRACT

Population characteristics, growth patterns, reproduction, mortality, food habits, denning, movements, and habitat use of black bears in bottomland hardwood forest were studied on White River National Wildlife Refuge in eastern Arkansas from June 1979 to May 1982. A total of 51 bears was captured 64 times, and 2104 telemetry locations of 28 radio-instrumented bears were obtained. Estimates of population size and density on the 457 km^2 Refuge were 130 bears and 1 bear/4.5 km^2, respectively. The genetically effective number of bears in the lower White River basin was estimated to be 53 to 130, indicating that the long-term fitness of this closed population is precarious. The composite ratio of males to females in the capture sample was 1.56:1; it did not differ significantly from 1:1 ($P<0.05$). Capture data suggested a stable age structure, and that females, which reached 14 years of age, were longer-lived than males. Growth was curvilinear in both sexes. Males attained peak body weight by 5 years of age, but females added weight until 9 or 10 years old. Mean weight of adult males (102 kg) was twice that of adult females (52 kg). Approximately one-third of the females successfully bred as 3-year-olds, and all had produced cubs by 6 years of age. All males appeared to be sexually mature by 4 years of age. Mean breeding interval of radio-collared females was 2.4 years. Most litters were born in early February, and mean litter size was 2.3 cubs. Mean annual cub mortality was 32 percent. Annual mortality rate of radio-collared bears $\geq$ 1 year old was approximately 5 percent. In spring, herbage predominated in the

the diet. Soft fruit was the staple summer food, but substantial amounts of animal matter also were consumed. In fall/winter bears relied on acorns. Den entry occurred in 40 of 42 bear-winters. Pregnant females denned earlier ($\bar{X}$ = 15 Dec) and longer ($\bar{X}$ = 134 days) than other cohorts. Two subadult males did not den in 1 winter. Females utilized elevated tree dens exclusively, apparently to enhance reproductive success in seasonally flooded bottomland forest. Males denned in trees and ground nests at similar frequencies. Dormancy behaviors of black bears in Arkansas were consistent with those in other geographic regions. Mean annual home range of males was 128 km^2 (range = 26-266 km^2) compared to 12 km^2 (range = 7-22 km^2) for females. Seasonal ranges were related to food availability and were larger in summer than in fall or spring. No radio-collared bears dispersed from the Refuge. Habitat use followed phenological development. Diverse habitats were preferred in spring and summer, but homogeneous oak stands were utilized in fall/winter. Swamps were important in all seasons, apparently for cover.

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CHAPTER I

INTRODUCTION

Black bears (_Ursus_ _americanus_) evolved from small, carnivorous, tree-climbing miacid mammals of the Oligocene epoch, and by mid-Pleistocene had dispersed from Eurasia to the Nearctic region (Kurten and Anderson 1980). Unlike brown bears (_Ursus_ _arctos_), which later immigrated to this continent adapted to open habitats created by glaciation, black bears retained an affinity to forests, and their primitive range eventually included all forested areas of North America (Hall 1981).

Apparently due to their wide distribution and anthropomorphic characteristics, black bears were well-known in aboriginal and colonial civilizations where they assumed both cultural and biological significance. Native North Americans relied on this species for sustenance (Malone 1922), but utilized it symbolically as well, and apparently they had little, if any, impact on its distribution or abundance. Later, however, as white civilizations expanded, forest habitats were altered, and black pear populations were over-exploited. Despite their adaptability to a variety of environmental conditions and relative tolerance of human encroachment, black bears required large, forested areas to maintain viable populations, and the distribution of this species steadily declined through the 19th and 20th centuries.

Large populations of black bears continue to occur where densely forested, relatively remote areas exist in Alaska, Alberta, British Columbia, Idaho, Maine, Michigan, Oregon, Pennsylvania, Washington, and Wisconsin (Cowan 1972). However, in those portions of North America where urbanization and especially agricultural development have largely replaced forests, the species has been extirpated or persists in small isolated populations on protected public land or in remote mountains and swamps.

The impact of human settlement and loss of forested habitats on black bears has been greatest in the southeastern United States. Based on a recent map of the distribution of black bears in eastern North America (Maehr 1984), this species occupies only 5 to 10 percent of its former range in the southeastern United States. Populations have been estimated at less than 1500 in 12 of the 13 states in this region where black bears still occur. Seven states apparently have populations of fewer than 500 individuals (Cowan 1972).

In the coastal plain of southeastern North America, agriculture and timber industries have focused attention on the rich floodplains of major river systems, and habitats occurring in these areas, particularly bottomland hardwood forests, have been dramatically modified (Wharton et al. 1982). Losses have been particularly high in the alluvial plain of the Mississippi River. In 1937, 11.8 million acres (4.8 million ha), or roughly half, of the original acreage of bottomland hardwood forest remained in this valley; by 1977 this had been reduced to 5.2 million acres (2.1 million ha), and given current trends, bottomland hardwood forest acreage in the Mississippi River floodplain will decrease to less than 4 million acres (1.6 million ha) by 1995 (McDonald et al. 1979).

Among temperate forests, the bottomland hardwood forest is one of the most productive (Conner and Day 1976). Apparently, dense populations of black bears once occurred in the 3.6 million ha of this habitat originally occurring in the lower Mississippi River delta. Natives relied on bears for oil, meat, and clothing (Le Page du Pratz _in_ Tregle 1975, Malone 1922), and accounts during early settlement of the region indicated that black bears were especially abundant in the bottomlands of Louisiana, Mississippi, and Arkansas (Roosevelt _in_ Schullery 1983, McKinley 1962); Arkansas was once unofficially known as the "bear state" (Sealander 1979).

The 2 million acres (809,000 ha) or so of bottomland hardwood forest which remain in the lower Mississippi River valley are being continually subdivided and reduced (Spencer 1981), and few large tracts of this habitat exist today. Those which have persisted were at one time heavily exploited, and it is not surprising that the black bear has been largely eliminated from this area of its former range. An exception is the White River National Wildlife Refuge (Refuge) which encompasses 113,000 acres (45,731 ha) along the lower White River in eastern Arkansas. Unique as the largest publicly owned tract of bottomland hardwood forest in the Lower Mississippi River valley, this area has even greater significance due to the remnant black bear population which has survived there, essentially unnoticed.

In most areas of North America where relatively large populations of black bears remain, the species has been intensively studied, primarily due to its value as a game animal. Documentation of the population ecology of black bears has been made in Alberta (Young and Ruff 1982, Kemp 1976), Arizona (LeCount 1982, 1983), California (Graber 1982, Piekelek and Burton 1975), Idaho (Beecham 1983, Reynolds and Beecham 1980), Maine (Hugie 1982), Michigan (Erickson et al. 1964), Minnesota (Rogers 1977), Montana (Jonkel and Cowan 1971), North Carolina (Hamilton 1978, Landers et al. 1979, Collins 1974), Pennsylvania (Alt 1977, 1982, Alt et al. 1980), Tennessee (Garshelis and Pelton 1981, Johnson and Pelton 1980b, Beeman 1975), Virginia (Raybourne 1976, Stickley 1961), and Washington (Lindzey and Meslow 1976a, 1976b, 1977a, 1977b, Poelker and Hartwell 1973). These studies and others have demonstrated that black bears are extreme generalists, sensitive to the vicissitudes of nature but adaptable to many ecological situations, a model K-selected species.

Research also has shown that behaviors of black bears are relatively uniform across the species' range, but variations observed in the dynamics of different populations and the complex interactions which occur between population structure and resource availability preclude applications of data from one population to management of another. Bottomland hardwoods habitat is particularly distinct due to periodic flooding which may be a major selective force on black bears.

Little is known and less is documented of the ecology of black bears in bottomland hardwood forests and other wetland habitats.

Hamilton (1978) and Landers et al. (1979) reported on a population in the coastal plain of North Carolina where hardwood swamps and Carolina bays constituted 14 and 42 percent, respectively, of the study area. This coastal habitat type is distinctly different, however, from bottomland hardwood forests of the Mississippi River floodplain. Taylor (1971) gathered limited information on the movements and denning of 6 black bears in Louisiana bottomlands, 4 of which had been relocated to Louisiana from Minnesota. Maehr and Brady's (1984) report on food habits of Florida black bears included samples from cypress swamps.

Given the precarious status of bottomland hardwood forests and the paucity of knowledge of the ecology of black bears in this unique habitat type, the situation on White River National Wildlife Refuge (NWR) provided an opportunity to not only add to our knowledge of the natural history of black bears, but also to contribute to our understanding of bottomland hardwood forest ecology, a primary concern of contemporary natural resource management (Wharton et al. 1982, McDonald et al. 1979, Frederickson 1978, 1980, Forsythe and Gard 1980).

Specific objectives of this study were:

1. To estimate density and sex and age structure of the black bear population on the Refuge.
2. To establish an index of relative density for monitoring gross trends in the Refuge population.
3. To delineate important aspects of the reproductive biology of this species in bottomland hardwood forest, e.g., age of

sexual maturity, mating season, breeding interval of females, and litter size.

4. To identify mortality factors and estimate survival rates.
5. To describe food habits and feeding behaviors of black bears in bottomland hardwood forest.
6. To delineate the denning ecology of black bears on the Refuge, i.e., define denning chronology and describe den characteristics and dormancy behaviors.
7. To estimate home range, identify patterns of seasonal distribution, and determine the effects of habitat components on these movement parameters.

CHAPTER II

THE STUDY AREA

General Description

White River NWR encompasses approximately 46,000 ha in Arkansas, Desha, Monroe, and Phillips counties in eastern Arkansas and extends for 87 km along the lower White River to within 10 km of its confluence with the Mississippi River (Figure 1). Bottomland hardwood forest predominates on the Refuge, covering more than 39,000 ha of its acreage. Interspersed within this forest are 4,000-6,000 ha of water including more than 160 lakes, cypress swamps and beaver impoundments, and many kilometers of bayous, sloughs, and seasonal streams. Similar, but privately owned, and more intensely managed (i.e., commercially harvested) bottomland forest remains along the White River 45-50 km North of the Refuge and 40 km south along the lower White and Mississippi rivers (Figure 2). No substantial tracts of forest remain to the east or west of the Refuge where the land is cultivated for soybeans, rice, cotton, and winter wheat.

Topography of the area is very subtle, and annual prolonged floods due to overflow of the White and Mississippi rivers are typical. Flooding generally occurs in late winter and early spring and may inundate as much as 85 percent of the Refuge for 1-4 months or longer (Figure 3). Characteristic of bottomland habitats (Wharton et al. 1982), water flow and sediment deposition during the flooding period determine the geomorphic, landform, and biotic features of the lower White River basin.

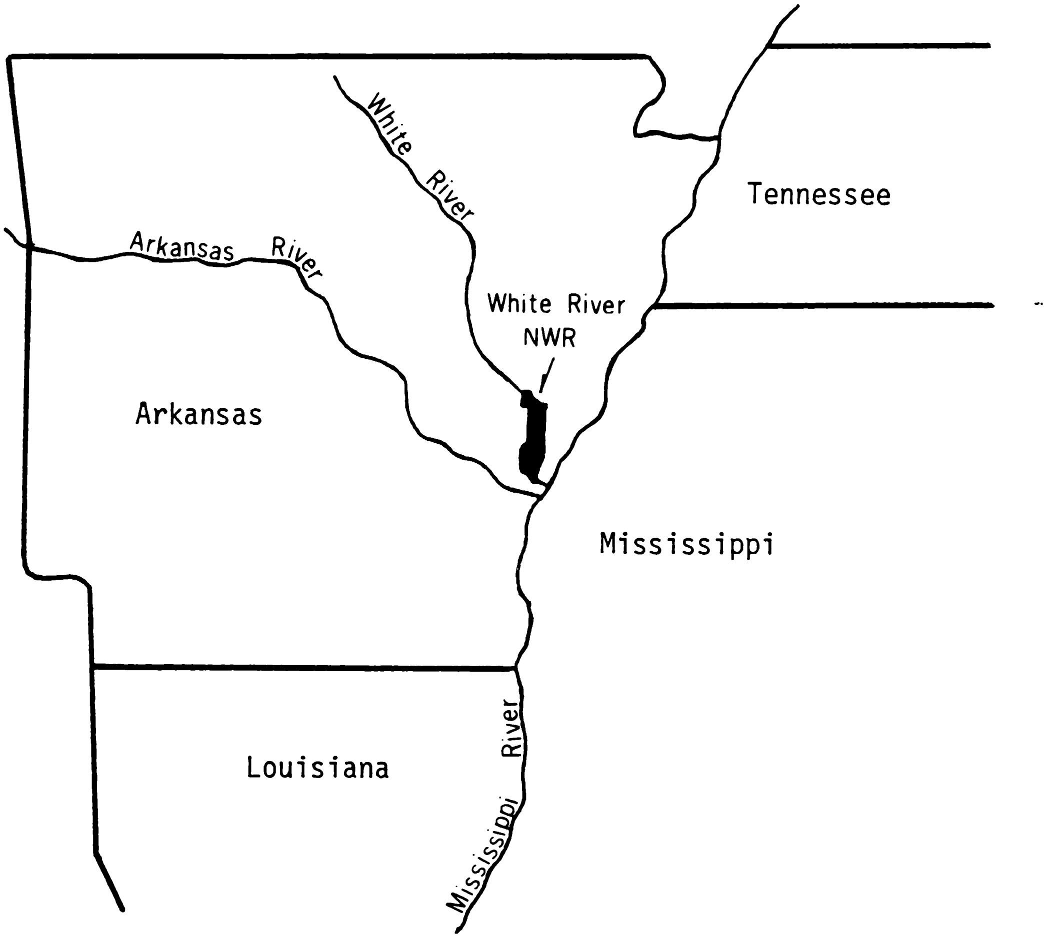


Figure 1. Location of White River National Wildlife Refuge (NWR) along the lower White River in eastern Arkansas.

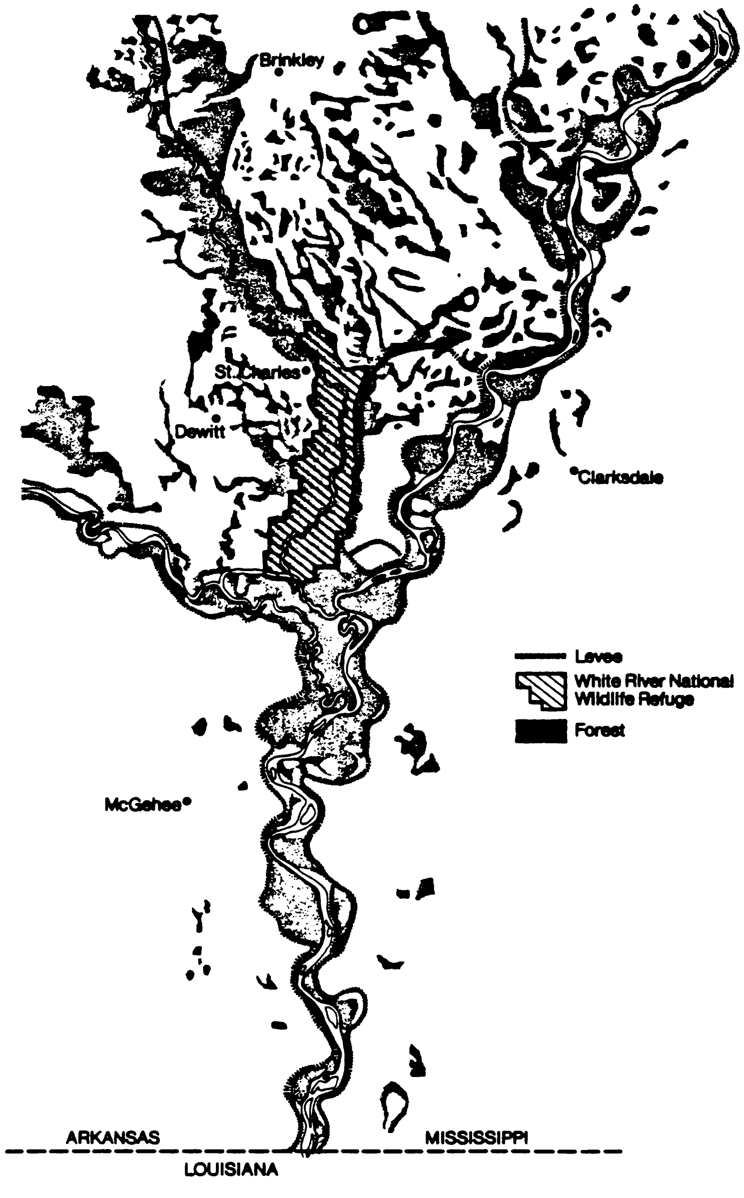


Figure 2. Distribution of bottomland hardwood forest in the vicinity of White River NWR in eastern Arkansas. (Taken from a map compiled by the U.S. Army Corps of Engineers in 1954.)

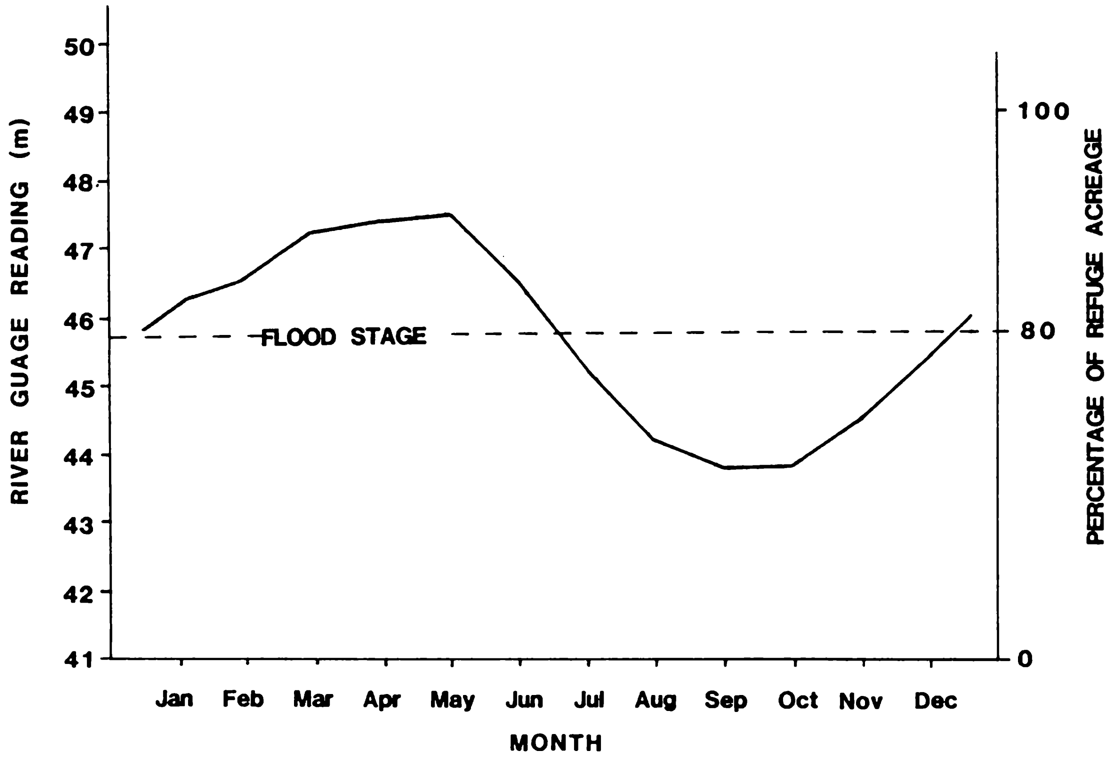


Figure 3. Mean monthly maximum stages of the White River at St. Charles, Arkansas, 1941-1980. (Unpublished data, U.S. Dep. Inter., Fish and Wildl. Serv., White River NWR, DeWitt, AR.)

The temperate climate of the area is characterized by hot humid summers, mild winters, and generally abundant rainfall. July is the hottest month and January the coldest (Figure 4). Seasonal temperatures range from a summer mean of 26.1°C to a winter mean of 7.8°C. Spring and fall mean temperatures are 18.3°C and 14.4°C, respectively (Reinhold 1969). Annual precipitation averages about 128 cm. Rainfall is common throughout the year, however, June-October is relatively dry and November-May relatively wet (Figure 5). Snow accumulation is uncommon, and when occurring rarely exceeds 15-20 cm or persists for more than a few days.

Topography and Soils

Elevation on the Refuge ranges from 41 m to 49 m above mean sea level. Approximately 60 percent of the acreage lies under 45 m, 20 percent between 45 m and 47 m, and the remainder above 47 m. Natural levees occur along the White River and its larger tributaries, and numerous parallel ridges and swales have been formed by the meanderings of major waterways during overflow.

Soil conditions, particularly depth and texture of the surface soils, are consequently greatly influenced by flooding, and interaction between elevation, overflow, and sedimentation has created a variety of soil conditions on the Refuge. In the northern third Dundee and Sharkey clays are overlain by relatively deep deposits of Dundee silt loam which is highly fertile, moderately acidic, and relatively well drained. Further down the floodplain, Sharkey clays lie below

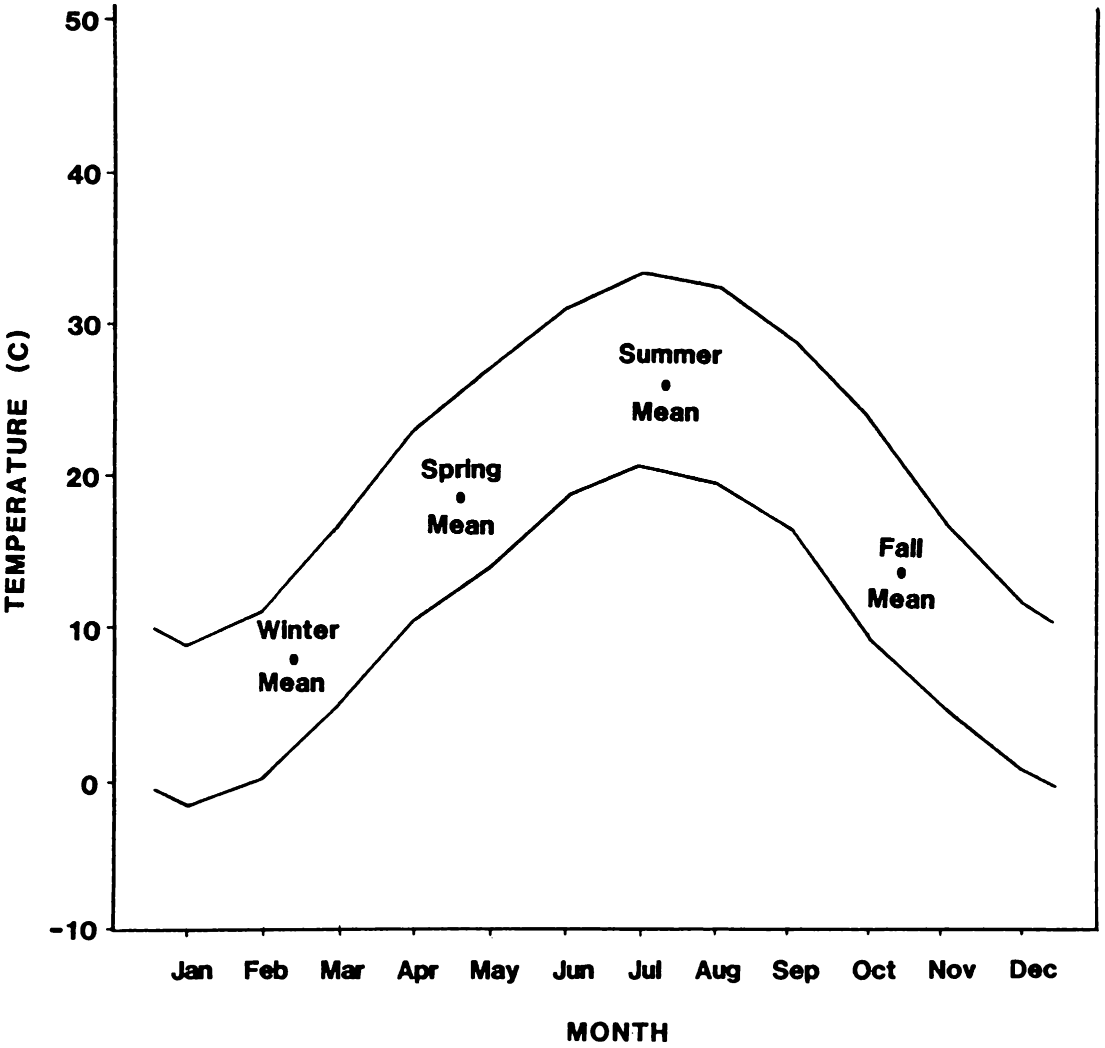


Figure 4. Mean monthly minimum and maximum temperatures on White River NWR, Arkansas, 1965-1980. (Unpublished annual narrative reports, U.S. Dep. Inter., Fish and Wildl. Serv., White River NWR, DeWitt, AR.)

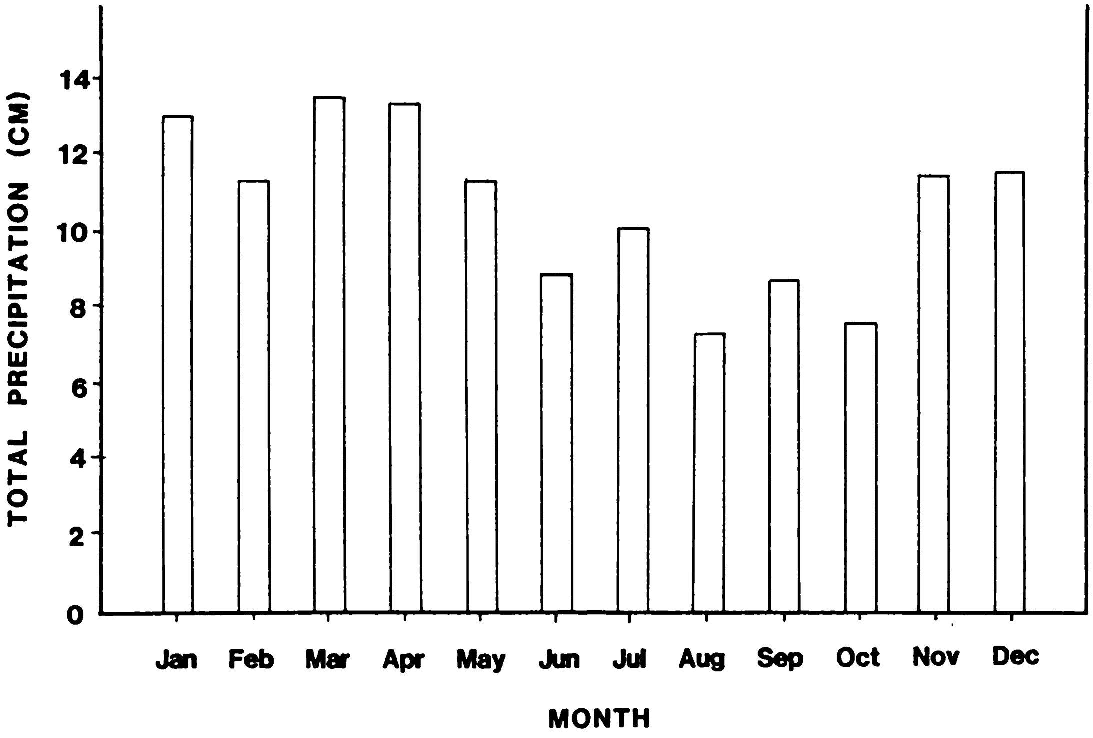


Figure 5. Mean monthly precipitation on White River NWR, Arkansas, 1938-1980. (Unpublished annual narrative reports, U.S. Dep. Inter., Fish and Wildl. Serv., White River NWR, DeWitt, AR.)

shallow layers of Acadia silty clay loam which is highly fertile but less acidic and well drained than Dundee loam. In the southern third of the Refuge soils are composed of Sharkey and Tunica clays, and aside from ridges associated with Scrubgrass and Honey Locust bayous in the eastern and western portions, respectively, of this area, surface loams are extremely shallow or nonexistent. Soils in this region of the Refuge are fertile, slightly acidic to mildly alkaline, and generally very poorly drained. These gradients in soil moisture, chemistry, and texture are reflected in the characteristics of plant and animal communities which occur throughout the Refuge.

Vegetation

Principle overstory species of the Refuge forest include overcup oak (*Quercus lyrata*), sugar hackberry (*Celtis laevigata*), Nuttall oak (*Q. nuttalli*), water hickory (*Carya aquatica*), green ash (*Fraxina pennsylvanica*), baldcypress (*Taxodium distichum*), common persimmon (*Diospyros virginiana*), sweetgum (*Liquidambar styraciflua*), honey locust (*Gleditsia triacanthos*), American elm (*Ulmus americana*), cedar elm (*U. crassifolia*), sweet pecan (*C. illinoensis*), sycamore (*Platanus occidentalis*), willow oak (*Q. phellos*), water oak (*Q. nigra*), black willow (*Salix nigra*), and several species of maple (*Acer*).

Forest acreage on the Refuge has been classified and inventoried by timber types (unpublished forest management plan, White River NWR, DeWitt, AR) (Table 1) which basically follow forest cover type classifications of the Society of American Foresters (SAF) (1954, 1980).

Table 1. Forest acreage on White River NWR, Arkansas.

Timber type[a]	Area (ha)	Percentage
Overcup oak-water hickory	22613	57.78
Oak-elm-ash[b]	6871	17.50
Hackberry-American elm-green ash[c]	5139	13.09
Nuttall oak-willow oak-sweetgum[d]	1833	4.67
White oak-red oak-hickory	767	1.95
Cypress[e]	564	1.44
Willow oak[f]	492	1.25
Sweetgum	267	0.68
Willow[g]	432	1.10
Cottonwood	194	0.49
Sycamore-pecan-American elm[h]	92	0.23
Loblolly pine	6	0.02
Totals	39270	100.0

[a] Taken from an unpublished forest management plan, White River NWR, DeWitt, AR.

[b] Not a recognized forest cover type (SAF 1980).

[c] Synonymous with sugarberry-American elm-green ash (SAF 1954, 1980) which will be used hereafter.

[d] Synonymous with sweetgum-Nuttall oak-willow oak (SAF 1954) and sweetgum-willow oak (SAF 1980). The former will be used hereafter.

[e] Synonymous with baldcypress (SAF 1954, 1980) which will be used hereafter.

[f] Not recognized as distinct forest cover types (SAF 1954, 1980). These are considered components of the sweetgum-Nuttall oak-willow oak type hereafter.

[g] Synonymous with black willow (SAF 1954, 1980) which will be used hereafter.

[h] Synonymous with sycamore-sweetgum-American elm (SAF 1980). Sycamore-pecan-American elm will be retained hereafter.

Exceptions are noted in Table 1 as well as nomenclature which has been adopted herein. The overcup oak-water hickory type is by far the most common, particularly in the southern half of the Refuge where clayey soils and extended overflow periods favor these species. The oak-elm-ash and sugarberry-American elm-green ash types are relatively abundant. The latter is a transitional component occurring on moderately well-drained soils between the overcup oak-water hickory type at lower elevations and the oak-elm-ash, sweetgum-Nuttall oak-willow oak, sycamore-pecan-American elm, and white oak-red oak-hickory types at higher elevations. Considerable variation may occur in the species associations within these forest cover types depending upon soil characteristics and inundation regimes across the Refuge.

Important understory species include swamp privet (*Ligustrum acuminata*), waterelm (*Planera aquatica*), buttonbush (*Cephalanthus occidentalis*), possumhaw holly (*Ilex decidua*), hawthorn (*Crataegus* spp.), and American hornbeam (*Carpinus caroliniana*). Numerous vines including poison ivy (*Toxicodendron radicans*), peppervine (*Ampelopsis arborea*), trumpetcreeper (*Campsis radicans*), Alabama supplejack (*Berchemia scandens*), grape (*Vitis* spp.), common greenbrier (*Smilax rotundifolia*), dewberry (*Rubus* spp.), honeysuckle (*Lonicera* spp.), and morning glory (*Ipomoea* spp.) contribute to a dense understory and ground cover in the bottomland forest of the Refuge. Other common ground cover species are stinging nettle (*Urtica dioica*), stalkless spanglegrass (*Uniola sessiliflora*) and sedge (*Carex* spp.).

Fauna

Despite habitat modifications which have occurred in the lower White River basin in recent years, the area continues to maintain a diverse fauna typical of bottomland hardwood forests. U.S. Fish and Wildlife Service (USFWS) personnel have developed tentative checklists of amphibians, reptiles, birds, and mammals on the Refuge which include 20, 46, 227, and 30 species, respectively. Fishes and invertebrates occurring on the area have not been documented.

Other than black bears, commonly observed mammals on the Refuge include white-tailed deer (*Odocoileus virginianus*) coyote (*Canis latrans*), raccoon (*Procyon lotor*), bobcat (*Felis rufus*), river otter (*Lutra canadensis*), mink (*Mustela* vison), opossum (*Didelphis virginianus*), muskrat (*Ondatra zibethica*), armadillo (*Dasypus novemcinctus*), swamp rabbit (*Sylvilagus aquaticus*) fox squirrel (*Sciurus niger*), and gray squirrel (*S. carolinensis*). Prior to settlement of the area, the eastern cougar (*Felix concolor*) and red wolf (*C. rufus*) were common in this bottomland forest, and buffalo (*Bison bison*) occurred on the tall grass prairie just west of the Refuge.

Migratory waterfowl are a highlight of the avifauna of the area, with winter populations as great as 300,000 censused on the Refuge. The mallard (*Anas platyrhynchos*) and resident wood duck (*Aix sponsa*) are most common, but all waterfowl species which utilize the Mississippi River Flyway as a migratory route may be observed. Great blue heron (*Ardea herodias*), little blue heron (*Florida caerulea*), and green heron (*Butorides virescens*) are common among the dozen or so species of wading birds occurring on the Refuge, and as many as 30 species of shore birds may be observed in riparian habitats of the area.

During late winter considerable numbers of migratory bald eagle (Haliacetus leucocephalus) and osprey (Pandion haliactus) utilize the Refuge, foraging along the White River and associated lakes and swamp impoundments. Other common predaceous birds resident to the bottomland forest and adjacent fields include red-tailed hawk (Buteo jamaicensis), marsh hawk (Circus cyaneus), Mississippi kite (Ictinia misisippiensis), barred owl (Strix varia), screech owl (Otus asio), and great horned owl (Bubo virginianus).

Spring migrations of song birds, particularly warblers, are spectacular and include upwards of 100 species. Christman (1984) observed breeding activity by 31 species, the most common including carolina wren (Thryothorus ludovicianus), tufted titmouse (Parus bicolor), prothonotary warbler (Protonotaria citrea), yellow-breasted chat (Icteria virens), cicadian flycatcher (Empidonax cirescens), indigo bunting (Passerina cyanea), and yellow-bellied cuckoo (Coccyzus americana). Woodpeckers are also a conspicuous component of the avifauna, particularly the pileated woodpecker (Dryocopus pileatus), yellow-shafted flicker (Colaptes auratus), red-headed woodpecker (Melanerpes erythrocephalus), and downy woodpecker (Dendrocopus pubescens).

Representative amphibians of the bottomland habitats of the Refuge include dwarf American toad (Bufo americanus charlesmith), green treefrog (*Hyla cinerea*), bullfrog (*Rana catesbeiana*), Louisiana waterdog (*Necturus maculosus louisianensis*), and marbled salamander (*Ambystoma opacum*). The herpetofauna of the area is particularly well represented by reptiles. Among 14 turtle species one may observe Alligator snapping turtle (*Macroclemys temmincki*), Mississippi map turtle (*Graptemys kohni*), and spiny soft shell (*Trionyx spiniferus spiniferus* x *hartwegi*). The five-lined skink (*Eumeces fasciatus*) is most common of 6 lizard species listed for the area.

Twenty-six species of snakes are known to occur on the Refuge. I commonly observed broadbanded water snake (*Nerodia fasciata confluens*), diamondback water snake (*N. rhombifera*), and western cottonmouth (*Agkistrondon piscivorous leucostoma*) during field work. The American alligator (*Alligator mississippiensis*) has been reintroduced to the area, but there is no indication that a viable population has been established.

A few commercial fishermen continue to make a livelihood from the fisheries resource of the lower White River. While their interest lies in several species of catfishes (*Ictalurus*) and buffalofishes (*Ictiobus*), less commercial carpsucker (*Carpoides carpio*) and fresh-water drum (*Aplodinotus grunniens*) are common in their barrel nets. Several relic species are also found in the White River drainage, including bowfin (*Amia calva*), alligator gar (*Lepisosteus spatula*), paddlefish (*Polyodon spathula*), and shovelnose sturgeon (*Scaphirhynchos platorynchos*). Sportfishing is a major recreational activity on the Refuge and limits of white crappie (*Pomoxis annularis*), bluegill (*Lepomis macrochirus*), and other centrarchids are frequently taken.

History and Management

Written accounts of the lower White River basin date back to the early 16th century exploration of the Mississippi River Valley by Ferdinand de Sota (Wilmar 1858) who "discovered" a pristine wilderness with spectacular diversity and abundance of life, including an enterprising aboriginal civilization. While the indigenous people of the area were victimized and soon displaced by white men, the White River bottomlands persisted as a wilderness through the 18th and 19th centuries despite increased settlement and Civil War of the late 1800's.

The natural processes of this wetland ecosystem began to erode, however, near the beginning of the 20th century when private individuals and companies began acquisition and exploitation of the land. Forests occurring on the "second bottoms" of the alluvial floodplain were cut and much of the land was converted to row crop farming, particularly for rice and cotton. Concurrently, the U.S. Army Corps of Engineers constructed levees and dams along the Mississippi, Arkansas, and White rivers which deterred natural flooding and allowed extensive exploitation of thousands of acres of "first bottom" forest which had previously been inaccessible. Settlement in the area also increased, especially by houseboat dwellers who hunted, fished, and trapped in the White River bottomland without control.

By the time the Refuge was established in 1935, the entire forest acreage of the area had been harvested, and wildlife populations had been severely reduced (USDI 1972). Furthermore, timber rights of previous landowners were not relinquished until several years after the Refuge was founded and an additional 20 million board feet of lumber had been high-graded. By the early 1940's, when all timber rights had expired and control of hunting and trapping had begun, the floral and faunal communities of the lower White River basin were noticeably impoverished compared to those so admiringly described by Antoine Simon le Page du Pratz (_in_ Tregle 1975) two centuries earlier.

Hence, early management on the Refuge consisted primarily of protection and inventory of the regenerating forest and wildlife resource. When the canopy began to close in the mid-1950's, a forest-wildlife management plan for the Refuge was designed with a broad objective "to produce the maximum amount of wildlife that could be enjoyed by the public consistent with the carrying capacity of the land" (U.S. Fish and Wildl. unpubl. for. manage. plan, White River NWR, 1980). To obtain this goal, a 15-year selective cutting cycle was initiated which would allow manipulation of the density and composition of the Refuge forest. Water control, road construction and improvement, and managed hunts were other areas of emphasis in Refuge management at that time.

In the initial cutting cycle, Refuge foresters hoped to clear the forest of culls and undesirable species and open the forest canopy to stimulate growth of ground cover. By 1976 over 164 million board feet of timber were removed from the residual forest. Public use had also increased significantly on the Refuge. In 1980, a revised and considerably expanded forest management plan was developed. Philosophically similar to the original plan, this version emphasized continued manipulation of the Refuge forest to "provide optimum wildlife habitat conditions and to yield economic return from the sale of forest products." The latter part of this statement illustrated the existing philosophy of the U.S. Fish and Wildlife Service at that time and differed greatly from that of the original Migratory Waterfowl Refuge program. The new plan focused increasing attention on public, particularly consumptive, use (e.g., hunting and fishing) of Refuge resources.

Currently, the Refuge is open to the public from March through October. Fishing and all non-consumptive use (e.g., camping, boating, and birding) are permitted throughout this period. Non-permit hunting of turkey and squirrel are allowed in specified areas at certain times of the year. Between late October and late November several 2- or 3-day managed deer hunts are held in which as many as 5,000 permits may be issued per hunt. Two 3-day raccoon hunts are also held during December. Duck hunting is permitted on 2 acres of the Refuge on alternate days during the regular state waterfowl season, and commercial fishing and furbearer trapping of resident species are legal along the White River in accordance with state and federal regulations.

Presently, as the second 15-year cutting cycle nears its end, Refuge personnel are updating the forest inventory and developing treatment prescriptions for compartments of the Refuge forest for the third cycle. Considerable effort is also being directed at controlling the beaver population on the Refuge and maintaining roads and water control structures.

CHAPTER III

METHODS AND MATERIALS

Choice of a Study Area Core

Due to the size (457 km^2) and elongated shape (52 km x 5-15.3 km) of the Refuge, I did not consider trapping and radio telemetry feasible over the entire area. Consequently, the initial phase of the study was to select a core area in which to concentrate these research activities. Based on accessibility by vehicle and boat, width and insular quality of the forest, and existing knowledge of the distribution and abundance of black bears on the Refuge, I selected an area of approximately 200 km^2 in the southern half of the Refuge (Figure 6). This area was characterized by a relative abundance of maintained roads, logging roads, and navigable waterways. It also represented the widest portion of the Refuge and lay in the central section of the remaining continuous bottomland hardwood forest of the lower White River basin (Figure 2, page 9). Information available from annual narrative reports of the Refuge and conversations with local trappers and commercial fishermen indicated that black bears had historically been relatively abundant in this area.

Prebaiting and Trapping

During June and July 1979 I conducted a reconnaissance of the study area core to familiarize myself with the area and identify a network of prebait-trap lines which included 120 km of roads and waterways partitioned into three sections (Figure 6).

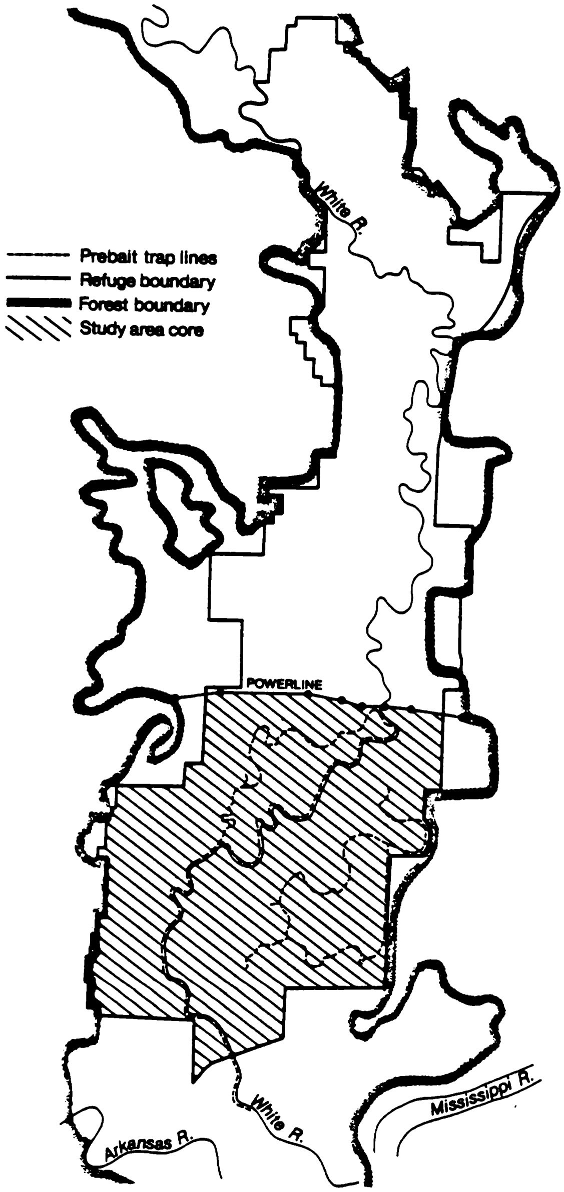


Figure 6. Location of black bear study area core and prebait-trap lines on White River NWR, Arkansas, 1979-1982.

Prebaiting and trapping procedures followed those described by Johnson and Pelton (1980a). Prebait sites were established at intervals of approximately 2 km along each line. Fresh fish, sardines, or pork scraps were placed in nylon-mesh fruit bags and suspended from tree limbs with nylon cord; baits were adjusted to hang about 3 m above ground and 1 m from the tree trunk. Smooth-barked trees (e.g., sugarberry) were selected to facilitate recognition of bear claw marks. Prebait sites were inspected at 5-day intervals or less to determine the occurrence of bear activity and replenish prebaits. Traps were set at sites visited by bears within 15 days of prebait establishment. If no bear visitation had occurred within that period, the prebait was removed and the site discontinued.

Two types of traps were utilized in this study; spring-activated foot snares (Aldrich Animal Trap Co., Clallam Bay, WA) set in cubbies (Johnson and Pelton 1980a) and barrel traps constructed of two 50-gallon oil drums (Eiler 1981). Due to their cumbersome nature and potential bias toward capture of smaller bears, barrel traps were used only occasionally. Generally this was when the recapture of a previously snared animal was anticipated.

Traps were baited with fresh fish or sardines and inspected daily during the morning. Trapped bears were immobilized with an intramuscular injection of either M99 (etorphine hydrochloride, D-M Pharmaceuticals, Rockville, MD) at a dosage of 1 mg per 45 kg estimated body weight or a compound of Ketaset (ketamine hydrochloride, Bristol Laboratories, Syracuse, NY) and Rompum (xylazine, Haver-Lockhart, Inc., Shawnee, KS) at dosages of 200 mg and 100 mg per 45 kg estimated body weight, respectively. Immobilization drugs were administered to snared bears with a dart syringe fired from a carbon dioxide-powered pistol (CAPCHUR, Palmer Chemical Co., Douglasville, GA) and to barrel-trapped bears from a 10 ml syringe mounted on a wooden jabstick.

After being immobilized, bears were removed from traps, their weights and a series of linear body measurements were recorded, and a first premolar tooth was extracted for age determination. A numbered, color-coded metal ear tag was placed in each ear, and a corresponding number was tattooed inside the upper lip. The location and extent of wounds and scars were recorded, and bears were inspected for trap injuries. Reproductive condition (i.e., swollen vulva or lactation) of females was noted, and testicular measurements of males were made.

Once processing was complete immobilizations with M99 were reversed with intravenous injection of the antagonist M50-50 (diprenorphine, D-M Pharmaceuticals, Rockville, MD) at a dosage of 2 mg per 45 kg body weight. Bears immobilized with Ketaset-Rompum were observed at the capture site until they had regained motor ability.

Radio Telemetry

Selected individuals in the capture sample were equipped with motion-sensitive radio transmitters (Telonics, Inc., Mesa, AZ) functioning at the 150-152 mhz range. For immature bears of both sexes, radio transmitter packages were affixed to breakaway collars designed to deteriorate and drop from the animal within 12-24 months, the estimated life expectancy of the transmitter batteries. Transmitters for adults of both sexes were mounted on permanent or static collars and were estimated to function for approximately 30 months.

Locations of radio-instrumented bears were made by ground and air utilizing a Telonics TR-2 receiver with TS-1 scanner and either a 2-element or 3-element directional antenna. Aerial locations were made from single engine aircraft (e.g., Cessna 152 or 172) at altitudes of 100-200 m. One 2-element "H" antenna was mounted on each wing strut with the beam positioned perpendicular to the axis of the strut. Antennae were wired to a switch box inside the aircraft that allowed isolation of the signal from either antenna. Once a signal was received from an individual transmitter, a series of 90 degree and 180 degree maneuvers was made to box in its origin. From altitudes of 100-200 m, radio signals were received within 4-5 km of the aircraft, and the position of the bear could be determined within 5 minutes of initial signal reception. Hence, 20 or more radio-collared bears were generally located during a 2-hour aerial radio tracking period.

Ground radio telemetry locations were made by triangulation of radio signal vectors from known landmarks. Due to the lack of topography on the Refuge, few elevated radio tracking sites were available. Denseness of the vegetation between June and October also reduced radio signal reception distances from ground tracking. Several attempts were made to overcome this situation. Levees occurring on the eastern and western extremeties of the study area core were used whenever possible. I also climbed trees to heights of 10-15 m to make radio locations, but this technique increased reception distances only marginally and was very time consuming. A permanent elevated radio tracking station was established near the center of the study area core in a tree house 12 m above ground. An 11-element directional antenna (Cushcraft Corp., Manchester, NH) was mounted to a mast which extended 14 m above the tree house. This 26 m height advantage increased reception distances by 25 to 50 percent during summer, but this improvement did not warrant construction of a system of these tracking stations. This structure proved to be very useful, however, for monitoring activities of bears during inclement weather and the denning period.

All radio telemetry locations were assigned to 1-ha grid cells numbered by 6-digit coordinates of the Universal Transverse Mercator (UTM) grid coordinate system. Bear locations from ground tracking were generally based on 3 or 4 azimuth readings and were considered to have an error radius of $\leq$ 200 m. Aerial radio locations provided greater accuracy, and field tests indicated that the error radius was generally $\leq$ 100 m.

Population Characteristics

Population structure. Ages of bears in the capture sample were determined from counts of cementum annuli (Willey 1974) in premolar teeth extracted at the time of capture. Decalcification, sectioning, and staining procedures followed those described by Eagle and Pelton (1978). I inspected tooth sections of each bear a minimum of 3 times, making independent age estimates after each inspection. For those estimates which remained questionable, I had 2 or 3 people experienced with the technique inspect the sections and make age estimates. Definitive assignment of age was then based on all estimates.

Population size. Estimates of the size of the black bear population on the study area core were made applying the single mark-recapture/reobserve or Lincoln-Petersen method (Seber 1973, Tanner 1978) to capture and observation samples for 1980 and 1981. These data were partitioned into two groups: mark-recapture (i.e., all marks) and mark-recapture/reobserve (i.e., radio-collar marks only) from which separate population estimates were generated.

Due to the absence of cubs in capture samples, yearlings in the 1980 and 1981 samples had a zero probability of being recaptures, and I excluded them from the capture sample. Hence, Petersen estimates were for bears $\geq$ 1-year-old. I estimated the sizes of cub cohorts by the equation:

$$\hat{N}_c = \frac{\hat{N}(P_f)}{B_f} \times (\bar{L})$$

where:

$\hat{N}_c$ = estimate of surviving cubs,

$\hat{N}$ = estimate of bears $\geq$ 1-year-old,

P_f = proportion of adult females in $\hat{N}$,

B_f = breeding frequency of adult females, and

$\bar{L}$ = mean litter size at 9-12 months after birth,

and added these to Petersen estimates to give estimates of total population size.

Population density. Based on population estimates for the study area core, an index of absolute density (number of km^2 per bear) was calculated for comparison with black bear population densities in other geographic regions. Due to evidence that density was not uniform across the Refuge, this estimate was adjusted based on the distribution of bears observed by hunters during managed deer hunts.

Two indices of relative density were also generated: prebait visitation rate and the number of bear observations per hunter-day during managed deer hunts. The latter was derived from responses by hunters on permit questionnaires; the number of hunters which observed bears was divided by the product of the number of days of that hunt times the number of permits issued. Follow-up questionnaires also were mailed to hunters who observed bears to obtain information on litter size and fall distribution of black bears on the Refuge.

Reproduction. Reproductive parameters of interest were age of sexual maturity, timing of estrous and parturition, litter size, and breeding frequency.

Age of sexual maturity of males was determined from testicular measurements and the occurrence of fighting wounds and scars. Width, length, and circumference of testicles and the extent and condition (i.e., old, cicatricose, or fresh) of fighting scars were recorded at the time of capture. Sexual maturity of females was determined from teat condition and measurements, observation of cubs or lactation of captured individuals, and/or the birth of cubs by radio-instrumented females.

Criteria used to estimate the timing of estrous included the occurrence of vulval swelling in captured females, family breakup of radio-instrumented females and their yearling young (Rogers 1977), and spatial relationships (i.e., pair bonds) between radio-instrumented adult males and females.

Timing of parturition was determined by inspecting dens of adult females through the denning period. At each visit a microphone attached to a portable cassette recorder was lowered into the den cavity to within 2 m of the female, and a 15-minute recording was made. Eiler (1981) found this method effective for determining the presence of suckling cubs in dens, and Alt (1983) reported that cub vocalizations were easily audible at distances of 15 m from the den entrance.

The size of newborn litters was also estimated from recordings at maternal dens. Delineation between 1-cub and $\geq$ 2-cub litters was easily made, however, the presence of more than 2 cubs was difficult to determine (Eiler 1981). During the third year of the study, I verified litter sizes by locating families of radio-instrumented females within one week of den emergence. Approaching with care, I generally intercepted these families while the cubs were on the ground. If not, the cubs climbed trees, and in either case, observation of the entire litter was easily accomplished. This technique was very effective for determining litter sizes and may result in less disturbance than inspections of maternal dens.

The frequency of breeding (i.e., interval between litter production) of adult females was estimated from the reproductive histories of radio-instrumented individuals.

Mortality. Mortality rates of bears $\geq$ 1-year-old were estimated from fates of radio-instrumented individuals during the course of the study. Cub mortality was estimated from observed reductions in mean litter sizes from birth to 9-12 months postpartum.

Denning

Chronology of denning, characteristics of dens, and degree of winter dormancy were of particular interest in this investigation because of flooding which occurs on the Refuge during late winter and early spring. Date of den entry was designated as the mean date between the first location at a den site and the location preceding it. Similarly, date of den emergence was defined as the mean date between the last location at the den and the first away from it.

Dens of radio-instrumented bears were located by walking in on their radio signals after they had become stationary. During these operations, den trees were often conspicuous at distances of 50-100 m. If so, I circled the origin of the signal to verify the position of the bear and flagged a trail out without approaching the den. During the first winter of the study, 2 bears abandoned ground dens after I approached too closely. Subsequently I avoided approaching bears which I believed were denned on the ground, but rather, circled the signal taking compass readings from marked locations. A trail was flagged out, and I did not return until the bear had emerged from the den. Bears denning in tree cavities were less susceptible to disturbance provided it did not occur soon after den entry. During the second winter of the study, 3 adult females abandoned tree dens after early inspections. Thereafter, I delayed these procedures until 2-3 weeks following den entry, and no further abandonments occurred which could be attributed to my presence.

After den emergence, tree and ground dens were inspected to obtain information on den characteristics. For tree dens, I recorded the following data: tree species, diameter at breast height (dbh), and aspect; height of cavity entrance above ground; entrance height, width, and aspect; cavity depth, width, and height; and height of cavity floor above ground. For ground dens I measured the diameter of the bed and height of the bed walls. The type of substrate and bedding material and the position of cover (e.g., logs, tree tops, and vine mats) to the bed also were recorded. Untransformed mean values for characteristics of dens utilized by population cohorts were compared with the t-test and chi-square procedures.

The degree of winter dormancy was determined from activity levels of radio-instrumented bears during the denning period, fidelity of bears to dens, and behavorial responses of bears to den inspection. During the wirst winter of the study, I monitored radio signals of bears confined to dens for extended periods of time (2-14 hours). Based on changes in signal mode frequency, and adjusting for the 2-minute reset mechanism of radio transmitters, percentage activity, minimum number of movements per hour, and lengths of activity periods were calculated.

Between October and April of the second year, I conducted bi-monthly, 24-hour activity monitoring sessions to determine activity levels of radio-instrumented bears prior to, during, and immediately following the denning period. Signal mode for all bears within reception range of the radio receiver were recorded hourly. Interpretation of activity from signal mode changes followed the logic of Quigley et al. (1979). Activity level was expressed as the percentage of active readings recorded during the 24-hour period.

Home Range

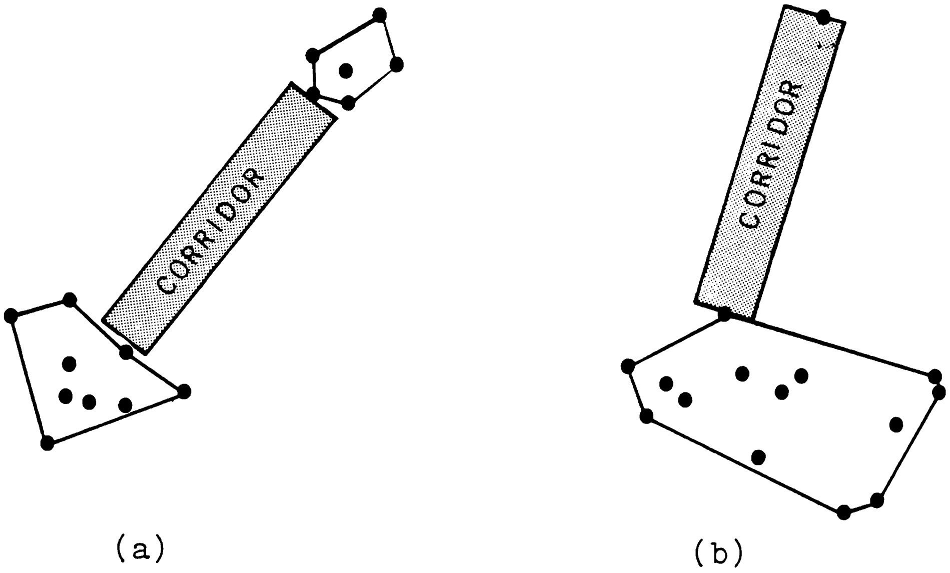
Seasonal and annual home range sizes of radio-instrumented black bears were estimated by the convex polygon or maximum area method utilizing Program TELEM (Koeln 1980). Polygons were subjectively adjusted to exclude areas which were considered unsuitable habitat (e.g., cultivated fields). If the area enclosed by the polygon was distinctly inflated due to a single outlying location point, which represented a known temporary excursion or the first or last in a seasonal series of locations, the polygon was constructed ignoring that point. A 1-km-wide corridor between the polygon and the outlier was then constructed and that area added to the home range estimate. The corridor adjustment also was applied to minimize areas which apparently were used only for travel between disjunct activity centers (Figure 7).

Due to small sample sizes, seasonal and annual home range estimates of population cohorts were compared by nonparametric tests utilizing the SAS (1982b) RANK and General Linear Model (GLM) procedures.

Food Habits

Seasonal foods and feeding behaviors of black bears on the Refuge were determined from analyses of scats collected during research activities and from field observations. Scats were collected as encountered at trap sites, along prebait-trap lines, and during radio telemetry procedures. Date, location, and estimated age of scats were recorded, and they were frozen in plastic bags within 12 hours of collection.

In the laboratory scats were washed through a series of sieves (6.7 mm, 4 mm, 2 mm, and 0.5 mm) to separate equal-sized particles. Contents were oven dried at 100°C and identified to species or the lowest taxa possible. References for seed identification included Martin and Barkley (1961) and Landers and Johnson (1976). Hairs were identified following keys of Moore et al. (1974) and Spiers (1973).



(a) (b)

Figure 7. Examples of home range polygons which were modified by a "corridor" method to minimize areas between (a) disjunct clusters of locations and (b) single outlying locations.

Unidentified grasses, other herbaceous material, and green leaves and stems were placed together in a general category. All fish were placed in one category as well.

An ocular estimate of percentage volume of each food item was made, and pooling data from all samples, the mean monthly percentage volume and frequency of occurrence of each category of food was calculated. Scats estimated to be more than 2 weeks old were excluded from the analyses. In addition, when radio telemetry observations indicated that one or more bears were concentrating activities at a specific site, possibly for food, an effort was made to locate the site and determine the nature of the activity by direct observation of the bear(s) or sign.

Habitat Utilization

The overall and seasonal distributions of black bears on the Refuge were analyzed in relation to habitat variables taken from forest cover (i.e., timber) type and USGS topographic maps of the area. Twenty-seven basic habitat parameters were initially inventoried and from these, 17 variables were selected or derived for analysis (Table 2).

Due to the low representation of certain forest types in the study area core (Table 1, page 15), forest cover was categorized as low forest, transitional forest, high forest, or riparian forest. Low forest included only the overcup oak-water hickory type which is generally restricted to poorly drained soils subject to extended

Table 2. Variables used in analysis of habitat utilization by black bears on White River NWR, Arkansas, 1979-1982.

Variable		Definition
Low forest	-	overcup oak-water hickory forest type
Transitional forest	-	sugarberry-American elm-green ash forest type
High forest	-	sum of sweetgum-Nuttall oak-willow oak, sycamore-pecan-American elm, oak-elm-ash, and white oak-red oak-hickory types
Riparian forest	-	sum of baldcypress, cottonwood, and willow forest types
Open water	-	sum of lakes, large perennial streams and bayous, and the White River
Swamps	-	wooded swamp/marsh, including beaver impoundments and dead timber reservoirs
Streams	-	small perennial streams and intermittent streams
Logging roads	-	unmaintained logging roads
Maintained roads	-	graveled and unsurfaced maintained roads
Miscellaneous	-	sum of levees, dredge spoils, and rights-of-way
Edge	-	sum of open water/forest edge, swamp/forest edge, streams, logging roads, and maintained roads
Contour	-	sum of contour lines
Forest diversity	-	Simpson (1949) index based on low forest, transitional forest, high forest, and riparian forest
Elevational diversity	-	Simpson (1949) index based on < 145 ft, 145-150 ft, and > 150 ft.
Habitat diversity	-	Simpson (1949) index based on first bottom (i.e., low forest), second bottom (i.e., sum of transitional forest and high forest), riparian forest, swamps, open water, and miscellaneous
Refuge boundary	-	same
White River	-	same

inundation on first bottom terraces below 44.2 m (145 ft). The sugarberry-American elm-green ash type (transitional forest) also was considered a discrete forest component because it occurs on transitional areas between the overcup oak-water hickory type at lower elevations and the sweetgum-Nuttall oak-willow oak, sycamore-pecan-American elm, white oak-red oak-hickory, and oak-elm-green ash types at higher elevations. These latter types, which occur on well drained soils on river fronts, first bottom ridges, and second bottom terraces above 45.1 m, were grouped into the high forest classification. Riparian forest comprised the baldcypress, black willow, and cottonwood types. While these forest and timber types may occur over a wider range of sites than these, they generally conform to these specifications on the Refuge (J. Johnson, pers. communication).

Variables expressing total edge, total contour, and 3 indices of diversity also were generated from basic habitat parameters. Diversity indices were calculated by the formula of Simpson (1949).

To quantify the availability of habitat variables on and adjacent to the study area core, the area was subdivided into approximately 1100 25-ha habitat quadrats which were assigned unique identification numbers based on the UTM grid coordinate system; this facilitated merging habitat and telemetry location data. Each quadrat was further subdivided into 25 1-ha cells; values for habitat variables were expressed as the number of 1-ha cells which the variable encompassed (e.g., forest cover) or the number of cells in which it occurred (e.g., streams).

I initially examined the frequencies of values for each habitat variable over all quadrats and found that many were skewed toward low values. Subsequently, I converted these continuous values to categorical ones (i.e., low-moderate-high or absent-present). The chi-square distribution was employed to test the null hypothesis that bear use of categories of each habitat variable was proportional to their frequencies on the study area core. When significantly ($P<0.05$) disproportionate utilization of categories for a given habitat variable was identified, simultaneous confidence intervals were constructed for observed category frequencies (Neu et al. 1974; Byers et al. 1984) to determine which categories were utilized more or less than expected.

Following the utilization-availability procedure, habitat and telemetry data were subjected to a multiple regression analysis utilizing the SAS 1982b) GLM procedure. The square root-transformed (Sokal and Rohlf 1969) number of bear observations in habitat units was the dependent variable of the model upon which independent habitat variables were regressed. Rather than enter all variables into the model, I subjectively chose those which appeared to be most important based on the initial chi-square analysis.

References

Vernacular and scientific names used herein were taken from the following sources: mammals, Jones et al. (1979; birds, American Ornithologist Union (1957); reptiles and amphibians, Conant (1975); fishes, Robins et al. (1980); insects, Sutherland (1978); and plants, Scott and Wasser (1980).

CHAPTER IV

RESULTS AND DISCUSSION

Prebaiting and Trapping

Prebaiting. There were two objectives for utilizing a prebaiting procedure: first, to identify areas of bear activity and hence increase the probability of capture at trap sites (Johnson and Pelton 1980a), and second, to define procedures and generate baseline index data for monitoring trends in black bear abundance on the Refuge in the future.

Eleven prebaiting sessions were conducted over the 3 years of the study, 5 in 1979 and 3 in each of 1980 and 1981 (Table 3). In the first 2 sessions of 1979 canned sardines and pork were used for bait, and no bear visitations occurred at all (N = 34) prebait sites. Line I was then rebaited with fresh fish, and a 27 percent visitation rate was observed within 15 days. Thereafter, I utilized only fresh fish for prebaiting. Also, due to the urgency of radio-collaring bears during the first year of the study, prebaiting and trapping were extended into the fall and winter on Line III. Results of these 2 sessions were likely biased by bait type and time of sampling, respectively, and were excluded from total year and area visitation rates.

The prebaiting procedure appeared to enhance trapping success. At trap sites where a bear had visited the prebait within 5 days

Table 3. Characteristics of prebait lines and chronology of prebaiting for black bears on White River NWR, Arkansas, 1979-1981.

Prebait line	Area	Length	Sampling period	
			Year	Dates
I	Scrubgrass Bayou-East Moon Lake	33 km	1979	11 Jul-19 Jul
			1979	20 Jul- 4 Aug
			1980	12 May-29 May
			1981	10 Jun-26 Jun
II	Lower White River-Levee B	46 km	1979	28 Jun-15 Jul
			1979	12 Sep-27 Sep
			1980	30 Jun-15 Jul
				31 Jul-24 Aug
			1981	11 Aug-27 Aug
III	Upper White River-Brooks Bayou-LaGrue Bayou	41 km	1979	1 Nov-21 Nov
			1980	3 Sep-26 Sep
			1981	7 Jul-27 Jul

following bait placement, capture success (6.2 percent) was higher than at sites where visitation occurred 6-10 days after prebait establishment (4.9 percent) (Table 4). The few trapnights effort at sites where prebaits were visited at 11-15 days produced no captures. Occasionally traps were set at prebait sites which were not visited but near which bear sign had been observed. Capture success at these sites was a relative low 2.9 percent. During a brief trapping session in the Parish Lakes area in June 1980, I did not prebait, but rather chose trap sites subjectively. Capture success during this session was also relatively low at 1.7 percent.

Although prebaiting (i.e., bait stations) is currently receiving much attention as an index of relative density of black bears, its use in conjunction with trapping has not been reported since the study of Johnson and Pelton (1980a). While based on somewhat small sample sizes, the results of my study support the conclusion of these researchers that capture success and hence trapping efficiency may be increased when prebaiting is employed.

The results of prebaiting and discussion of its value as a population index will be presented later in a section on relative density (page 62).

Trapping. Sixty-three captures of 51 individual black bears were made in 1453 trapnights (TN) during the 3 years of sampling (Table 5). In addition, a yearling male was immobilized from a tree in floodwater in May 1980. The 1980 sample included 3 recaptures,

Table 4. Relationship between black bear capture success and prebait visitation on White River NWR, AR, 1979-1981.

Prebaiting circumstances	No. of trapnights	Capture success (%)
Prebait visited at 1-5 days	445	6.3
Prebait visited at 6-10 days	336	4.9
Prebait visited at 11-15 days	83	0.0
Prebait not visited but bear sign observed nearby	70	2.9
Trapline not prebaited	168	1.8

Table 5. Results of black bear trapping on White River NWR, AR, 1979-1981.

	1979			1980			1981			Area Totals		
Trapline	No. TN[a]	No. captures	Capture success[b]	No. TN	No. capture	Capture success	No. TN	No. captures	Capture success	No. TN	No. captures	Capture success
I	198	5	2.5	135	6	4.4	239	17	7.1	572	28	4.9
II	68	5	7.4	260	12	4.6	172	6	3.5	500	23	4.6
III	50	1	2.0[c]	71	4	5.6	143	5	3.5	264	10	4.2
IV[d]				117	2	1.7[e]				117	2	
Year Totals	316	11	3.7	583	24	4.7	554	28	5.1	1453	63	4.7

[a] Trapnights.

[b] Percentage.

[c] Excluded in calculation of capture success totals due to seasonal bias.

[d] Parish Lakes area.

[e] Excluded in calculation of capture success totals due to lack of prebaiting.

one of an animal caught in the same year. In 1981, 10 recaptures were made; 4 individuals were originally captured in 1979, 5 were marked in 1980, and one was caught earlier in 1981. One adult male was captured in each year of trapping. Data from 2 trapping sessions were excluded from calculations of total capture success by year and area due to biases in sampling procedures (i.e., season and prebaiting).

Over 92 percent of the trapping effort was accomplished with spring-activated foot snares. Barrel traps were generally utilized when a snare was repeatedly robbed and/or the capture of a previously snared bear was anticipated. Capture success was similar with snares (4.4 percent) and barrel traps (3.4 percent).

Capture success varied considerably within year and area samples, however total capture success did not vary significantly ($P>0.05$) between years or areas. Phenological development (Reynolds and Beecham 1980, Garshelis and Pelton 1981) and dispersal (Rogers 1977) affect the temporal distribution and activities of black bears and could have accounted for the degree of variation observed in capture success on the Refuge.

Overall capture success in this study was relatively high compared to those from other black bear investigations. Reports of snaring success based on large sample sizes have been 0.5 percent in New York (Miller et al. 1973), approximately 5.0 percent in Arizona (LeCount 1980), and 11.4 percent in east Tennessee (Johnson and Pelton 1980a). Trapping success with barrel or culvert traps has ranged from 2.4-3.4 percent in Michigan (Erickson 1957), Minnesota (Rogers

1977), New York (Miller et al. 1973), and Virginia (Stickley 1961) to 16.9 percent in Tennessee (Johnson and Pelton 1980a).

Four bears died at trap sites after being immobilized (1 in 1979, 2 in 1980, and 1 in 1981). Three of these (1 adult male, 1 adult female, and 1 subadult female) died within 10 minutes of normal intramuscular injection of M99, apparently due to respiratory failure. One adult male did not recover and died 5 hours after initial injection of Rompum-Ketamine. All of these drug-related deaths occurred during mid-summer (9 July-14 August) and were probably related to high humidity and temperature (V. Nettle, Southeastern Cooperative Wildlife Disease Study, pers. communication).

Radio Telemetry

Twenty-eight black bears were equipped with radio collars at capture sites and monitored for periods of 17 to 1001 days (Table 6). Radio contact was maintained with 4 bears (3 adult males and 1 adult female) for more than 30 months (including 3 winters), with 11 bears for 18-24 months, and with 8 for 11-15 months. The radio transmitter of one subadult female functioned for only 38 days, and 2 adult females captured in the summer of 1979 died (1 shot, 1 undetermined) less than 2 months after being radio-collared. A 3-year-old female and a 2-year-old male removed their breakaway collars 53 and 132 days, respectively, after being radio-equipped.

A total of 2104 telemetric locations were made between 23 July 1979 and 26 May 1982. No monitoring was conducted from 12 September 1981 to 11 December 1981 while I was away from the study area. The

Table 6. Summary of radio telemetry data for black bears on White River NWR, Arkansas, 1979-1982.

Bear No.	Sex	Age[a]	Period of monitoring	No. days monitored	No. telementry locations
403	F	3	23 Jul 79-23 Sep 79	53	11
405	F	3	23 Jul 79- 7 Sep 79	38	9
407	M	6	18 Aug 79-15 May 82	1001	152
408	F	11	18 Aug 79-15 Oct 79	48	8
409	M	2	6 Sep 79-16 Jan 80	132	32
410	M	4	18 Sep 79-15 May 82	796[b]	127
411	M	8	21 Sep 79- 6 Apr 82	928	153
412	M	2	25 Sep 79-27 Mar 81	549	117
413	F	9	26 Sep 79-12 Oct 79	17	3
415	F	10	18 Nov 79- 5 May 82	899	160
416	M	1	2 May 80- 7 Aug 81	462	101
417	M	5	28 May 80-15 May 82	717	103
418	F	2	6 Jun 80-31 Aug 81	451	94
419	M	6	8 Jun 80-15 May 82	706	101
420	M	3	8 Jun 80-15 May 82	706	94
421	M	5	12 Jun 80-15 May 82	702	103
423	F	2	14 Jun 80-11 Sep 81	454	91
425	M	2	23 Jun 80-12 Jun 81	354	66
428	F	11	18 Jul 80-15 May 82	666	95
429	F	5	25 Jul 80-15 May 82	659	98

Table 6. (Continued)

Bear No.	Sex	Age[a]	Period of monitoring	No. days monitored	No. telementry locations
430	F	3	26 Jul 80-15 May 82	658	81
438	F	10	27 Aug 80-24 May 82	635	76
439	F	9	26 Sep 80-26 May 82	607	71
451	F	4	27 Sep 80-15 May 82	595	74
452	F	7	13 Jun 81-15 May 82	336	18
458	M	1	20 Jun 81- 5 May 82	329	24
459	F	11	20 Jun 81-15 May 82	329	18
460	F	3	24 Jun 81-15 May 82	325	17
				TOTAL	2104

[a] Age when radio-collared.

[b] Removed radio-collar in March 1980. Recollared in August 1980.

flat topography of the area and denseness of vegetation during the 8-month growing season considerably hindered radio tracking from the ground, and approximately 80 percent of the telemetry locations were made by air. Outside of the denning period, the mean interval between locations was 5.2 days, ranging from 4.2-4.4 in 1979 and 1980 to 6.1 in 1981.

Population Characteristics

Size. Given three sampling periods separated by one-year intervals, an open multiple mark-recapture model (e.g., Jolly-Seber method (Seber 1973)) would generally be appropriate to generate estimates of population size. However, the small size of the 1979 sample (N=11), and subsequently low number of recaptures (N=3) in the 1980 sample, precluded the application of this type model. The best alternative was to apply the single mark-recapture or Petersen method (Seber 1973, Tanner 1978) to larger samples from 1980 and 1981.

Although the Petersen method is a closed model and assumes no gain or loss to the population between sampling periods, the closure assumption can be relaxed if either additions or deletions, but not both occur. Assuming recruitment, the estimate applies to the time of the second sample, and conversely, assuming random loss (i.e., emigration and/or death) between marked and unmarked individuals, the estimate is valid for the time of the first sample.

While both reproductive recruitment and death occurred between the sampling periods, telemetry observations indicated that immigration to, and emigration from the study area core were minimal. Only 6 of 24 bears which were radio-instrumented in the study area core and monitored for 10 months or longer made known movements outside this area. These movements were temporary excursions (i.e., seasonal or less), and the geometric home range centers of all 24 individuals lay inside the study area core (Figure 8). Undoubtedly, some animals in the capture sample may have been largely resident outside the study area core, but telemetry data indicated that most were not, and I had no reason to believe that the 212 km^2 study area core did not encompass the sampling "area of effect." Consequently, by excluding captures of cubs (which did not occur) from the 1980 sample and captures of yearlings from the 1981 sample, the condition of unbiased loss with no recruitment could be reasonably assumed. Hence, the population estimate applied to the time of the first sample (i.e., 1980) and represented the number of bears $\geq$ 1-year-old.

Separate Petersen estimates were generated from two sources of data: mark-recapture, which included all capture data, and mark-recapture-reobserve, which considered radio-collar marks only and included observational data as well as capture data. Applying the formula of Bailey (1952) to reduce the bias of small sample size, estimates of the number of black bears $\geq$ 1-year-old on the study area core for 1980 were 82 and 77 (Table 7). The 95 percent confidence interval for the estimate based on mark-recapture-reobserve data was much narrower than that based on mark-recapture data, and 77 appeared to be the best estimate.

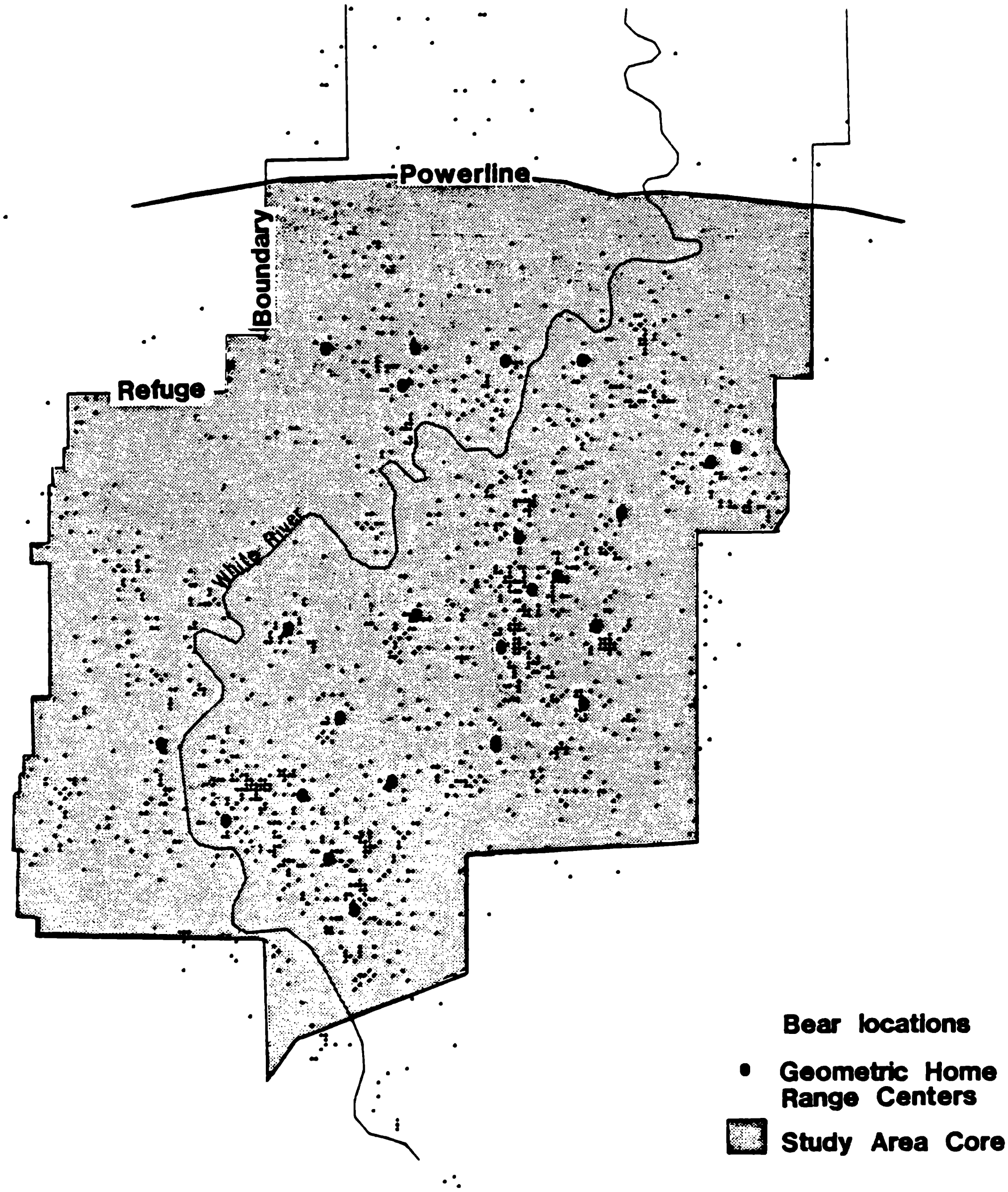


Figure 8. Distribution of radio-locations and geometric home range centers of black bears captured in the study area core on White River NWR, Arkansas, 1979-1982.

Table 7. Petersen estimates of black bears $\geq$ 1-year-old on a 212 km^2 section of White River NWR, Arkansas, 1980.

Data source[a]	Sample size (C)	No. of recaptures (R)	No. marked in population (M)	Petersen[b] estimate ($\hat{N}$)	95% confidence interval
Mark-recapture	25	6	22	82	50——226
Mark-recapture-reobserve	29	6	18	77	56——124

[a] See text, page 52.

[b] Derived from the formula of Bailey (1952): $\hat{N} = \frac{M(C+1)}{R+1}$

As outlined in Chapter III (page 30) a formula was derived for estimating the number of cubs present in a given population during fall based on:

1. The proportion of adult females in the capture sample,
2. observed breeding frequence of radio-collared females,

and

3. mean fall litter size.

In a population of 77 individuals $\geq$ 1-year-old, I estimated that 10 cubs would survive to the fall. Hence, my estimate for the total number of black bears on the study area core was 87.

Extrapolation of the Petersen estimate for the 212 km^2 study area core to the 457 km^2 Refuge would give an estimate of 177, but there was evidence that the abundance of black bears was not uniform across the Refuge and that such an exercise would overestimate the number of bears on this area. Annual narrative reports of the Refuge since 1937, as well as information from local trappers and commercial fishermen, indicated that black bear density has historically been higher in the area which I sampled than elsewhere in the lower White River basin. Furthermore, an average of 67 percent of the black bear observations made during managed hunts between 1979 and 1982 occurred in the study area core (Table 8). This area represents only 46 percent of the total Refuge acreage. Assuming that this proportion reflected the actual distribution and density of bears over the Refuge, the estimate would be 130.

Table 8. Proportions of black bear observations within and outside the study area core during managed deer hunts on White River, NWR, Arkansas, 1979-1982.

		Bear observations			
		Outside study area core		Within study area core	
Year	Type hunt	N	%	N	%
1979	Youth-adult	12	35	22	65
	Gun	21	23	71	77
1980	Youth-adult	12	34	23	66
	Gun	16	35	30	65
1981	Youth-adult	2	3	59	97
	Gun	35	18	158	82
1982	Youth-adult	50	50	50	50
	Gun	144	45	175	55
	Total	292	33%	588	67%

Given the evidence that bear density was greater in the study area core than outside it, and considering that Petersen estimates may have been positively biased by migration of bears in and out of the sampling area, as well as by small capture samples, I believe an estimate of 130 probably lies closer to the actual number of black bears in the Refuge population.

Effective population size and long-term fitness. A specific estimate of the number of black bears in the lower White River basin cannot be made with confidence from available information. However given my estimates of the number and density of bears on the Refuge, and the finite size of habitat available to the population, broad limits can be defined which probably encompass the actual population size. Such an approximation is useful for estimating the genetically effective size of the population and for addressing the important subject of its adaptive potential and long-term fitness.

An optimistic approach would be to assume that black bear density is relatively uniform throughout the continuous forest in the lower White River basin, and that the total population size is roughly twice that estimated for the Refuge, i.e., approximately 260 bears. On the other hand, my data on the relative density of bears on the Refuge suggest that it is reasonable to assume that a population nucleus exists in the southern portion of the Refuge, away from which density progressively decreases. In this case, a conservative estimate of the total population size would be about 150 bears.

Using these numbers, assuming a 1:1 sex ratio, and applying my estimates of age structure and age at sexual maturity for bears in the study area core, the genetically effective size of this population is approximately 75 to 130. These figures are liberal since the assumption of equal reproductive effort among breeding individuals is probably not met for black bear populations. Males compete for females, and dominant males may contribute disproportionately to reproduction (Robers 1977). Fecundity of adult females also may vary by age (i.e., social position) (Rogers 1977) and maternal experience (Alt 1982). If I relax the assumptions, and assume that (1) the sex ratio of the capture samples (1.56:1) was representative of the population, and (2) 50 percent of the males $\geq$ 4 years old plus 25 percent of the 3-year-old males actually contributed to the reproductive effort, the estimate of the genetically effective size of this population is 53 to 92.

According to contemporary theory, effective population sizes in this range (i.e., 53 to 130), especially for large mammals, are dangerously low (Frankel and Soule 1981). A small population size generally results from a "bottleneck" event in which a larger population is reduced or subdivided. If this occurs rapidly, a substantial proportion of the genetic variation in the parent population may be lost. This situation is further compounded because with low effective numbers, the probability that rare advantageous alleles will be lost or disadvantageous alleles will be fixed is increased. The "bottleneck" event also may result in geographic isolation of the population, eliminating any effect which gene flow from other subpopulations might have in balancing genetic drift. Concomittantly, mutation pressure is likely to be unimportant when numbers are low, especially for generalist species with low reproductive rates.

The consequence of low effective population size and loss of genetic variation is reduction of fitness (i.e., survival and reproductive potential). Franklin (1980) proposed that a minimum effective population size of 500 is necessary to preserve useful genetic variation and provide reasonable assurance of long-term survival of a population. While this number is somewhat tentative, it is empirically derived and appears, at least, to be in the right order of magnitude. It can be shown (Frankel and Soule 1981), that a population which maintains an effective number of 100 will lose approximately 40 percent of its genetic variation within 100 generations.

These theoretical considerations suggest that the long-term fitness of the black bear population in the lower White River basin is extremely low. If this remnant population is to survive the reduction in genetic variation which appears likely to occur, every measure must be taken to maintain an effective population number equal to or greater than that which presently exists.

Absolute density. Assuming estimates of 87 bears for the study area core and 130 for the entire Refuge, the density of black bears ranged from approximately 1 bear per 2.4 km^2 to 1 bear per 5.7 km^2 ($\bar{X}$ = 1 bear/3.5 km^2). These estimates are relatively high compared to reported black bear densities across North America (Table 9). There appears to be limited value, however, in comparing these density estimates due to the variety of methodologies and interpretations of population estimates, especially with respect to model assumptions and area sampled, upon which they were based.

Possibly the only obvious trend in these data is that densities of highly exploited (i.e., hunted) populations in Maine, Michigan, and North Carolina are noticeably lower than those for less or unexploited populations in Alberta, Arizona, Arkansas, Montana, and Tennessee. Otherwise, existing density estimates are probably of little use for comparing the quality of different habitat types for black bears.

Relative density. Estimates of absolute size and density are fundamental to describing the characteristics of a population and approaching ecological questions concerning its status, but procedures for generating these estimates are costly and time consuming. If, however, measures of absolute and relative density are made concurrently, a relationship between absolute and relative abundance is established. Hence, the general status of the population may be monitored over long time periods based on more feasibly produced index values. This is particularly important for managed, multiple-use public areas such as the Rufuge where research funding and personnel may be limited, yet the status of the black bear population is of concern and may be influenced by management.

Table 9. Estimates of black bear density in different geographic regions of North America.

State	Density estimate (bear/km^2)	Source
Michigan	1/8.8 km^2	Erickson and Petrides 1964
North Carolina	1/8.7 km^2	Hamilton 1978
Maine	1/4.8-16.7 km^2	Hugie (in press)
Minnesota	1/4.5 km^2	Rogers 1977
Arkansas	1/2.4-5.7 km^2	This study
Montana	1/2.1-4.4 km^2	Jonkel and Cowan 1970
Tennessee	1/3.75 km^2	Eagar 1977
Arizona	1/3.0 km^2	LeCount 1982
Alberta	1/2.6 km^2	Kemp 1976
Idaho	1/1.3 km^2	Beecham 1980

Two indices of the relative density of black bears on the Refuge were explored in this study: prebait visitation rate and the number of bear observations per hunter-day during managed deer hunts. A summary of prebait visitation rates is given in Table 10. Distinct variation occurred within year and area samples, but a chi-square analysis indicated no significant differences ($P>0.05$) in prebait visitation rates between years or areas. Three years of index data are generally not adequate (nor were they meant) to identify population trends, especially since experimentation with procedures reduced replication of sampling.

A second index of relative abundance was generated from permits returned by hunters following managed deer hunts (Table 11). This index declined dramatically from 1979 (0.048) to 1980 (0.014). However, given the relatively high survival rate of black bears (Jonkel and Cowan 1971, Rogers 1977, this study, page 87), these figures cannot represent an actual population fluctuation. Prebait visitation rate and capture success did not vary substantially between 1979 and 1980.

I could not identify any unusual climatic or management factors which might have biased bear observations in 1980, however, the distribution of bears during fall of that year was somewhat unusual. Acorns were abundant but very localized in low overcup oak flats. Bears concentrated their activities in these areas, and this may have reduced the overall probability of bear observations among more evenly dispersed hunters.

Table 10. Black bear prebait visitation rates on White River, NWR, AR, 1979-1981.

	Prebait Line							
	I		II		III		Year Total	
Year	No. of prebaits	Visitation rate	No. of prebaits	Visitation rate	No. of prebaits	Visitation rate	No. of prebaits	Visitation rate
1979	19	.00[a]	14	.00[a]	19	.16[b]		
	22	.27	8	.50	-	-	30	.33
1980	17	.59	23	.43	19	.26	59	.42
1981	26	.54	19	.53	31	.35	76	.46
Area Total	65	.47	50	.48	50	.31	Grand Total 165	.39

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[a] Excluded from totals due to bait type bias.

[b] Excluded from totals due to seasonal bias.

Table 11. Black bear observations by hunters during managed deer hunts on White River National Wildlife Refuge, Arkansas, 1976-1982.

Year	Type hunt	No. days	No. permits returned	No. hunter days	No. bear observations	No. observations/ hunter-day
1976	Gun	2	1855	3710	207	0.056
1977	Gun	3	1750	5250	219	0.042
1978	Gun	3	2011	6033	295	0.049
1979	Gun	3	914	2742	131	0.048
1980	Gun	3	2270	6810	93	0.014
	Youth-Adult	2	2645	5290	121	0.023
1981	Gun	3	4138	12414	381	0.031
	Youth-Adult	2	1794	3588	125	0.035
1982	Gun	3	3460	10380	604	0.058
	Youth-Adult	2	2410	4820	244	0.051

It appeared that prebait visitation rate was the most reliable method for long-term monitoring of the black bear population on the Refuge. However, data on bear observations by hunters may be easily obtained and can provide valuable information on the fall distributions and litter sizes of black bears on the Refuge.

Sex ratio. More males (N = 39, 61 percent) than females (N = 25, 39 percent) were captured during the study, however, sex ratios of capture samples in different years varied considerably. In 1979 and 1980, male:female ratios of 1.2:1 and 1.1:1, respectively, approximated the theoretical 1:1, but in 1981, significantly more males than females were captured (2.5:1, $P<0.025$). The overall sex ratio of 1.56:1 deviated only marginally ($0.1>P>0.05$) from a 1:1 ratio (Table 12).

A greater proportion of males in black bear capture samples may result from inherent differences in trapability between sexes. Males range over larger areas, increasing their exposure to traps (LeCount 1980), and the aggressive nature of males also may increase their vulnerability to capture (Hamilton 1978). Yearlings of both sexes and 2-year-old females typically utilize very small home ranges (Rogers 1977), and wide intervals between traps may reduce the probability of capture in these cohorts. If I assume that these sampling biases were reduced or eliminated by utilizing camouflaged foot snares and maintaining a relatively small trap-spacing (e.g., less than the home range length of juveniles and 2-year-old females),

Table 12. Sex ratios in black bear capture samples on White River NWR, Arkansas, 1979-1981.

Year	Male	Female	Ratio
1979	6	5	1.2:1
1980	13[a]	12	1.1:1
1981	20	8	2.5:1
Total	39	25	1.56:1

[a] Includes one "free-range" capture (page 44).

the preponderance of males in the capture sample indicated an unbalanced sex ratio in favor of males in the Refuge population. Beecham (1983) hypothesized that such a situation was indicative of unexploited (i.e., unhunted) black bear populations and that sex ratios favoring females should occur in capture samples from exploited populations. Results of my study support this hypothesis.

Sex ratios reported from other black bear populations include 0.8:1 in Washington (Lindzey and Meslow 1977a) and Minnesota (Rogers 1977), 1.15:1 in Pennsylvania (Matula 1976), 1.2:1 in Arizona (LeCount 1980) and Tennessee (Beaman 1975), 1.3:1 in Idaho (Beecham 1983), 1.5:1 in Michigan (Erickson 1964), and 2.5:1 in North Carolina (Hamilton 1978). Clearly a greater proportion of males in capture samples has been observed most often.

Age structure. Capture samples were used to estimate the age structure of the population. Data from 1979, 1980, and 1981 were pooled due to small yearly samples (11, 25, and 28, respectively). Given the relatively low reproductive potential of black bears (Jonkel and Cowan 1971) and the low mortality rate of radio-instrumented bears during this study (page), it is unlikely that a major change occurred in the age distribution of bears in this unexploited population over this time period.

There was considerable uncertainty over the accuracy of the base of the age pyramid derived from the capture sample (Figure 9). The estimate of the cub cohort was based on the proportion of mature

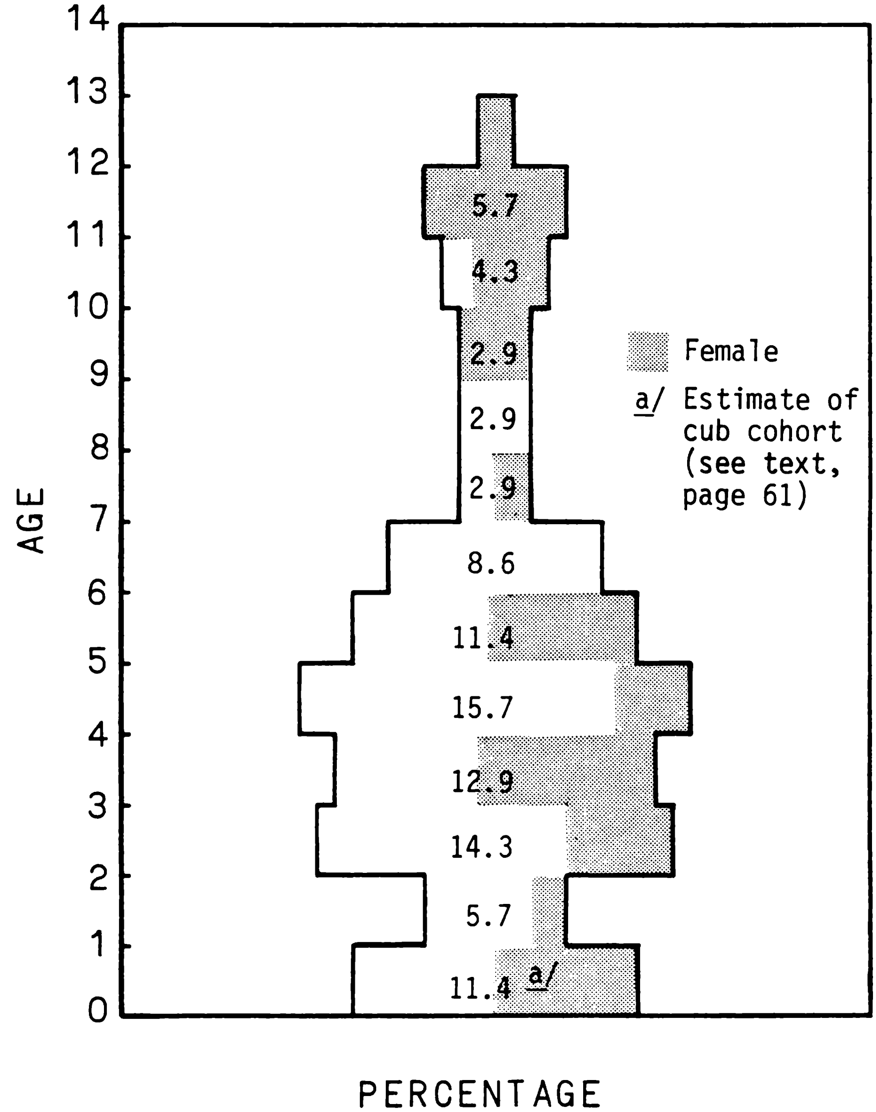

Figure 9. Age pyramid of black bears captured on White River NWR, Arkansas, 1979-1981. (Annual capture samples were pooled assuming a stable age distribution over the sampling period.)

females in the capture sample, fecundity of radio-collared females, and cub survival. I believe that this estimate approximated the actual proportion of cubs in the population. However, the probability of capture for yearlings may have been low and if so, this age class was likely underrepresented in the capture sample.

Reproductive recruitment in black bear populations may be dramatically reduced when nutritional stress leads to unsuccessful breeding or high cub mortality (Robers 1977). The low proportion of yearlings in the Refuge capture sample was not likely due to a single year of high cub mortality since my sampling was done over a 3-year period. Furthermore, consecutive years of depressed cub recruitment would have been reflected in proportions of other age classes (i.e., 2- and 3-year-olds) in the capture sample. Reproductive success of radio-collared bears, cub survival, and the number of litters observed by deer hunters between 1979 and 1981 indicated no marked decrease in reproductive recruitment over this period. It is more likely that behaviors (i.e., reduced movements and ranges) lowered the probability of capture of yearlings and that this age class constituted a greater proportion of the population than capture data indicated. Nonetheless, assuming that the yearling estimate was accurate, the proportion of immature ($\leq$ 2.5 years old) bears (31 percent) was not unusually low for an unexploited black bear population (LeCount 1982).

Females appeared to be longer-lived than males. Seven (28 percent) of 25 females captured were 9-12 years of age. No males (N = 37) greater than 10 years old were captured, and only 3 (8 percent) were $\geq$ 7 years of age. Subsequent radio-telemetry observations indicated, however, that both sexes reached greater ages on the Refuge than shown by capture data. Two females were known to attain 14 years of age, and 2 others were 12 years old when field work was terminated. In May 1982, 1 11-year-old, 1 9-year old, and 2 8-year-old radio-collared males were present in the population. With the exception of Hugie's (in press) data from Maine, longevity appears to be greater in female than male black bears (e.g., Beeman 1975, Rogers 1977, and Beecham 1983). In these and other studies (Hamilton 1978, Sauer 1975), a few individuals 15-25 years old were observed.

Growth Patterns

Relationships between age and body measurements of black bears captured on the Refuge indicated that growth was curvilinear in both sexes. For males, length and girth measurements were strongly related to age (Figure 10). Relationships between body size and age of females were less distinct and limited to measures of girth (Figure 11).

Rate of growth was somewhat greater for males, which reached peak body weight by 5 years of age, than for females. Females attained adult stature (i.e., length and height) earlier, possibly by 2 or 3 years of age, but continued to add weight and girth until they were 9 or 10 years old. Sauer (1975) reported that female black bears in New York attained adult size and sexual maturity by 2.5 years of age, but that long bone closure was not complete until about 8.5 years.

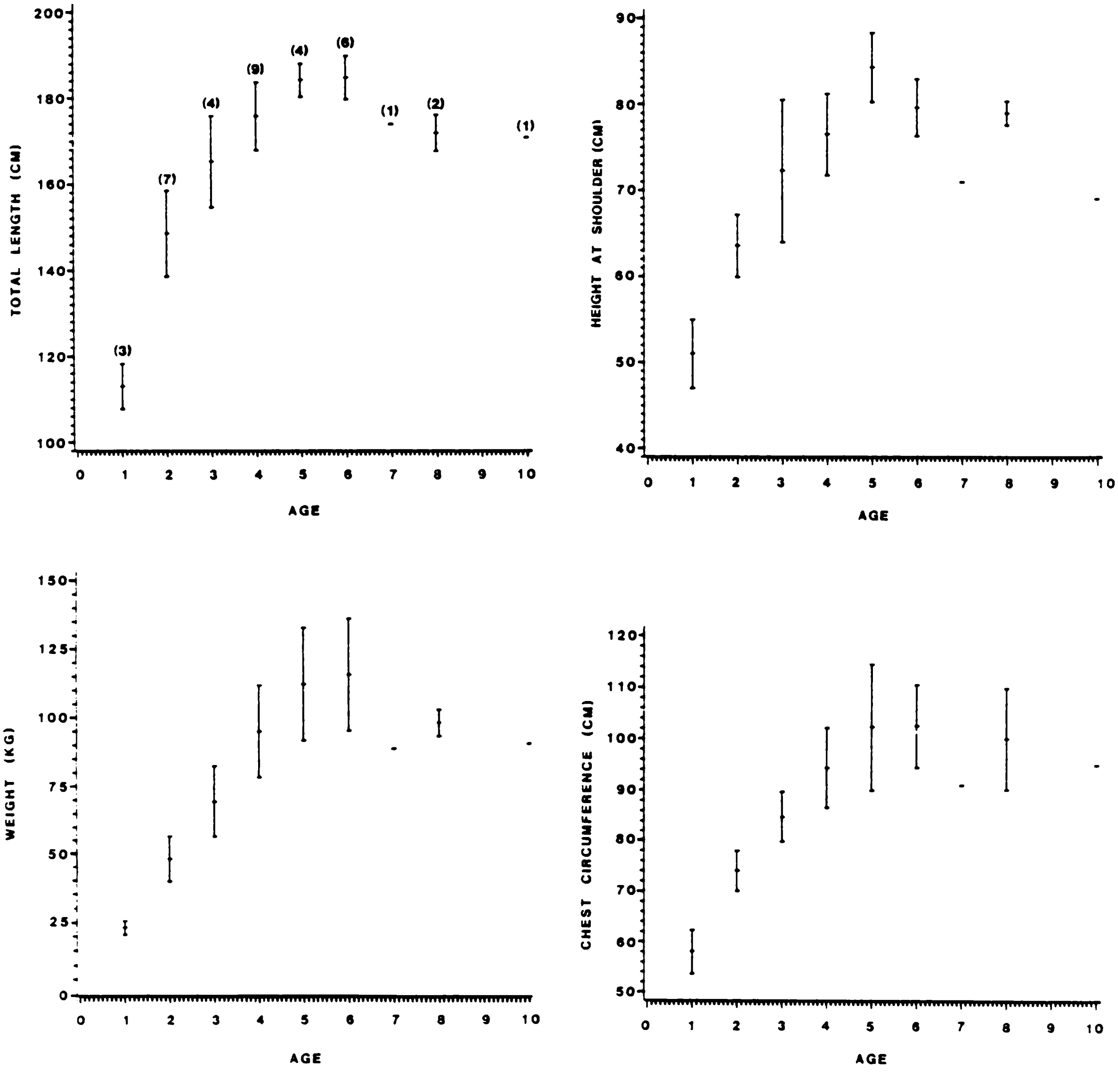

Figure 10. Relationships between body measurements (mean ± standard deviation) and age of male black bears captured on White River NWR, Arkansas, 1979-1981. (Numbers in parentheses represent sample sizes.)

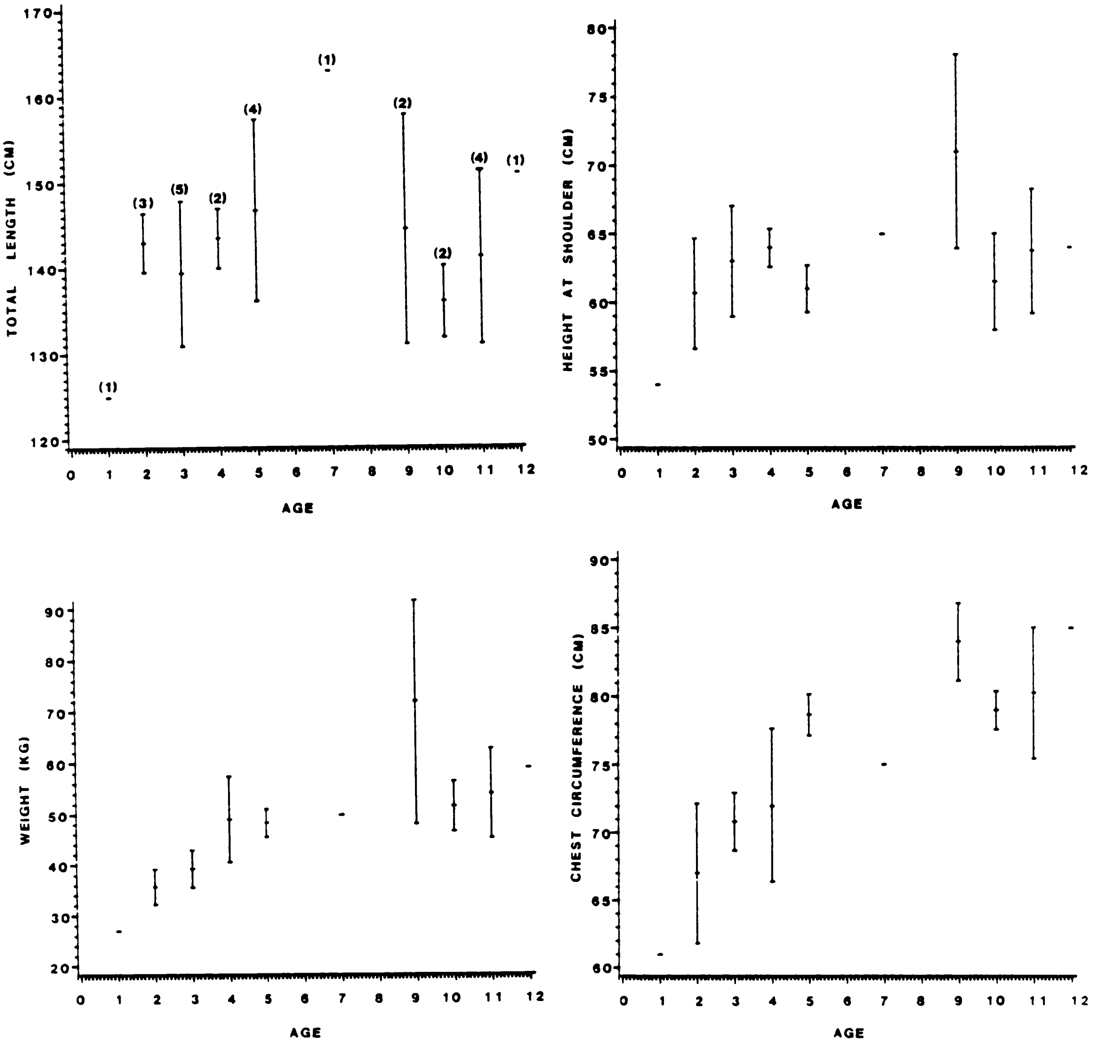

Figure 11. Relationships between body measurements (mean ± standard deviation) and age of female black bears captured on White River NWR, Arkansas, 1979-1981. (Numbers in parentheses represent sample sizes.)

Sexual dimorphism was apparent by age 3, and mean weight of adult males (102.1 kg) was twice that of adult females (52.2 kg). Sauer (1975) noted that 1.5-year-old males and females were dimorphic, and Beecham (1980) reported distinct differences in weights of male and female black bears by 2.5 and 5.5 years in 2 Idaho populations, respectively. Rausch (1961) found that skulls of male and female black bears in Alaska were similar until 5 years of age.

In my study, sample sizes were very small, data were pooled over 3 years of sampling, and bears in the sample were captured between May and November. These factors may have added to the variation which I observed in body size within age-sex classes. This is particularly true for weight, which may vary between seasons and years due to food availability (Jonkel and Cowan 1971), and for females, by their reproductive condition (Rogers 1977). Considerable variation also was observed in linear measurements (e.g., total length, height at shoulder, and head length). These results indicate that body size has limited value as an index of age for black bears on the Refuge.

Reproduction

Age of sexual maturity. The age at which females became sexually mature (i.e., successfully bred) was determined from teat condition and measurements, lactation, or the presence of cubs for captured bears and the birth of cubs to radio-instrumented individuals (Table 13).

No female in the capture sample whose reproductive history could be reconstructed (N = 9) had successfully bred as a 2-year-old.

One radio-collared female which produced a litter at 4 years of age and 1 4-year-old which was lactating when captured had bred at 3 years of age. Two radio-instrumented females had their first litters at 5 years, 1 5-year-old was accompanied by cubs when captured, and another 5-year-old had previously nursed cubs, indicating that these females had bred at $\leq$ 4 years of age. A female which was radio-tagged as a 5-year-old and produced a litter the following winter and a 7-year-old which was accompanied by yearlings when captured had bred as 5-year-olds.

Based on these cases, one-third of the female black bears on the Refuge first bred successfully at 3 years of age, 75 percent had bred by 4 years of age, and 100 percent by age 5. Although derived from limited data, these results were consistent with most reports of sexual maturity in female black bears. In Idaho (Beecham 1980) and Washington (Poelker and Hartwell 1973), 33 percent of the females successfully bred as 3-year olds; in the Idaho population 93 percent had bred by 5 years of age. A higher proportion of sexually mature 3-year-old females was reported in North Carolina (80 percent) (Collins 1973) and Pennsylvania (88 percent) (Kordek and Lindzey 1980). In these two populations, as well as those in New York (Sauer 1975), Tennessee (Eiler 1981), and California (Graber 1982), there was evidence that 2-year-old females occasionally reached sexual maturity.

Nutrition has been shown to influence maturation and reproductive fitness of female black bears (Jonkel and Cowan 1971, Rogers 1976, Beecham 1980). The relatively young age of sexual maturity and

Table 13. Reproductive data for female black bears captured on White River NWR, Arkansas, 1979-1981.

Bear No.	Age	Weight (kg)	Teat width (mm)	Teat length (mm)	Was or had lactated no	Was or had lactated yes	Age of first[a] or known litter[b]	Reproductive status immature	Reproductive status mature
450	1	27	5	5	x		-	x	
418	2	36	4	4	x		-	x	
423	2	39	4	3	x		-	x	
434	2	45	7	6	x		-	x	
467	2	32	5	6	x		-	x	
403	3	36	-	-	x		-		?
405	3	36	-	-	x		-		?
430	3	39	7	7	x		4[a]		x
460	3	40	8	9	x		4[a]		x
451	4	55	8	5	x		5[a]		x
465	4	43	11	11		x	4[b]		x
429	5	45	8	7	x		6[a]		x
436	5	52	13	8	x		-		?
471	5	48	8	9	x		-		?
473	5	48	15	19		x	5[b]		x
452	7	50	15	25		x	5[b]		x
439	9	89	12	25		x	-		x
415	10	48	15	19		x	-		x
438	10	58	12	10		x	-		x
459	11	57	14	20		x	-		x
428	12	59	10	14		x	-		x

reproductive success of female black bears on the Refuge during this study suggest that the nutritional quality of this bottomland hardwood forest is high. My data on growth (page 70) and home range size (page 131) support this interpretation.

Age of sexual maturity of males was determined from testicular size and the occurrence of fighting scars. Testicular weights correlated with sexual maturity of black bears in Michigan (Erickson et al. 1964), and fighting scars and wounds have been associated with breeding activity of males (Rogers 1977), particularly in unexploited populations (LeCount 1982).

Fighting scars were absent on all yearling and 2-year-old males ($N = 10$) and 2 of 4 3-year olds (Table 14). All males $\geq$ 4 years old ($N = 23$) exhibited signs of fighting. Testes of yearlings and 2-year-olds were distinctly smaller than those of males $\geq$ 3 years of age. The testes of 1 3-year old, which did not show signs of fighting, were distinctly smaller than those of other males 3 years old or older.

These data indicate that male black bears on the Refuge may become sexually mature at 3 years of age but probably are not successful breeders at that age. Mean body weight of 3-year-olds (70 kg) was significantly less ($P<0.02$) than that of 4-year-olds (95 kg). Given the large proportion (62 percent) of males $\geq$ 4 years old and relatively high density of the population, it is doubtful that many younger, smaller 3-year-olds compete successfully for females. Erickson and Nellor (1964) found that few males lighter than 59 kg or less than

4 years old were sexually mature. Hugie (in press) concluded that no males less than 3 years of age were capable of breeding and reported that 12 and 48 percent of the 3-year-old males in two populations were mature. Rogers (1977) observed no males less than 4 years old paired with a female in Minnesota.

Breeding period. A limited number of observations were made relative to the breeding period of black bears on the Refuge. No females captured during the study exhibited swollen vulvae characteristic of breeding. Three females examined on 13 June, 27 June, and 18 July, respectively, had slightly stretched vulvae, and 2 females handled on 24 July and 24 August, respectively, exhibited unusual red spots on the inside margin of the vulva. These conditions may have been related to breeding activity.

The female captured on 24 July was paired with an adult male on 18 July. Three other male/female pairings of radio-collared individuals were observed by telemetry on 13 July, 18 July, and 13 August, respectively. Each of these females produced litters the following winter. On 10 July a large adult male was observed following the trail of a smaller bear (apparently a female) minutes after she passed.

A single case of family breakup involving a radio-collared female and her yearling male offspring occurred on 11 July. Fresh or cicatrizing fighting wounds were observed on adult males (N = 8) between 27 June and 27 August.

Table 14. Criteria for determining age of sexual maturity of male black bears on White River NWR, Arkansas, 1979-1981.

Age	N	Weight (kg) $\bar{X}$ ± S.D.	Mean testes measurements			Signs of fighting		Reproductive status	
			width (cm)	length (cm)	circ. (cm)	N	%	immature (%)	mature (%)
1	3	23 ± 3	1.6	3.4	-	0	0	100	0
2	7	48 ± 8	2.5	4.5	8.0	0	0	100	0
3	4	70 ± 13	4.0	8.0	11.5	2	50	50	50
4	9	95 ± 17	4.0	7.5	11.8	8	89	11	89
5	4	113 ± 21	-	-	-	4	100	0	100
6	6	116 ± 20	4.5	8.7	12.8	6	100	0	100
≥7	4	94 ± 6	3.8	7.3	11.3	4	100	0	100

Based on these observations, black bears may breed from mid-June to late-August on the Refuge. I believe that the most reliable of these data are cases of male/female bonds and that most breeding occurs between mid-July and mid-August.

The mating period of black bears has been reported to peak between mid-June and mid-July in Alaska (Rausch 1961), Michigan (Erickson and Petrides 1964), Minnesota (Rogers 1977), Montana (Jonkel and Cowan 1971), and Washington (Lindzey and Meslow 1977a). Rausch and Rogers believed that there was little geographic variation in the chronology of breeding, however, data presently available indicate that the breeding period of black bears may vary between years and geographic regions and extend over a long time period, particularly into August.

Jonkel and Cowan (1971) observed breeding activity between late May and August in Montana. In California, estrous females were captured from April through September (Graber 1982). Stickley (1961) and Alt (1982) also reported substantial breeding activity during August. In the Great Smoky Mountains National Park, Beeman (1975) noted breeding between 17 June and 17 August, and later, Eiler (1981) and Wathen (1983) observed females in estrus from 5 June-12 September and 22 June-18 August, respectively. Hence, observations related to breeding activity of black bears on the Refuge fall within the broad limits of the mating season reported for this species across its range.

Breeding frequency. The frequency of breeding (i.e., litter production) by adult females on the Refuge was estimated from the reproductive histories of 6 individuals. One female produced litters in 1979, 1981, and 1983; two others bore cubs in 1980 and 1982. Three females were known to have skipped at least 1 year (i.e., $\geq$ 3-year interval) between litters. From these data, the mean breeding frequency for females was estimated at 2.4 years.

There are no reports of female black bears maintaining their potential breeding frequency of 1 litter every 2 years in wild populations, although it has been approximated in Tennessee (Wathen 1983) and possibly in Virginia (Stickley 1961). Graber (1982) reported an average interval of 2.8 years in Yosemite National Park, and Reynolds and Beecham (1980) observed a 31 percent litter frequency (i.e., approximately 3-year interval) in an Idaho population. Rogers (1977) and Jonkel and Cowan (1971) found considerable fluctuation in litter frequencies between years with some females producing cubs at intervals of 4 years or longer.

Availability and quality of mast may greatly influence the fecundity of female black bears (Rogers 1976), and the scarcity or low nutritional value of foods may cause complete reproductive failure (Jonkel and Cowan 1971, Rogers 1977, Wathen 1983). This relationship between food and reproduction also may lead to reproductive synchrony among the adult females in a population (Lindzey and Meslow 1977a, Free and McCaffey 1972). There was no indication that either of these factors was operating in the Refuge population. In 1981, following good overcup oak mast production in the fall of 1980, 4 of 6 adult females produced litters. In 1982, following relatively low food availability in the fall of 1981, 5 of 6 females bore cubs.

Birthing dates. Approximate birth dates of 9 litters born by radio-collared females were determined during this study. Due to the inaccessibility of certain maternal dens and the effort to minimize disturbances to pregnant females, some birth dates were not well-defined (Table 15). Most litters were born during the last week of January and the first two weeks of February. Of 7 births between 30 January and 29 February, 5 apparently occurred during the first half of February. One litter was born prior to den inspection on 21 January and another between inspections on 8 January and 19 February.

Parturition in black bears has generally been assumed to occur in late January and early February (e.g., Poelker and Hartwell 1973, Erickson and Nellor 1964, Rausch 1961). Alt (1983) argued that there is little evidence for this assumption and that data which exist are mostly from captive bears. He reported that 32 black bear litters were born in Pennsylvania between 3 January and 24 January and suggested that parturition in this species may occur earlier than traditionally assumed. My observations do not support this notion. Rather, they suggest that birthing dates for black bears probably vary between geographic regions.

Litter size. Sizes of 9 litters born by radio-collared females, plus 1 litter of an unmarked female observed in May, were used to

Table 15. Approximate dates of birth of litters of radio-instrumented black bears on White River NWR, Arkansas, 1980-1982.

Winter	Female	Date of litter birth
1980-81	415	7 February ± 9 days
	428	9 February ± 8 days
	429	12 February ± 8 days
	451	Between 8 Jan. and 19 Feb.
1981-82	460	31 January ± 1 day
	439	6 February ± 4 days
	430	5 February ± 5 days
	438	20 February ± 9 days
	452	Before 21 January

[a] Mean date between the last den inspection when cubs were not present and the first den inspection when they were.

estimate the mean size of black bear litters at birth (Table 16). Sizes of 2 litters were estimated because recordings of cub vocalizations at these dens could not be confidently interpreted. A minimum of 2 cubs was verified, but in each case a third cub may have been present. These litters were not censused visually and since litters of 3 were not uncommon on the Refuge, I estimated their size at 2.5 cubs each.

The observed average litter size at birth of 2.3 cubs (Table 16) closely approximated reports from other black bear populations in the eastern United States. There is evidence that litter sizes are larger in the east than in western regions, and several authors (e.g., Jonkel and Cowan 1971, Beeman 1975, Hamilton 1978, and Reynolds and Beecham 1980) have summarized existing data on litter sizes to demonstrate this trend. In habitats or geographic regions most closely related to the Refuge, reported litter sizes have been 2.2 in Florida (Harlow 1961) and North Carolina (Collins 1974) and 2.6 in East Tennessee (Eiler 1981, Wathen 1983).

Mortality

Cub mortality. Based on the reduction in mean litter size from birth (Table 16) to 9-12 months post-partum (Table 17), I estimated that the mean annual cub mortality rate on the Refuge was 32 percent between 1979 and 1982. This estimate is relatively high compared to reports from other studies. In Arizona (LeCount 1980) and Tennessee (Wathen 1983) cub mortality rates of 52 percent and 38 percent,

Table 16. Black bear litter sizes at birth on White River NWR, Arkansas 1979-1981.

Year	Female	Litter size
1979	unmarked	3.0
1980	415	2.0
	428	2.0
	429[a]	2.5[b]
	451[a]	2.5[b]
1981	430[a]	3.0
	438	1.0
	439	2.0
	452	2.0
	460[a]	3.0
	Total =	23.0, $\bar{X} = 2.3$

[a] First litter.

[b] Estimate (see page 83).

Table 17. Black bear litter sizes at 9-12 months after birth on White River NWR, Arkansas, 1979-1982.

Data source	Year	No. litter observations	No. cubs observed	Mean litter size
UT and Refuge personnel	1979	12	18	1.50
	1980	2	4	2.00
	1981	6	10	1.67
	1982	2[a]	1	0.50
	Subtotal	22	33	1.50
Hunter observations	1979	13	21	1.62
	1980	5	10	2.00
	1981	43	69	1.60
	1982	45	67	1.49
	Subtotal	106	167	1.58
	Grand total	128	200	1.56

[a] Includes 1 litter which drowned in a maternal den in April 1982.

respectively, were observed, however, in other studies (Alt 1982, Erickson and Petrides 1964, Jonkel and Cowan 1971, Kemp 1972, Lindzey and Meslow 1980, Rogers 1976) cub mortality ranged from 13 to 30 percent.

Survival of black bear cubs appears to be related primarily to food abundance and the subsequent nutrition of parturient females (Jonkel and Cowan 1971, LeCount 1982, Reynolds and Beecham 1980, Rogers 1977, Wathen 1983). Infrequent causes of cub mortality include cannibalism (Lindzey and Meslow 1977a, LeCount 1982), flooding of maternal dens and inexperience of young mothers (Alt 1982), and predation (Rogers 1977). Mast production on the Refuge appeared to be high, and the age of sexual maturity, breeding interval, and litter size of females indicated that they were well-nourished. I did not handle parturient females or their newborn cubs, but observations of 7 litters shortly after den emergence gave no indication that malnutrition was related to cub mortality. There also was no indication that litters of new mothers were either less well-nourished or experienced higher mortality than those of multiparous females. There were no observations or suspected cases of cannibalism, but this or other more indirect social factors (e.g., harassment of litters) cannot be ruled out.

Two cubs which drowned in a tree den constituted 13 percent of the mortality observed in litters of radio-collared females. Given the types of dens utilized by females (pages 124-125) and frequency of spring flooding on the Refuge, such occurrences may not be uncommon.

However, they probably do not account for the degree of cub mortality which I observed. Flooding may indirectly contribute to cub mortality by delaying phenological development and restricting the movements of females with young cubs.

My inspections of maternal dens following den emergence indicated that no cubs died in dens other than the litter which drowned. It appeared, however, that most cub mortality occurred prior to fall, possibly shortly after den emergence. Two females that gave birth to 2 or more cubs in early February 1981 were accompanied by only 1 cub on 5 July and 8 July, respectively. Alt (1982) reported a "number" of cases of cub mortality in dens, primarily due to flooding or collapse of the den. Rogers (1977) and LeCount (1980) found that most cub mortality occurred shortly after den emergence.

Mortality of bears ≥ 1-year-old. Radio telemetry data indicated that mortality rate was low for bears ≥ 1-year-old. Of 26 individuals radio-monitored for periods of 6 months or longer, 2 died. One 11-year-old female was shot in late September or early October 1979 near the edge of a soybean field at the periphery of the Refuge. At approximately the same time, a 9-year-old female died within the interior of the Refuge. Due to the degree of decomposition of the carcass, the cause of her death was not determined.

Based on observed survival of radio-collared individuals, annual mortality rate of bears ≥ 1.5 years old was approximately 5 percent. Reported mortality rates from other black bear populations have been considerably higher. In Michigan (Erickson and Petrides 1964), Minnesota (Rogers 1976), and Alberta (Kemp 1972) yearling mortality rates of 4 percent, 18 percent, and 27 percent, respectively, were observed. Mortality rates of 2-year-olds were 21 percent in Michigan (Erickson and Petrides 1964) and Washington (Lindzey and Meslow 1980) and 27.5 percent in Alberta (Kemp 1972). For bears $\geq$ 3 years of age and $\geq$ 5 years of age, mortality rates of 12.5 percent (Kemp 1972) and 21 percent (Lindzey and Meslow 1980) have been reported.

Mortality of males during their first and second years of independence may be high due to dispersal, nutritional stress, and human-related causes (Rogers 1977). In the closed Refuge population, there was no evidence of long dispersal by young males. However, conflicts between young and adult males may have occurred as the young attempted to establish permanent ranges. Before losing radio contact, 2 yearlings survived to 2.5 years of age, and 3 2-year-olds survived to 3.5 years of age. Two males captured at an age of 2.5 years were recaptured when 3.5 and 4.5 years old, respectively.

Refuge records and my observations indicated that illegal killing of black bears was not uncommon on the Refuge, often occurring during managed deer hunts. This may be an important source of mortality among subadult and adult bears on this area.

Food Habits

Contents of 195 scats collected between June 1979 and May 1982 included 26 food items and 4 forms of debris (Table 18). Plant foods

Table 18. Items identified in black bear scats collected on White River NWR, Arkansas, 1979-1982.

Type	Category	Item
Plant	Herbage	Green stems and leaves (unidentified)
		Grass (unidentified)
		Winter wheat
		Naiad
		Oak flowers
	Soft fruit	Common persimmon
		Common pokeberry
		Dogwood (*Cornus* spp.)
		Greenbrier
		Muscadine grape
		Peppervine
		Possumhaw holly
		Red mulberry
		Rubus spp.
		Swamp privet
	Hard mast	American lotus
		Oak (*Quercus* spp.) acron
Animal	Insect	Ant (Formicidae)
		Beetle (Coleoptera)
		Honeybee (insects and wax)
		Insect larvae (unidentified)
		Yellow jacket
	Fish	Fish (unidentified)
	Mammal	Muskrat
		Rabbit (*Sylvilagus* spp.)
		White-tailed deer
Debris	Debris	Stems and leaves (dried)
		Wood (chewed)
		Soil and/or rock
		Black bear hair

were partitioned into three conventional categories: herbage, soft fruits, and hard mast. Herbage included unidentified green stems and leaves, grass, winter wheat, naiad (*Naja guadalupensis*), and oak (*Quercus* spp.) flowers. Soft fruits or berries of common persimmon, common pokeberry, dogwood (*Cornus* spp.), greenbrier, muscadine grape (*Vitis* spp.), swamp privet, peppervine, possumhaw holly, red mulberry (*Morus rubra*), and dewberry/blackberry (*Rubus* spp.) were represented. Hard mast included oak acrons and the nuts of American lotus (*Nelumbo lutea*).

Animal foods were categorized as insect, fish, or mammal. Insects included ants (Formicidae), yellow-jackets (*Vespa maculifrons*), honeybees (*Apis mellafera*), unidentified larvae, and beetles (Coleoptera). Beeswax occurring with honeybees was included as insect matter. Fish remains were not identified to species and were considered categorically. Mammals represented in the sample were white-tailed deer, muskrat, and rabbit (*Sylvilagus* spp.). Dried stems and leaves, chewed wood, soil, and rock debris were apparently incidentally ingested with food items, particularly insects. Black bear hair also was considered debris.

Due to small sample sizes, scat data were pooled over years. While plant phenology and the availability of certain foods may have varied between years, field observations indicated that annual differences were minor, at least within food categories.

Initially I examined mean monthly percentage volumes of important food categories to identify temporal patterns of diet (Figure 12).

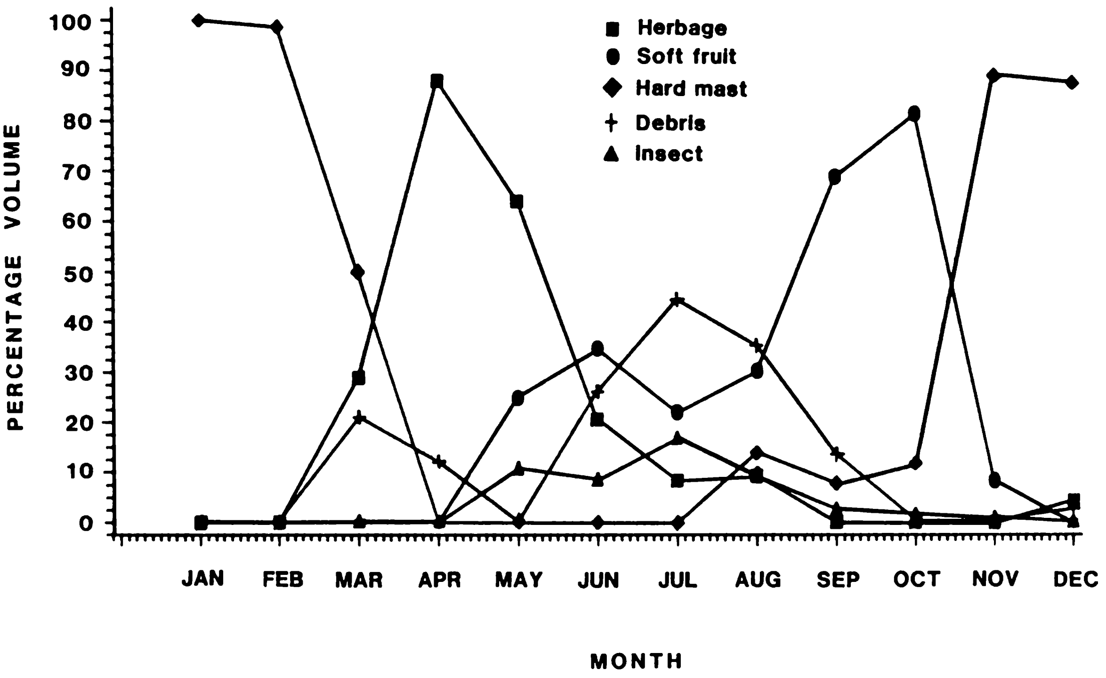

Figure 12. Mean monthly percentage volume of 4 food categories and debris in black bear scats collected on White River NWR, Arkansas, 1979-1982.

This delineated three dietary periods which corresponded to seasonal availability of foods and were consistent with the opportunistic, omnivorous, but mostly vegetarian food habits of black bears confirmed in numerous studies of this species across its range (Maehr and Brady 1984, Eagle and Pelton 1983, Graber and White 1983, Landers et al. 1979, Hatler 1972, Bennett et al. 1943). These and other studies have demonstrated that plant foods predominate in the diet of black bears in all seasons with herbaceous plants utilized in spring, fleshy fruits in summer, and depending on the geographic region, soft fruits or hard mast in the fall. Animal foods, mostly insects, are utilized less frequently and in small proportions but may be an important source of protein throughout the year.

Spring. Few foods are available to black bears in spring, and they depend upon a high fiber diet of largely undigestible and nutritious green plant material (Eagle and Pelton 1983). Poelker and Hartwell (1973) termed this the "negative foraging period" in which bears lose weight (Rogers 1976, Beeman 1975, Jonkel and Cowan 1977). This weight reduction apparently represents the loss of fat reserves (Eagle and Pelton 1983).

Relatively few scats were collected on the Refuge during spring (N = 31, 16 percent), but it was clear that herbage predominated in the diet in that season (Figure 13). Grass and green stems and leaves were most common and constituted 31 and 21 percent, respectively, of the herbage volume. Oak flowers and winter wheat also were represented.

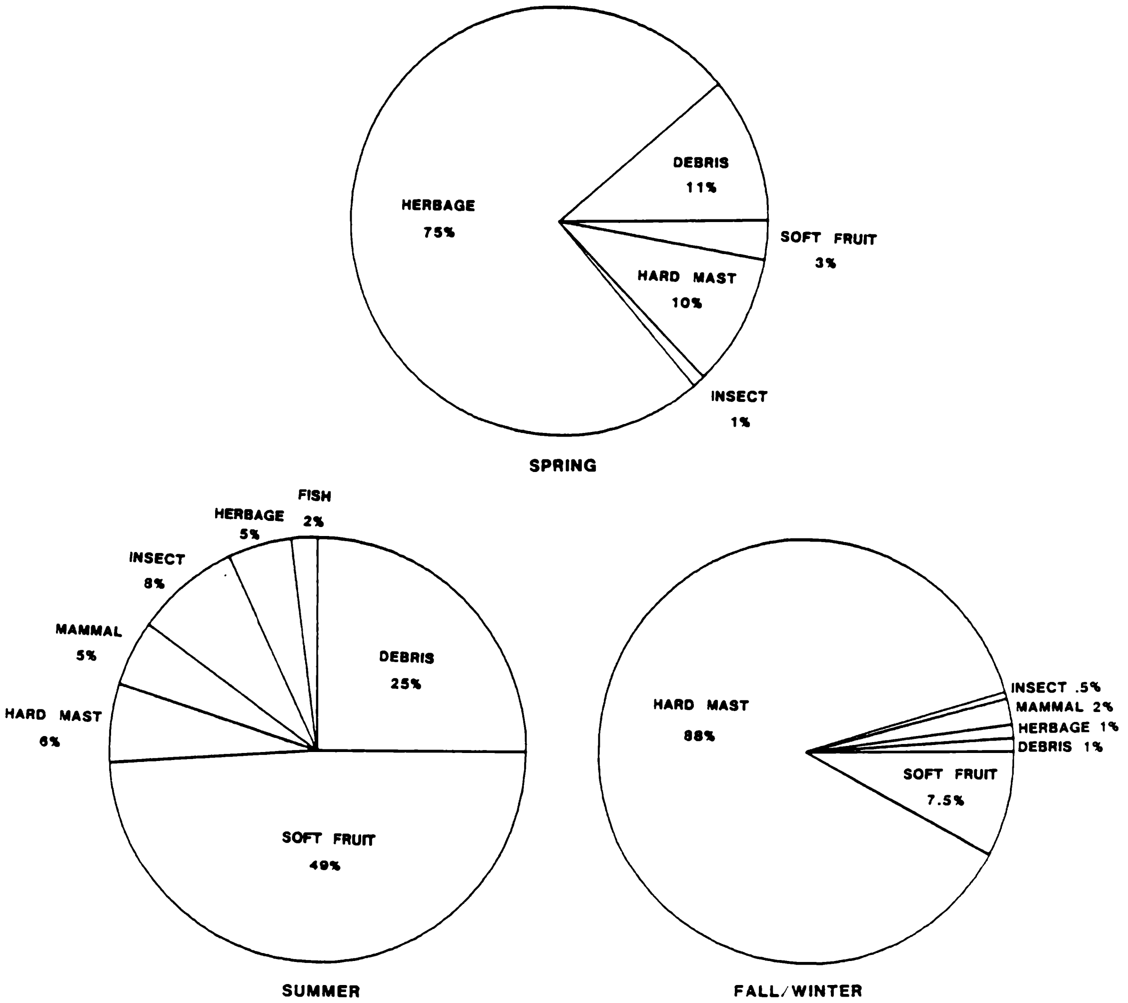

Figure 13. Seasonal mean percentage volume of items occurring in black bear scats collected on White River NWR, Arkansas, 1979-1982.

A 3-year-old male consumed large amounts of oak flowers in an unflooded portion of the Refuge following den emergence in early April 1980, and I commonly observed bears high in the branches of trees both during and following the flood period. I believe that this represents a common feeding behavior of black bears in bottomland hardwood forest. In certain years or areas of the Refuge, spring flooding delays phenological development of understory plants, leaving the buds, new leaves, and flowers of canopy trees as the primary food source. Grenfell and Brody (1983) observed small amounts of oak flowers in July scats in California, and Roosevelt (_in_ Schullery 1983) wrote that black bears fed on ash (_Fraxina_ spp.) buds in Louisiana and Mississippi during spring.

For approximately 2 weeks during late spring 1981, an adult male concentrated his activity near the corner of a winter wheat field adjacent to the Refuge and fed exclusively on the maturing wheat. Residents of the area also reported bears in wheat fields during spring of that and other years, indicating that utilization of this food source was not uncommon.

A 3-year-old female consumed nuts of American lotus after emerging from her den about 1 March 1981. At that time of year vegetation on the Refuge had not begun to green-up, and over-wintered nuts and acrons were the only food available. This was the only case of hard mast occurring in spring scats, and I believe it is an unusual event. Oak acrons constituted 45 percent of the total volume of spring scats in Pennslyvania (Bennett et al. 1943). Grenfell and Brody (1983) found oak acorns in two spring scats in California. Nozaki et al. (1983) also reported that the Asiatic black bear (*Selenarctos thibetanus*) utilized over-wintered beech nuts and oak acorns in Japan.

Animal food occurring in spring scats was limited primarily to adult and larval beetles. This evidence and field observations indicate that bears frequently forage for grubs in decaying logs during this season. Beetles and chewed wood together represented 10 percent of the volume and occurred in 20 percent of spring scats. Beetles have been frequently observed in black bear scats, but their importance remains unclear. Landers et al. (1979) felt that they contributed little to the diet of black bears in coastal North Carolina, however, in East Tennessee beetles occurred in scats more frequently than other insects and composed 5 percent of the total volume (Beeman and Pelton 1980).

Bear hair was frequently observed in spring scats, two of which contained substantial amounts of this material. These samples were collected under den trees and consisted of matted hair mixed with green, amorphous mucous. They apparently were over-wintered gastro-intestinal contents. Johnson (1978) collected similar scats near den trees in the Great Smoky Mountains National Park, and several researchers have observed this type of material in and around dens of brown bears (*Ursus arctos*) and polar bears (*Ursus maritimus*) as well as black bears (Jonkel 1972). The common hypothesis is that these contents are packed in the lower intestine as bears groom during dormancy.

Summer. During summer, black bears on the Refuge maintained a relatively diverse diet. Protein- and carbohydrate-rich soft fruits replaced herbage as the staple food and considerable amounts of animal matter were incorporated into the diet. Red mulberry, dewberry, and swamp privet became available in late May and early June, the latter appearing to be mostly undigestible. Blackberry matured in late June and was frequently (38 percent) observed in July scats. In August, peppervine was the the most important fruit followed by muscadine grape, common pokeberry, and greenbrier. At that time bears also began to make limited use (14 percent volume) of immature oak acorns.

September was a distinct time when common persimmon fruits ripened and dominated the diet, occurring at a frequency of 92 percent and comprising 65 percent of the mean volume of 13 scats collected. Oak acorns continued to be utilized in small proportions. The importance of persimmon increased still further in October, when it composed 95 percent of the total volume and occurred in 19 of 20 scats. By late October, the availability of persimmon fruits declined sharply, and a dietary shift to matured oak acorns ensued.

During the first three months of summer small amounts of green plant material appeared in scats, but by September herbage had completely disappeared from the diet. An interesting observation was the occurrence of naiad, a submersed pondweed, in the stomach of an adult male which died at a trap site in early August 1979. I frequently radio-located bears near swamps and shallow lakes which had abundant aquatic vegetation, and on two radio-tracking occasions, bears were observed wading in lakes. Hatler (1972) reported that a black bear was shot in Alaska while feeding on emergent vegetation in 0.5 m-deep water and stated that observations of bears feeding "belly-deep in swamp water" were numerous. Landers et al. (1979) reported that bears fed on arrowarum (*Peltandra virginica*) in North Carolina swamps, and Maehr and Brady (1984) found substantial amounts of alligator flag (*Thalia geniculata*) in the spring diet of Florida black bears. Algae and rushes were commonly consumed by black bears in California (Grenfell and Brody 1983, Graber and White 1983).

The mean volume of animal matter in summer scats was 15 percent. Debris associated with these foods constituted an additional 25 percent of the total volume, indicating the importance of animal foods to bears during that season. Animal tissues are highly digestible, and their volumes in scats may be greatly reduced from those actually ingested (Poelker and Hartwell 1973, Hatler 1972). This discrepancy in plant and animal food digestibilities is evident when the frequency of occurrence and mean percentage volume of these food types are compared (Figure 14).

Insects, mostly social hymenopterans, were the most common animal food during summer (Figure 13). Carpenter ants occurred in 53 and 39 percent, respectively, of June and July scats and comprised 9 percent of the total volume in these months. The frequency of ants in August scats remained high (35 percent), but their importance in the diet may have begun to diminish since they represented only 2 percent of the total volume. Beeman and Pelton (1980), Grenfell and

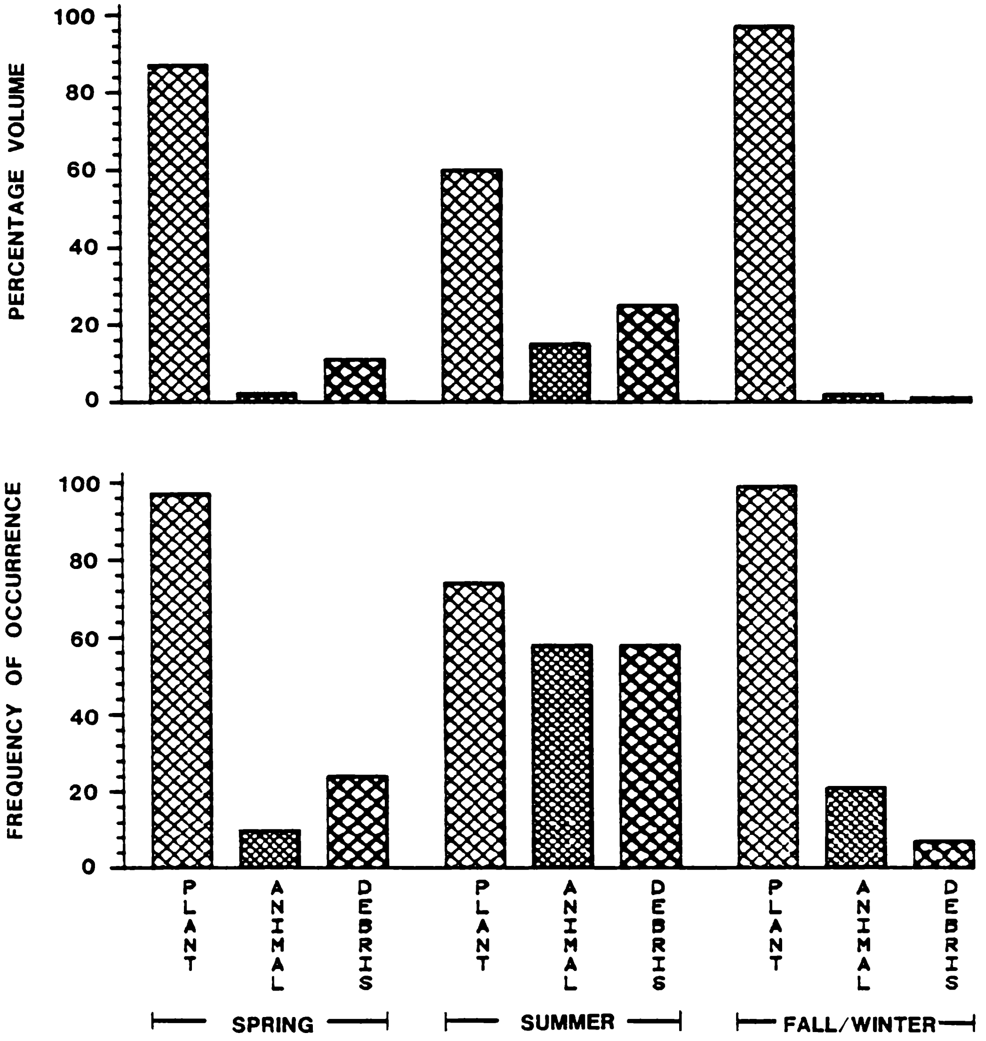

Figure 14. Relationship between seasonal mean percentage volume and frequency of occurrence of plant, animal, and debris matters in black bear scats collected on White River NWR, Arkansas, 1979-1982.

Brody (1983), and Graber and White (1983) found ants in black bear scats throughout the year, while Maehr and Brady (1984), Landers et al. (1979), and Hatler (1972) reported that the utilization of ants was greatest in spring and summer. Honeybees occurred in one scat in each of July and August. Maehr and Brady (1984), Landers et al. (1979), and Bennett et al. (1943) found that honeybees were most commonly used by black bears in fall.

As the utilization of ants declined, yellow-jackets assumed greater importance in the diet, occurring in 24 and 23 percent of August and September scats and constituting 1.3 and 2.5 percent of the total volumes, respectively. Other researchers (Maehr and Brady 1984, Beeman and Pelton 1980, Grenfell and Brody 1983, Hatler 1972) also have found that wasps (i.e., Vespula spp.) were more common in the fall diet of black bears than in other seasons. The utilization of insects declined in October when they occurred in 2 of 20 scats.

Fish appeared in the scat sample during late June and became increasingly important in the diet through September when it occurred at a frequency of 31 percent and a mean volume of 7.4 percent. I believe, however, that fish may contribute much more to the diet of black bears on the Refuge than scat contents indicated. Several radio-collared bears concentrated their activities near lakes which experienced a fish kill and complete desiccation, respectively, in the summers of 1980 and 1981. At the latter site I observed bears foraging on rotting carcasses of rough fish. During the late summer drought of 1980, I also observed a radio-collared female "fishing" gar (Lepisosteus spp.) from water less than 20 cm deep in a drying stream bed. On several occasions, I found the remains of gars, which had been consumed by bears, near a productive trap site off the bank of the White River. This site was above a permanent log drift in a bend of the river where dead fish, particularly gar killed by commercial fishermen, frequently accumulated.

Although fish is a preferred food of captive black bears (Bacon and Burghardt 1983), it has not been commonly reported as a food item in wild populations. Bears apparently catch and consume salmon in California (Graber and White 1983, Piekelek and Burton 1975) and Alaska (Frame 1974), and Juniper (1978) found fish in the stomachs of black bears in Quebec. Fish were not found in scats and stomachs from swamp-type habitats in Florida (Maehr and Brady 1984) and North Carolina (Landers et al. 1979).

The remains of three mammals, white-tailed deer, muskrat, and rabbit (Sylvilagus spp.), occurred in summer scats. Deer hair was found in 3 (16 percent) and 2 (15 percent) scats collected in June and July, respectively. Remains in one of the scats collected in June contained the hoof of a fawn. Grenfell and Brody (1983), Landers et al. (1979), and King (1967) reported increased incidences of deer remains in black bear scats during the fawning season.

Muskrat remains appeared as a trace in one July scat and composed nearly 100 percent of a scat collected in mid-October. Rabbit hair constituted approximately 50 percent of a scat from June. Snowshoe hare (Lepus americanus) was the most commonly occurring vertebrate in black bear scats in Alaska (Hatler 1972), and trace amounts of rabbit were found in scats in North Carolina (Landers et al. 1979) and Pennsylvania (Bennett et al. 1943). I am not aware of muskrat having been previously reported as a food item of black bears.

Fall/winter. A shift in the diet of black bears in fall to fat- and carbohydrate-rich nuts and acorns has been commonly observed (Maehr and Brady 1984, Eagle and Pelton 1983, Grenfell and Brody 1983, Landers et al. 1979, Bennett et al. 1943, and others). This behavior was strongly demonstrated by black bears on the Refuge where oak acorns occurred in 93 percent of fall/winter scats and accounted for 88 percent of the total volume. It appeared that the utilization of acorns in bottomland hardwood forest may be greater than in other habitats where black bear food habits have been studied. Grenfell and Brody (1983) reported that oak acorns occurred at a frequency of 92 percent and constituted 76 percent of the aggregate volume of scats during one October of their study, but the overall values for acorns during fall were well below these figures. Bennett et al. (1943) reported that oak acorns comprised 55-66 percent of the volume of fall scats in Pennsylvania. Beech nuts also were available in that area and represented 20 to 97 percent of the fall diet.

Overcup oak is the most abundant and consistent mast producing species on the Refuge, especially in the study area core. During falls of 1979 and 1980, radio-instrumented bears focused their activities on low flats where mature homogeneous stands of overcup oak occurred. In 1981, when overcup oak mast failed, red oak (e.g., water, willow, and Nuttall oaks) acorns and sweet pecans were abundant, and bears moved to ridges where these foods were located. Apparently, this alternate, but relatively limited, source of fat-rich food was nutritionally adequate. Reproductive success of radio-collared females in the following winter was high. Given the choice (e.g., in the fall/winter of 1980), however, black bears on the Refuge appear to prefer the acorns of white (i.e., overcup) oak over red oaks. Garshelis and Pelton (1981) noted that during fall black bears preferred areas of white oak abundance in the Great Smoky Mountains National Park. Possibly due to lower tannin, white oak acorns are preferred over red oak acorns by many species (Martin et al. 1951, Petrides 1972).

In fall/winter, animal food utilized by black bears on the Refuge was limited primarily to white-tailed deer. This item occurred in scats at a frequency of 18 percent and mean volume of 2 percent during this season. My observations and hunter reports indicate that bears scavenge wounded deer on the Refuge during managed hunts in October and November. Hatler (1972) and Bennett et al. (1943) commonly found deer in black bear scats during the hunting season, and it is generally believed that the use of deer and other cervids for food represents scavenging (Graber and White 1983, Beeman and Pelton 1980, Hatler 1972).

Beetles and yellow-jackets were the only insects present in fall/winter scats, and contributed little to the diet. During that period, they occurred at frequencies of 1 and 3 percent, respectively, and together comprised only 0.5 percent of the total volume of scats.

Results of this analysis, as well as field observations, indicate that the diversity and abundance of foods in the bottomland hardwood forest of the Refuge is high. Sources of protein, carbohydrate, and fat appear to be available to bears at high quantities in all seasons.

Denning

During the 3 years of the study, 42 cases of winter activity were monitored. Four individuals were followed through 3 winters, 11 through 2 winters, and 8 through 1 winter. A 2-year-old male and a 3-year-old male did not den in the winter of 1980-81. All other cases involved den entry, and with few exceptions dates of den entry and emergence, length of the denning period, den type, and den characteristics was determined. In addition, types of dens utilized by 4 radio-collared individuals (3 females, 1 male) during the 1982-83 winter were known.

Denning chronology. During the first winter of the study only 5 bears were radio-monitored. In the 2 subsequent winters, however, sample sizes of 19 and 18, respectively, were maintained, and distinct patterns of den entry and emergence were observed which indicated that denning chronology was related to sex, age, and reproductive condition (Table 19).

Pregnant females entered dens first ($\bar{X}$ = 15 Dec, N = 9), followed by barren adult females ($\bar{X}$ = 22 Dec, N = 4) and 2-year-old

Table 19. Denning chronology of black bears on White River, NWR, Arkansas, 1979-1982.

Sex	Age (reproductive condition)	1979-80				1980-81				1981-82				Total			
		N	Mean entry date	Mean emergence date	Mean No. days denned	N	Mean entry date	Mean emergence date	Mean No. days denned	N	Mean entry date	Mean emergence date	Mean No. days denned	N	Mean entry date	Mean emergence date	Mean No. days denned
M	Yearling	0	-	-	-	1	7 Feb	23 Mar	45	1	28 Feb	5 Apr	37	2	18 Feb	30 Mar	41
M	2-year-old	1	29 Jan	7 Apr	70	1	did not den			0	-	-	-		29 Jan	7 Apr	70
M	≥ 3-years-old	3	9 Feb	22 Apr (N=2)	80 (N=2)	8[a]	16 Jan	2 Apr	76	7	7 Jan	21 Mar	75	17	17 Jan	31 Mar (N=16)	76 (N=16)
F	2-year-old	0	-	-	-	2	4 Jan	3 Mar	59	0	-	-	-	2	4 Jan	3 Mar	59
F	≥ 3-years old (barren)	0	-	-	-	3	25 Dec	3 Apr	100	1	12 Dec	18 Apr	128	4	22 Dec	7 Apr	107
F	≥ 3-years-old (w/"coys")	1	25 Jan	1 May	97	0	-	-	-	4	17 Jan	13 Apr	85	5	19 Jan	15 Apr	87
F	≥ 3-years-old (pregnant)	0	-	-	-	4	17 Dec	26 Apr	131	5	14 Dec	28 Apr (N=4)	136 (N=4)	9	15 Dec	27 Apr (N=8)	134 (N=8

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[a] One individual did not den.

females ($\bar{X}$ = 4 Jan, N = 2). Adult males ($\bar{X}$ = 17 Jan, N = 17), adult females accompanied by cubs of the year ("coys") ($\bar{X}$ = 19 Jan, N = 5), and 1 2-year-old male (29 Jan) entered dens considerably later. In 1982, a yearling male did not den until 28 February.

Similar to den entry, emergence occurred over a span of approximately 2 months. Two 2-year-old females emerged distinctly earlier ($\bar{X}$ = 3 March) than all other bears. Mean emergence dates for 2 yearling males (30 March), adult males ($\bar{X}$ = 31 March, N = 16), barren adult females ($\bar{X}$ = 7 April, N = 4), and 1 2-year-old male (7 April) were similar. Adult femaels with yearlings ("coys" at the time of den entry) emerged during mid-April ($\bar{X}$ = 15 April, N = 5). Females with newborn cubs remained in dens until late April or early May ($\bar{X}$ = 27 April, N = 8).

Parturient females denned for significantly longer periods ($\bar{X}$ = 134 days, N = 8) than barren adult females ($\bar{X}$ = 107 days, N = 4), adult females with yearlings ($\bar{X}$ = 81 days, N = 5), and adult males ($\bar{X}$ = 76 days, N = 16) ($P \leq 0.02$). Sample sizes of other groups were too small for valid statistical comparisons, nevertheless, distinct patterns existed. Two yearling males denned for much shorter periods ($\bar{X}$ = 41 days) than other bears. Two 2-year-old females also denned for relatively short periods of 52 and 65 days ($\bar{X}$ = 59 days). One 2-year-old male denned for 76 days, the mean length of denning periods of older males.

The relatively mild flooding which occurred on the Refuge during the study occasionally forced bears to abandon dens and relocate to dry sites, but this appeared to have only minor effects on den emergence dates and the length of denning periods. In the spring of 1980, portions of the Refuge remained under 1 to 2 m of floodwater until the first week of May. This high water apparently held 1 adult female with a yearling and 2 adult males in their tree dens 2-4 weeks longer than usual. In the spring of 1981, when flooding did not occur, adult males and barren adult females emerged from dens during the first week of April.

In early April 1982, an adult male and a parturient female abandoned their tree dens when floodwater reached the den cavity. Both of these bears moved to alternate dens until flooding subsided 3 weeks later. Another adult male moved from ground dens twice in 1982 due to rising water. He also relocated to dry alternate areas where he remained through spring. Also in the spring of 1982, 1 adult male emerged from a dry tree cavity and swam through floodwater to another tree not having a cavity. He remained there for 2 weeks and then swam approximately 1 km to dry ground. In 1982, den emergence of a barren female (18 April) and 4 females with yearlings ($\bar{X}$ = 13 April) also may have been delayed by flooding. In 1981, when flooding did not occur, the mean den emergence date for 3 barren adult females was 3 April (Table 19).

It is not unusual for flooding to continue into May or June in the lower White River basin (e.g., 1968, 1973, 1983, 1984). In such cases females with young cubs are likely confined to den trees beyond the normal emergence period, and cub survival may be affected. Other bears appear to be less restricted by flooding, swimming from tree to tree or to higher ground. Except in extremely high water (e.g., in 1973), dry ridges and second bottom terraces are accessible to bears within or near their home ranges.

Patterns of denning chronology on the Refuge were similar to those reported in other black bear populations. Early den entry by pregnant females was observed in Idaho (Beecham et al. 1983), southern California (Novick et al. 1981), Alberta (Tietje and Ruff 1980), coastal Washington (Lindzey and Meslow 1976a), and Louisiana (Taylor 1971). In New York, pregnant and barren females denned before adult males (O'Pezio et al. 1983), and adult females denned earlier than all other groups in Arizona (LeCount 1983), Michigan (Erickson 1964), Montana (Jonkel and Cowan 1971), North Carolina (Hamilton and Marchinton 1980), and East Tennessee (Johnson and Pelton 1980b). In the North Carolina and Tennessee studies, order of entry was similar to that on the Refuge, i.e., adult females denned first, followed by adult males and subadults of both sexes. In Alberta, Michigan, Montana, and Washington, subadults entered dens before adult males. Beecham et al. (1983) and O'Pezio et al. (1983) found no difference in entry dates of subadults and adults.

The sequence of den emergence is generally the reverse of den entry. Subadults of both sexes, adult males, and females with yearlings emerge first (O'Pezio et al. 1983, Lindzey and Meslow 1976a, Jonkel and Cowan 1971, Erickson 1964, this study). Females with young cubs are the last to leave dens (O'Pezio et al. 1983, LeCount 1983, Novick et al. 1981, Johnson and Pelton 1980b, Tietje and Ruff 1980, this study). This pattern also has been observed in brown bears (Servheen and Klaver 1983, Craighead and Craighead 1972a).

The duration of dormancy in black bears on the Refuge approximated those reported from other areas of southeastern United States. In east Tennessee, Johnson (1978) observed den entry between 15 December and 15 February, emergence between 11 March and 4 May, and denning periods ranging from 59 to 119 days. In coastal North Carolina, Hamilton (1978) observed den entry by 3 adult females between 5 December and 22 December. An adult male and a subadult female denned on 28 December and 3 January, respectively. Denning periods ranged from 85 to 113 days with the latest emergence occurring on 22 April. In a bottomland hardwood forest in Louisiana, a pregnant female entered her den on 20 November and remained denned for 121 days; an adult male was denned between 10 December and 10 March (91 days), and an adult female with a "coy" was denned from approximately 31 December to 7 March (77 days) (Taylor 1971). Comparable denning periods also were reported for black bears in southern California, an area of relatively mild winters, where 7 males denned an average of 93 days, 1 female with a "coy" denned for 106 days, and a parturient female denned for 159 days (Novick et al. 1981).

The duration of dormancy increases with the severity and length of winters. LeCount (1980) observed mean denning periods of 116 days, 139 days, and 167 days for adult males, nonpregnant females, and pregnant females, respectively, in Arizona. In coastal Washington, the mean denning period for all bears was 126 days (Linzey and Meslow 1976a). Considerably longer denning periods (approximately 5.0-6.5 months) have been reported for black bears in Minnesota (Rogers 1977), Montana (Jonkel and Cowan 1971), Idaho (Beecham et al. 1983), Alberta (Tietje and Ruff 1980) and Alaska (Erickson 1965).

Variations in the timing and duration of dormancy in bears have been attributed to snowfall (Novick et al. 1983, Craighead and Craighead 1972b, Jonkel and Cowan 1971, Northcott and Elsey 1971, Erickson 1964), rain and temperature (Johnson and Pelton 1980b, Lindzey and Meslow 1976a), food availability (Beecham et al. 1983, O'Pezio et al. 1983, Johnson and Pelton 1980b, Jonkel and Cowan 1971, Erickson and Youatt 1961), and physical condition (Lindzey and Meslow 1976a, Spencer 1955). Lindzey and Meslow proposed that attainment of a certain physiological condition represents the ultimate requisite to denning and that the cumulative effects of lowered temperature and increased precipitation through late fall proximately stimulate the denning response. Variation in the denning chronology of age and sex groups can then be explained by varying thresholds to this stimulus and/or different rates of food assimilation and fat deposition.

Johnson and Pelton (1980b) argued that physical condition should not function as an ultimate denning stimulus because of its correlation with food supply, a highly variable resource, i.e., "denning behavior appears to follow a more consistent pattern" (than food abundance). They hypothesized that a circannual, endogenous physiological rhythm, similar to that in "true" hibernators, has evolved in black bears and represents the ultimate denning mechanism. Limited evidence from recent studies in relatively mild climates indicates, however, that if a circannual rhythm induces a physiological readiness to den, it may be flexible and is circumvented under certain conditions. In southern California, one subadult male either did not den or denned for a very short period (Novick et al. 1983). Two subadult males monitored by Hamilton (1978) in coastal North Carolina remained active throughout mid-winter. Carpenter (1973) reported that black bears low in body fat continued activity during winter in Virginia, and recently, Carney and Vaughn (1984) reported that a young male displayed no sign of denning in Shenandoah National Park. In my study, 1 2-year-old male and 1 3-year-old male did not den during the 1980-81 winter.

If denning behavior (i.e., hibernation) is an energy conservation strategy, it seems more reasonable that physical condition, specifically body weight:stored fat ratio, would be the ultimate prerequisite for dormancy. During late fall, if more energy is lost than gained in foraging, the denning response also may be stimulated, even if a high body weight:stored fat ratio has not been attained. Black bears have been observed to extend activity during fall and early winter when foods were abundant (O'Pezio et al. 1983, Johnson 1978, Jonkel and Cowan 1971), and conversely, enter dens earlier when fall foods were scarce (Beeman 1975). On the Refuge, when oak acorns were abundant in the falls of 1979 and 1980, bears denned later than after the fall of 1981 when mast production was poor.

Food availability may explain the failure of certain individuals to den in relatively mild climates. In colder regions, where snow accumulation may render existing foods unavailable, dormancy would be selectively advantageous over energy-deficient foraging, regardless of the bear's physical condition. In milder climates with little or no snow accumulation (e.g., eastern Arkansas, southern California, and coastal North Carolina), fall foods may remain available through the winter, and energy-efficient foraging may be the best alternative for a bear which has not attained an adequate body weight:stored fat ratio. This ratio may be more difficult to accomplish in subadult males which grow at faster rates (and probably assimilate fat slower) than other groups (Beecham 1980, Sauer 1975, Rausch 1961, this study).

Degree of dormancy.

Activity of denned bears. On 11 occasions between 30 January and 28 February 1980 I continuously monitored radio signals of bears in tree dens to determine the activity levels of dormant bears and whether they intermittently left and returned to dens. Four bears (2 adult males, 1 2-year-old male, and 1 adult female accompanied by a yearling) were represented in the sampling. Monitoring sessions ranged from 2.4 to 14.2 hours ($\bar{X}$ = 4.4 hrs) (Table 20). Mean percentage activity for all sessions was 13.6, ranging from 1.7 to 27.1 percent. Periods of activity occurred at a mean rate of 1.7 per hour and lasted an average of 6.6 minutes. Both of these measures varied considerably. Periods of continuous activity as great as 57 minutes

Table 20. Activities of denned radio-collared black bears on White River NWR, Arkansas, January-February 1980.

Date	Bear No.	Time monitored (hrs)	Percentage activity	Mean No. of active periods per hour	Mean length of active periods (min)	Longest active periods (min)
30 Jan	407[a]	2.8	12.4	0.4	21.0	21
6 Feb	412[b]	2.4	6.9	1.3	3.3	4
7 Feb	407	3.0	1.7	1.0	1.0	1
8 Feb	412	2.4	8.4	2.9	1.7	4
11 Feb	415[c]	2.6	22.2	1.9	7.0	17
12 Feb	407	2.9	8.7	2.1	2.5	4
12 Feb	412	5.3	26.3	1.7	9.3	50
14 Feb	407	3.9	27.1	1.0	15.8	57
15 Feb	415	3.7	16.7	1.6	6.2	10
22 Feb	415	14.2	12.5	2.2	3.5	28
28 Feb	411[d]	4.7	6.4	2.8	1.4	3
	Means	4.4 hrs	13.6%	1.7 hr	6.6 min	-

[a] Adult male.

[b] Subadult male.

[c] Adult female accompanied by a yearling.

[d] Adult male.

were noted, but no movements from den trees occurred. Frequency and duration of activity appeared to be random, and most movements were likely momentary comfort shifts. The length of some active periods indicated that behaviors such as grooming or scratching also are common for denned bears.

Between 30 October 1980 and 16 April 1981, I conducted 9 24-hour radio-monitoring sessions in which hourly activity (i.e., active or inactive) was recorded for 6 to 15 bears ($\bar{X} = 10$). Through fall and prior to the initiation of denning, percentage activity decreased from 47 to 29 percent (Figure 15). After the onset of denning, bears markedly reduced their activity to a mean level of approximately 5 percent. Concomitantly, mean activity of bears not denned was 42 percent. Two bears which did not den in the 1980-81 winter maintained activity levels of 33-68 percent through the denning season.

Fidelity to dens. Numerous inspections of occupied dens indicated that black bears on the Refuge either remained in their den until spring or left without returning to the original den. Several cases of den abandonment occurred during early winter, but all followed disturbances by research personnel. It was unclear why a 4-year-old female abandoned her den in mid-February 1981, but she immediately moved to a second den tree where she remained until late March.

Lethargy. Denned bears were typically observed in the classic dormant or hibernating posture (Folk et al. 1980). At my presence, bears either did not react or lethargically raised and lowered

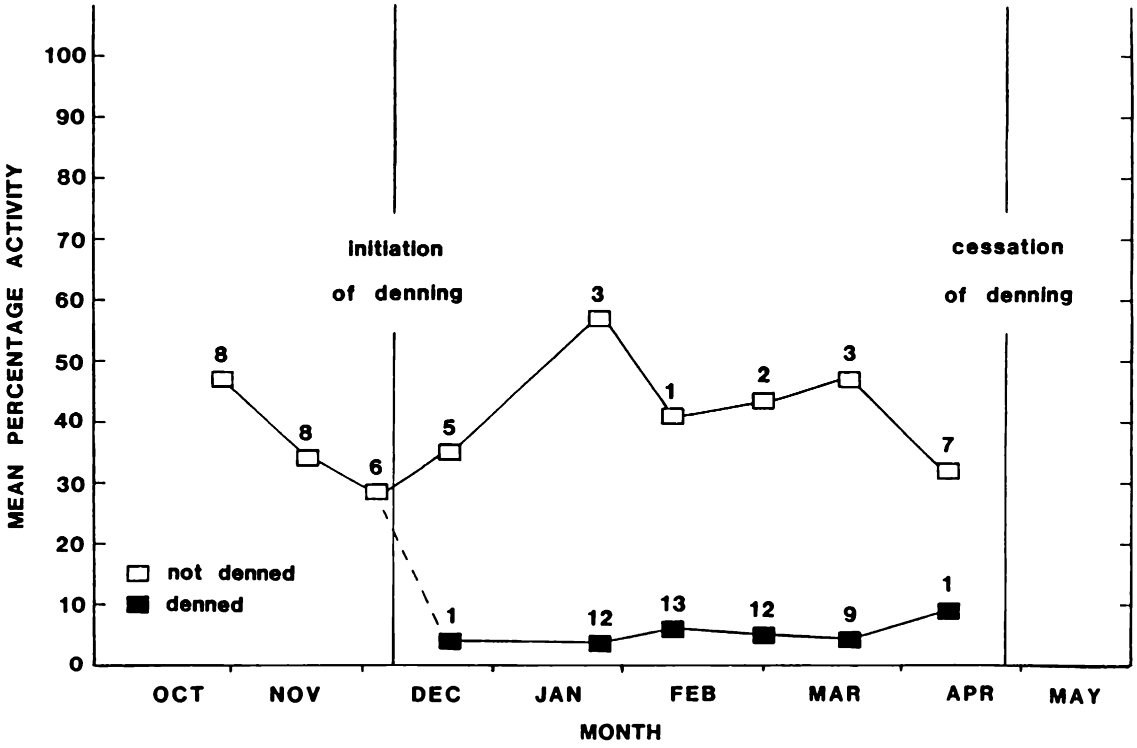

Figure 15. Percentage activity of radio-collared black bears prior to and during the denning period, White River NWR, Arkansas, October 1980-April 1981. (Numbers above plot points represent sample sizes.)

their head. One exception was a female which had recently (< 3 days) whelped 3 cubs and was located less than 2 m from the den cavity entrance. Although she did not react other than to raise her head, her eyes did not have the glazed appearance that I uniformly observed in dormant bears.

An interesting dormancy behavior was exhibited by a pregnant female in mid-December 1981. This bear bedded on the ground 125 m from a den tree which she entered 5-6 days later. When I observed her in the bed 3 days prior to den entry, she sensed me, raised her head, looked in my direction, and then dropped her head as if she could hardly hold it up. Johnson and Pelton (1979) reported that activities of black bears in GSMNP began to decrease and were concentrated around den sites as much as 1 month prior to denning. In Idaho, Beecham et al. (1983) observed marked predenning lethargy in black bears, particularly females, which moved to the vicinity of dens an average of 8 days prior to entry. Craighead and Craighead (1972b) observed prehibernation lethargy in brown bears, and Servheen and Klaver (1983) thought that 2 adult female brown bears which moved to den sites 3-4 weeks before entry may have experienced a similar lethargic state.

The dormant behavior of black bears in Arkansas was similar to that reported in other investigations of this species across its range. Nearly uniform (95 percent) den entry, strong fidelity to dens, depressed levels of activity during denning, lethargic reaction to human observation, and abandonment of dens following disturbance have been commonly observed in both northern and southern regions. This consistency across a broad environmental spectrum indicates that the intensity of dormancy of black bears does not vary according to the severity of winter conditions in different geographic regions. The differential timing of dormancy between regions appears to be explained by plant phenology and food availability.

Den types and characteristics. Two types of dens were utilized by black bears on the Refuge, elevated cavities inside standing, living trees, and ground nests constructed in forest gaps. Females used tree dens exclusively (N = 34) while males denned in ground nests (N = 13) and tree cavities (N = 15) at similar frequencies (Table 21).

Tree dens. Tree cavities used for denning were formed by heart rot following wind, ice, or lightning damage. In bottomland hardwood forest, trees appear to resist such disturbances well and continue to grow. Often, the entire crown breaks off leaving a living snag; sprouting ensues at the point of the break, a new crown develops, and a cavity forms with a top entrance. Other times a large limb, often a fork, breaks off initiating formation of a cavity accessible from the side of the trunk.

Tree dens on the Refuge were most commonly located in overcup oak (N = 30, 61 percent) and baldcypress (N = 13, 27 percent) (Table 21). Cavities in 3 Nuttall oaks, 2 sycamores, and 1 water tupelo also were utilized. Availability of den trees by species was not

Table 21. Types of dens selected by black bears on White River NWR, Arkansas, 1979-1982.

Sex	Age class (reproductive condition)	Ground dens	Tree dens	Tree species				
				OO[a]	BC[b]	NO[c]	SY[d]	WT[e]
M	Subadult	2	2	0	1	1	0	0
M	Adult	11	13	11	2	0	0	0
	Subtotal	13	15	11	3	1	0	0
F	Subadult	0	4	3	0	0	0	1
F	Barren adult	0	6	3	2	1	0	0
F	Pregnant	0	17	10	4	1	2	0
F	w/"coys"	0	7	3	4	0	0	0
	Subtotal	0	34	19	10	2	2	1
			Total	30	13	3	2	1

[a] Overcup oak; [b] Baldcypress; [c] Nuttall oak; [d] Sycamore; [e] Water tupelo.

determined, but it appeared that species were used in general proportion to their abundance on the study area. Lacking availability data, I could not test for preferences of age and sex classes for particular tree species. There was some indication, however, that adult males may prefer overcup oaks, possibly due to the relative ease with which these trees are climbed. Branches usually occur along the entire trunk of overcup oaks, and the bark is deep and rough. Conversely, baldcypress, sycamore, and water tupelo generally lack branches near the ground; the first limbs often are as high as 20 m, and the barks of these species are relatively thin and slick. One baldcypress used by a large male was atypical, having many low branches. The other was the den of a relatively small 4-year-old male which, as a subadult 3-year-old, used the same tree. There was no indication that females preferred cavities of particular tree species. In the southern Appalachians, where black bears commonly utilize tree cavities for denning (Johnson and Pelton 1981, Lentz et al. 1983), no preferences for particular tree species have been reported. Apparently, availability rather than species-specific characteristics determines the selection of individual tree species for denning.

Despite distinct sexual dimorphism, male and female black bears utilized den trees with similar dimensions. Mean diameter at breast height (dbh) of trees used by males was 116 cm compared to 107 cm for females. Mean width of the cavity floor (i.e., bedchamber) in males' dens was 76 cm compared to 72 cm for females' dens (Table 22). On the Refuge, and elsewhere, black bears apparently do not substantially

Table 22. Mean dbh, bedchamber width, and characteristics of cavity entrance of tree dens utilized by black bears on White River NWR, Arkansas, 1979-1982.

			Bedchamber	Cavity entrance							
		DBH	width	width	height above	position		aspect			
Sex	Cohort	(cm)	(cm)	(cm)	ground (m)	top	side	N	E	S	W
M	Subadult	113	72	44	12.3	1	1	1	1	0	0
M	Adult	117	77	59	9.7	4	5	0	5	3	0
	Males	$\bar{X}$ = 116	$\bar{X}$ = 76		$\bar{X}$ = 10.2	5	6	1	6	3	0
F	Subadult	101	69	32	10.2	3	1	1	1	0	1
F	Barren adult	112	77	38	9.7	1	5	2	1	1	2
F	Pregnant	103	72	41	9.5	10	7	4	2	4	4
F	w/"coys"	110	69	40	11.1	0	7	0	1	5	0
	Females	$\bar{X}$ = 107	$\bar{X}$ = 72		$\bar{X}$ = 9.9	14	20	7	5	10	7
					Total	19	26	8	11	13	7

[a] Cohort means.

modify tree cavities (but see Pelton et al. 1980), and bedchamber size is likely a function of availability, i.e., most bears would fit in most bedchambers. Conversely, where ground dens are excavated, den entrance and chamber sizes are related to body size (Beecham et al. 1983, LeCount 1983, Novick et al. 1981, Tietje and Ruff 1980).

On the Refuge I did observe a relationship between body size of bears and width of tree cavity entrances. Mean width of entrances of dens of females and subadult males (39 cm) was significantly smaller than that of entrances to dens of adult males (59 cm) ($P<0.004$). By selecting (or constructing) den entrances which will not accomodate body sizes greater than theirs, bears may reduce competition for dens. This would reduce disturbances from other bears (Tietje and Ruff 1980, Lindzey and Meslow 1976b) and predators (Rogers 1977). Elevated tree cavities further enhance protection from disturbances (Johnson and Pelton 1981). In east Tennessee, where considerable variation occurred in heights of tree cavity entrances above ground (5.1-27.5 m), females selected higher entrances than males (Wathen et al. in press). This was not the case on the Refuge, where the height to cavity entrances varied less (4.3-16.0 m) and was commensurate for males ($\bar{X} = 10.2$ m) and females ($\bar{X} = 9.9$ m). Above a certain height, increased elevation of the cavity entrance may not directly increase protection. Rather, the higher the entrance, the smaller the tree trunk at that point, and hence, the smaller the cavity entrance will be. If entrance width is a primary selection criterion, elevation of the entry may simply be an artifact of entrance width. This appeared to be the circumstance for several ($N = 8$) tree cavities used by females on the Refuge.

Minimizing entrance size may be of greater importance by reducing air circulation inside the den chamber and subsequent convective heat loss (Thorkelson and Maxwell 1974). Position of the entrance (i.e., top or side) will also effect heat conservation inside the den. Lentz et al. (1983) found that entrance position accounted for 11 percent of the variation in heat retention capacities of black bear dens in Georgia, and Thorkelson and Maxwell (1974) reported that side entrances reduced the "view effect" or exposure of the cavity floor to precipitation; the insulative capacity of the occupant's fur was decreased when wet. On the Refuge, neither adult males, nor females collectively, appeared to select tree den cavities based on entrance position. However, barren adult females and females with "coys" exhibited slight ($P<0.11$) and strong ($P<0.01$) preferences, respectively, for cavities with side entrances (Table 22).

Entrance aspect also may be important to a bear's ability to conserve energy in the den. In northern regions with heavy snowfall, bears apparently prefer ground dens located on north and west facing slopes where snow accumulation is greater and provides better insulation (Beecham et al. 1983, Tietje and Ruff 1980, Craighead and Craighead 1972a). In habitats where snow accumulation is uncommon or elevated tree cavities are used for denning, south and east facing entrances may be more advantageous, allowing greater solar radiation to reach the cavity and reducing exposure to prevailing westerly winds, respectively. On the Refuge, aspect of tree cavity entrances was not an important den selection criterion across the entire black bear population. However, two cohorts, adult males and females with "coys," utilized east and south facing cavities more than expected and north and west facing ones less than expected ($P \leq 0.05$) (Table 22). Females with "coys" used cavities with side entrances exclusively, and the east and south facing entrances would have increased solar radiation into these dens. Adult males did not exhibit a preference for side entrances, but interestingly, all 5 cavities with side entrances faced south ($N = 4$) or east. This pattern was not consistent for dens with side entrances which were used by other cohorts.

In northern Georgia, Lentz (1980) found that each of 7 tree den cavities with side entrances were exposed to the east. In the same region, however, Wathen et al. (in press) reported that more tree cavity entrances faced west than faced east and believed that entrance aspect was of minimal importance in den selection. In coastal Washington, another area with relatively mild winters and no significant snow accumulation, Lindzey and Meslow (1976b) concluded that exposure of slope and aspect of ground den entrances did not influence den selection.

Although side entrances increase shelter of the cavity floor, cavities with top entrances may be equally well protected if the cavity is sufficiently deep and/or the tree trunk is not absolutely vertical. I categorized vertical shelter (i.e., "view effect") of tree cavity floors as poor, fair, or good. Females selected a much greater proportion of cavities with fair and good shelter than males (Table 23). Assuming that differences between categories were equal, a t-test

Table 23. Characteristics of bedchambers in tree dens utilized by black bears on White River NWR, Arkansas, 1979-1982.

Sex	Cohort	Mean depth below entrance (m)		Vertical shelter			Mean height above ground (m)	Mean height above sea level (m)
				poor	fair	good		
M	Subadult	2.43		1	1	0	9.9	55
M	Adult	3.14		5	1	3	6.6	50
	Males	$\bar{X}$ = 2.99	Total	6	2	3	$\bar{X}$ = 7.2	$\bar{X}$ = 51
F	Subadult	5.41		0	3	1	4.8	49
F	Barren adult	4.26		0	2	4	5.4	49
F	Pregnant	5.35		3	8	6	4.2	47
F	w/"coys"	4.12		0	2	5	7.0	50
	Females	$\bar{X}$ = 4.91	Total	3	15	16	$\bar{X}$ 5.0	$\bar{X}$ = 48

indicated that cavities used by females were significantly more protected than those used by males ($P<0.05$). This was due, in part, to females using a greater proportion of cavities with side entrances, but cavity depth also contributed substantially to the difference. Mean depth of cavities used by females (4.9 m) was distinctly greater than that of cavities used by males (3.0 m) ($P<0.02$). Lentz et al. (1983) reported that bedchamber height accounted for 59 percent of the thermal efficiency of tree den cavities, but did not clarify if this was due to proximity of the bedchamber to ground surface or its depth below the cavity entrance. Their reference to the findings of Thorkelson and Maxwell (1974), which emphasize the role of air circulation inside the cavity, suggest that cavity depth was actually the relevant factor in their study.

In bottomland hardwood forests which are seasonally inundated, height of the tree cavity floor may be especially important in den selection. During spring floods of 1980 and 1982, 3 (15 percent) of 20 bears were forced from tree dens when rising water reached the cavity floors. In one case an adult female abandoned her 2 2-month-old cubs which drowned in the den cavity. Since females used tree cavities exclusively, it follows that selective pressure would also exist for choosing high cavities which are secure from flooding; however, this did not appear to be the case. Females utilized tree cavities with lower bedchambers than males; bedchambers of pregnant females were lowest of all cohorts (Table 23). Aside from the case of cub abondonment, 2 other pregnant females selected flood-susceptible tree dens. One abandoned the cavity, which later flooded, due to my disturbance, and the other used the cavity in a year when flooding did not occur. Possibly, the greater thermal efficiency and seclusion afforded by deep den tree cavities are selectively advantageous for females in bottomland hardwood forests, despite the increased risk of flooding.

Ground dens. Male black bears on the Refuge utilized ground nests as well as tree cavities for denning; some males appeared to be disposed to one or the other type of den. Three males monitored for 2 years and 1 monitored for 3 years denned exclusively in tree cavities. Two males used tree cavities as 4-year-olds and later denned on the ground as 5- and 6-year-olds; 1 continuing to do so as a 7-year-old. Another adult male denned on the ground in 2 consecutive years. Each of 2 yearlings denned on the ground as well.

All ground dens (nests) were located in forest gaps formed by natural tree falls or resulting from logging (Table 24). Canopy cover was either absent or less than 25 percent in the immediate vicinity (25 m radius) of all ground dens. Nests were generally situated in the most open part of the gap, and I frequently observed bears in ground dens from aircraft. Such exposure would have increased penetration of solar heat to the nest but exposed the nest to precipitation as well. It was common (N = 4), however, to find a secondary bed situated under a dense overhanging vine mat within 10 m of the primary nest. These alternate beds offered greater vertical protection

Table 24. Characteristics of ground dens utilized by male black bears on White River NWR, Arkansas, 1979-1982.

	Bed dimensions						
Age	width[a] (cm)	depth (cm)	ht. of wall (cm)	Type of lining	Site type	Associated cover	Canopy cover (%)
Subadult	40x60	17-29	17	Mixed debris[b]	Tree-fall gap	Fallen log/vines	0
Subadult	35x71	0	38	Mixed debris	Tree-fall gap	V-shaped log/vines	0
Adult	80x90	25	0	Leaves	Tree-fall gap	Vines/saplings	25
Adult	86x117	20	25	Leaves/vines	Logging platform	Vines/Saplings	0
Adult	87x104	15	18	Decayed log/ mixed debris	Heavily logged	Vines/*Rubus* spp.	25
Adult	111x132	15-25	0	Mixed debris	Tree-fall/gap	Vines/tree-top	25
Adult	130x142	9-20	15-30	Mixed debris	Logging platform	Vines	25
Adult	81x129	40	34	Leaves	Tree-fall gap	Base of large tree/ vines/saplings	25

---

[a] Narrowest x widest.

[b] Includes leaves, vines, soil, and sticks.

and may have been used during heavy rain. Three nests were associated with large logs or tree tops in vine thickets, 3 were in dense vine/sapling thickets without fallen logs, and 1 was positioned 1 m south of a 70 cm dbh overcup oak.

Nests were constructed by digging a shallow depression and pulling debris from around the depression to form a wall and line the oval nest. One bed was constructed totally of leaves which had either been carried or "raked" from a radius of 15 m of the nest. Dimensions of nests were related to the size of the occupant; nests of 2 subadults were distinctly smaller than those of adult bears (Table 24). The walls of 3 nests varied in height and in each case were substantially higher at the north end of the bed. Body impressions in 2 nests indicated that bears rested their heads on the nest wall.

Hamilton and Marchinton (1980) described a similar ground nest used by a 3-year-old female black bear in "Carolina bay" habitat in coastal North Carolina. Black bears also utilize ground nests in dense, open-canopy swamps in Florida (Mykytka, pers. communication) and Virginia (Helgren, pers. communication). Johnson and Pelton (in press) observed 9 elaborately constructed, nest-like winter beds of black bears in GSMNP; all were in dense understories, and 8 of 9 were associated with logs, trees, or rocks. They believed that these nests were used primarily during the predenning period. On the Refuge, I observed several beds used prior to and immediately following the denning period which were structurally and ecologically indistinguishable from nests used as dens; the only difference was the absence of scats around nests used as hibernacula.

Lindzey and Meslow (1976b) reported that adult black bears were more selective than subadults in choosing denning habitat and that adult females insulated (i.e., lined) their den chambers better than other cohorts. Johnson and Pelton (1981) felt that the disproportionately high use of tree cavities by both females and subadults of both sexes in Tennessee was strong evidence that these groups selected and prepared dens with greater care than adult males. Alt and Gruttadauria (1984) reported that female black bears in Pennsylvania used protective dens in cavities while males utilized exposed ground dens. Obviously there is selective pressure on females to choose secure dens which enhance successful parturition and care of young. Smaller males also may reduce their vulnerability to environmental (i.e., energy) and intraspecific stress if they select protected dens. My observations gave no indication that young males exercised particular care in den selection on the Refuge. However, the uniform utilization of tree dens by females indicates that they are highly selective of dens and that the availability of tree dens is important to the reproductive fitness of female black bears in bottomland hardwood forest.

Den reuse. Six dens (all trees) were monitored in 3 consecutive winters and 24 dens (21 tree, 3 ground) in 2 winters. In this total of 36 potential cases of den reuse, 9 (26 percent) occurred. Only tree dens were reused. Five bears (2 adult males, 1 subadult/adule male, 2 adult females) used the same den trees in 2 consecutive years.

Another adult male denned in the same tree in alternate years. One maternal den used by a radio-collared female in 1980-81 was occupied the following winter by an unmarked female and her 3 yearlings; meanwhile, the radio-collared female and her single "coy" denned in an overcup oak used 2 years earlier by an adult male. An unmarked adult male utilized a tree in the winter of 1981-82 that had been used by a radio-collared adult male 2 years before. After abandoning a flooded tree cavity, an adult female relocated to a den tree used the previous year by a pregnant female.

Den reuse by black bears on the Refuge appeared to be high, however, data on this behavior from other studies is limited, and there is considerable variation in that which exists. Based on 568 den years of availability over an 11-year period, Alt and Gruttadauria (1984) reported den reuse of approximately 5 percent by black bears in Pennsylvania. Their observations were limited almost exclusively to females. Most cases of reuse were by the same female bears (41 percent) or their female offspring (11 percent); 33 percent were not by the same bears nor their known daughters, and kinships of the remainder were unknown. Beecham et al. (1983) also reported 5 percent den reuse by black bears in Idaho; 2 cases were reuse of dens by yearlings. In the southern Appalachians, Johnson and Pelton (1981) and Lentz (1980) observed no reuse of dens, primarily tree cavities. Tietje and Ruff (1980) reported 2 cases (6 percent) of den reuse in Alberta but believed that they were unrepresentative because both individuals frequented dumps and exhibited atypical denning behaviors. In southern

California, 1 of 3 dens monitored in 2 consecutive years was reused (Novick et al. 1981), and in coastal Washington (Lindzey and Meslow 1976b) at least 6 of 12 dens used by bears in the population had been constructed in previous years.

Alt and Gruttadauria (1984) implied that den reuse may be inversely related to den availability. Johnson and Pelton (1981) interpreted the lack of den reuse by black bears in GSMNP as in indication of an abundance of dens. They found that tree dens were used less frequently in areas which had been extensively logged (i.e., contained relatively few den trees). Bromlei (1973) reported that reuse of tree dens by Asiatic black bears was high in an area with limited number of tree dens. To my knowledge, however, there have been no comparative studies of the frequency of den reuse and the availability of dens.

I do not believe that the relatively high rate of reuse of tree dens by black bears on the Refuge was due to a lack of den trees. Several (N = 7) bears used either 3 or 4 different tree dens during the study. Based on my casual field observations, den trees are abundant throughout the study area core. The strong preference exhibited by females for tree dens suggests that selection of this den type by females enhances reproductive success. The protection of existing and potential den trees and forest management which perpetuates the dynamics of den tree formation appear to be important to the long-term fitness of the black bear population on the Refuge.

Home Range and Movements

Estimates of annual and seasonal home range were made by the convex polygon or maximum area method. As outlined in Chapter III (page 35), dispersion of telemetry locations of each individual were examined, and in certain cases polygons were modified to either (1) exclude unsuitable habitat (e.g., cultivated fields, barge canal) or (2) minimize the size of unused areas enclosed by the polygon due to outlying locations or disjunct clusters of locations.

Annual home range. Estimates of annual home range size were based on locations between den emergence or capture in 1980 to den entry the following winter. For those individuals captured later in summer (July-September), estimates were based on locations between the date of capture and 1 year later.

Substantial variation occurred in estimates of annual home range size within population cohorts (Table 25). Greatest variation was exhibited by males; adults utilized areas ranging from 39 to 266 km^2, while subadults ranged over areas of 26 to 226 km^2. Annual ranges of females varied less; adults ranged over areas of 7 to 22 km^2, and subadults utilized areas of 8 to 10 km^2.

Collectively, males (excluding the yearling) utilized significantly larger areas ($\bar{X}$ = 128 km^2, N = 9) than females ($\bar{X}$ = 11 km^2, N = 9) ($P<0.03$). This relationship held for ages classes as well. The mean annual home range of adult males (116 km^2, N = 6) was significantly greater than that of adult females (12 km^2, N = 6)

Table 25. Estimates[a] of annual home range sizes of black bears on White River NWR, Arkansas, 1980-1981.

Bear	Sex	Age	Cohort	Number of locations	Home range estimate (km^2)		Cohort mean (km^2)	S.D.[b]
416	M	1	Yearling	51	14		---	---
412	M	2	Subadult	67	226			
425	M	2	Subadult	65	193	subadult male	148	107
420	M	3	Subadult	49	26			
410	M	5	Adult	41	73			
417	M	5	Adult	58	58			
421	M	5	Adult	48	61	adult male	116	91
419	M	6	Adult	49	39			
407	M	7	Adult	59	199			
411	M	9	Adult	59	266			
418	F	2	Subadult	49	10.3			
423	F	2	Subadult	49	8.5	subadult female	9.0	1.1
430	F	3	Subadult	34	8.2			

Table 25. (Continued)

Bear	Sex	Age	Cohort	Number of locations	Home range estimate (km^2)		Cohort mean (km^2)	S.D.[b]
451	F	4	Adult[c]	40	6.7	adult female	11.7	8.8
429	F	5	Adult[c]	38	6.6			
439	F	9	Adult	47	10.7			
438	F	10	Adult	30	16.5			
415	F	11	Adult	59	21.6			
428	F	12	Adult	37	7.8			

[a] Calculated by the convex polygon or maximum area method (see text, page 35).

[b] Standard deviation.

[c] Matured (i.e., first produced cubs) in the winter of 1980-81.

(P<0.02), and subadult males used larger areas ($\bar{X}$ = 148 km^2, N = 3) than subadult females ($\bar{X}$ = 9 km^2, N = 3) (P<0.03). There was no significant difference between sizes of areas used by subadults and adults of the same sex (P>0.55).

It is difficult to compare these estimates of home range size to those reported from other investigations. The frequency and number of locations from which range sizes are calculated (Smith et al. 1981) and the method of defining areas (Garshelis and Pelton 1981) substantially affect estimates of home range. Methodologies have not been consistent among studies of black bear movements, particularly with respect to sampling regimes. Hence, variation within range sizes reported for different populations may have little meaning.

Distinctly small areas were utilized by black bears on an island off the coast of Washington where annual home ranges of 5 males varied from 1.8 to 12.3 km^2 and 7 females used areas ranging from 1.4 to 3.8 km^2 (Lindzey and Meslow 1977b). Garshelis and Pelton (1981) reported annual home ranges of 13 to 28 km^2 for males (N = 10) and 2 to 23 km^2 for females (N = 14) in the mountains of east Tennessee, while in Arizona chapparal annual home range estimates ranged from 15 to 69 km^2 for males (N = 11) and 10 to 30 km^2 for females (N = 8) (LeCount 1980). Relatively small annual home ranges also were reported for black bears in the San Bernadino Mountains of southern California where 6 males used areas of 7 to 54 km^2, and 1 female ranged over 17 km^2 (Novick and Stewart 1982).

Larger annual home range sizes have been reported elsewhere. In Alberta, male black bears ranged over areas of 42 to 196 km^2, and females ranges varied from 3 to 63 km^2 (Young and Ruff 1982). Two males in Idaho used areas of 109 km^2 and 115 km^2, respectively, and 7 females utilized areas of 17 to 130 km^2 (Amstrup and Beecham 1976). In coastal North Carolina 2 males occupied annual ranges of 46 km^2 and 184 km^2 (Hamilton 1978), while in bottomland hardwood forest of Louisiana 1 adult male ranged over an area of 158 km^2, and the ranges of 2 adult females were estimated at 18 km^2 and 22 km^2, respectively (Taylor 1971).

Despite the biases in methodology between these studies, a general pattern of spatial utilization by black bears appears to be constant. Males consistently utilize much larger areas than females. Subadult males may range over areas equal to or greater than those of adult males (Hamilton 1978, LeCount 1980, Quigley 1982, Villarubia 1982), perhaps because of dispersal behavior of younger males and their attempts to establish breeding ranges (Rogers 1977). Adult males increase their reproductive fitness by utilizing areas which encompass the ranges of several adult females (Amstrup and Beecham 1976, Rogers 1977). Young females establish ranges within or overlapping their mother's home range (Lindzey 1976, Rogers 1977) and generally utilize smaller areas than adult females (Rogers 1977, LeCount 1980, Quigley 1982). Both male and female yearlings typically restrict movements during their first year of independence and use smaller home range areas than all other population cohorts (Amstrup and Beecham 1976, Rogers 1977, Reynolds and Beecham 1980). Hence, a complex social system in black bears appears to affect home range dynamics and, coupled with fluctuations in the resource base, may account for variations observed in home range sizes within cohorts of individual populations.

Differences in sizes of areas utilized by subadult males may directly reflect varying degrees of success at establishing permanent home ranges and indirectly relate to population structure (i.e., density and age composition of the male cohort). As males mature, competition for females should increase, and the heirarchical position of adult males will continually determine the sizes of areas which they use. Home range sizes of females may be more directly related to habitat quality (Amstrup and Beecham 1976, Rogers 1977). If females utilize small areas, the breeding effort of males should be concentrated in smaller areas and in turn reduce the sizes of areas (i.e., home ranges) required to maximize their reproductive fitnesses.

On the Refuge there was evidence of a relationship between home range sizes of adult males, habitat quality, and body size. The eastern portion of the study area core appeared to be relatively resource-rich and secluded. In this area, the home ranges of 3 adult males overlapped considerably (39-72 percent) (Figure 16) and were relatively small (39-61 km^2) (Table 25). These 3 individauls were among the largest males captured during the study (111, 130, and 148 kg). Within the composite area of these adults, a 3-year-old subadult male (420) ranged over 26 km^2, an area much smaller than

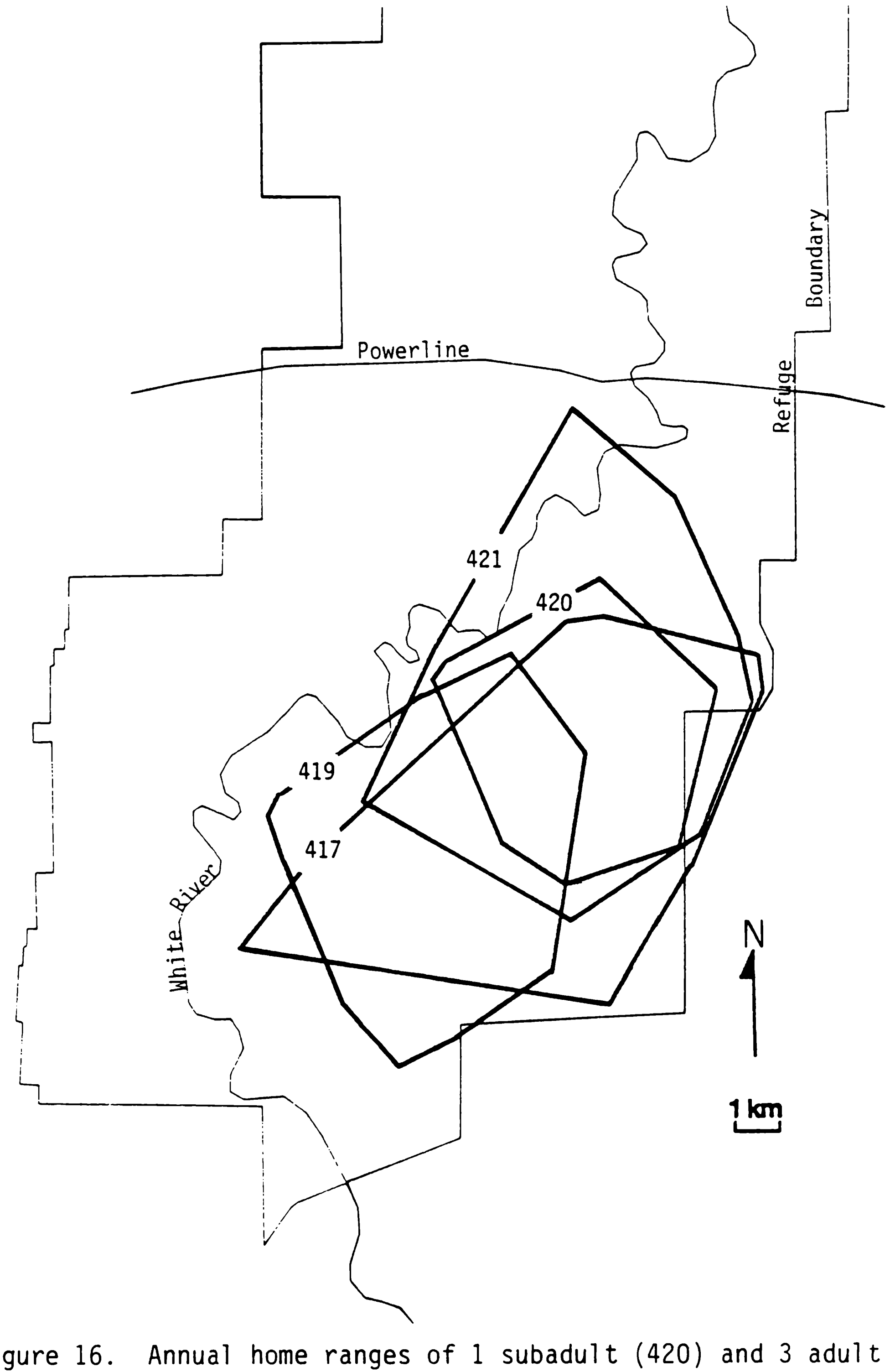

Figure 16. Annual home ranges of 1 subadult (420) and 3 adult male black bears on White River NWR, Arkansas, 1980.

those used by 2 more transient subadult males ($\bar{X}$ = 210 km^2) (Table 25). In the southern portion of the study area core, another large male (107 kg) occupied a relatively small area of 73 km^2.

Conversely, 2 relatively small (95 kg and 96 kg, respectively) adult males ranged over much larger areas of 199 km^2 and 266 km^2. These males were occasionally located in the eastern portion of the study area core, but they concentrated their activities west of the White River (Figure 17) where habitat quality appeared to be lower (i.e., less diversity and seclusion). In the southwestern portion of the Refuge, 12 km^2 are managed as a green tree reservoir (GTR) from October through April which significantly decreases understory cover (Christman 1984). Due to flooding, the availability of hard mast also is reduced in the GTR in the fall. Just north of the GTR, human traffic is heavy to a campground, boat ramp, residential houseboats, and Refuge maintenance shop. Radio-telemetry observations indicated that bears avoided this area. Several small settlements and fishing camps occur near the border of the Refuge further north. Interestingly, the largest male captured west of the White River (N = 9) weighed 96 kg, while 11 of 25 males captured east of the White River weighed more than 95 kg, and 5 weighed greater than 120 kg.

Home range sizes of adult females also indicated a disparity in the suitability of black bear habitat in the eastern and western portions of the study area core. Two females (415 and 438) which utilized areas west of the White River (Figure 18) had larger home ranges (16.5 km^2 and 21.6 km^2) than females which occupied areas east

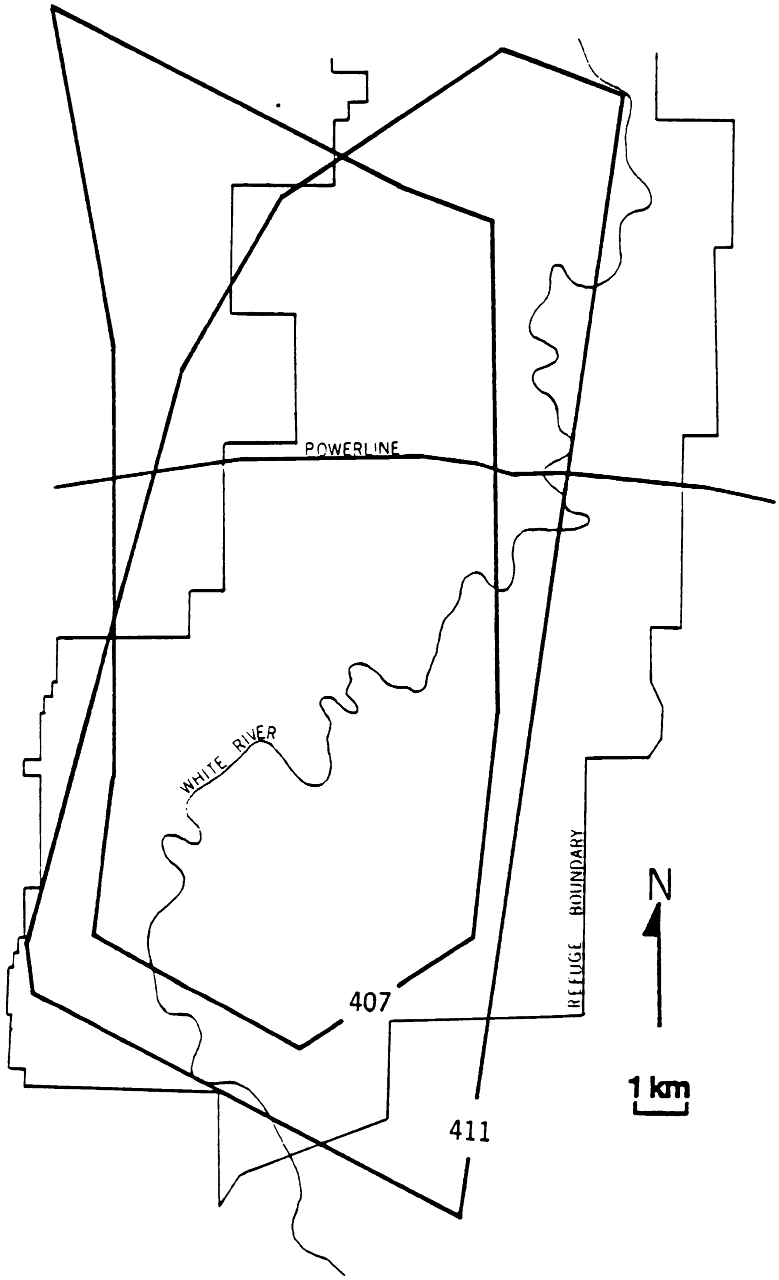

Figure 17. Annual home ranges of 2 adult male black bears on White River NWR, Arkansas, 1980.

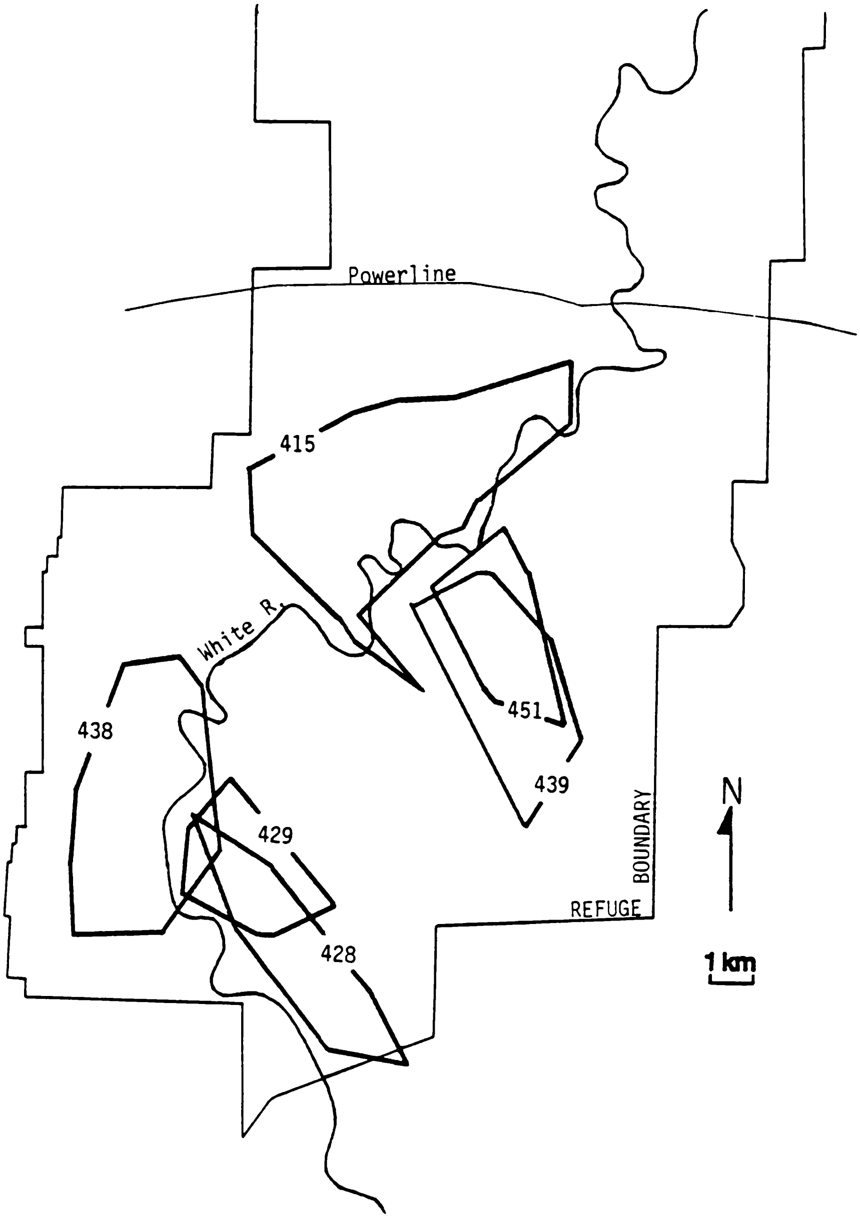

Figure 18. Annual home ranges of 6 adult female black bears on White River NWR, Arkansas, 1980-81.

of the White River (6.6-10.7 km^2, N = 7) (Table 25). These 2 females also moved to areas east of the White River during the fall of 1980 to feed on acorns, while none of the females with ranges east of the White River were ever located west of it. These findings concur with Refuge records and local information which indicate that black bears have historically been most abundant in the eastern portion of the study area core.

Seasonal range and movement. Several studies have demonstrated the influence of food availability on seasonal movements and ranges of black bears (e.g., Jonkel and Cowan 1971, Amstrup and Beecham 1976, Rogers 1977, Garshelis and Pelton 1981). On the Refuge, black bears exhibited 3 distinct dietary patterns which corresponded to phenological development (page 92). Consequently, seasonal ranges were calculated for these periods; spring was considered to extend from 1 March (or den emergence) to 7 June, summer from 8 June to 21 October, and fall/winter from 22 October to 29 February (or den entry).

Similar to and coincidental with annual home ranges, season range sizes varied substantially within cohorts (Table 26). Despite the variation, a general pattern of seasonal movements and range use was typical: relatively small areas were utilized in spring and fall, while during summer, bears traversed most (66-89 percent) of their annual ranges. Adult males ranged over significantly larger areas in summer ($\bar{X}$ = 97 km^2, N = 6) than in spring ($\bar{X}$ = 15 km^2, N = 11) ($P<0.008$) or fall ($\bar{X}$ = 27 km^2, N = 10) ($P<0.03$). Areas used by

Table 26. Estimates of seasonal home range size of black bears on White River NWR, Arkansas, 1979-1982

		Spring[a]			Summer[b]			Fall/Winter[c]		
Sex	Cohort	N	Mean (km^2)	Range	N	Mean	Range	N	Mean	Range
M	Juvenile	-	-	-	1	10.3	-	1	2.3	-
M	Subadult	3	25	3-62	3	103	25-145	5	26	13-40
M	Adult	11	15	5-41	6	97	27-264	10	27	8-66
F	Subadult	3	5.3	4.2-6.6	3	5.9	5.7-6.1	3	4.8	3.8-6.6
F	Barren adult	3	3.1	1.5-6.3	4	10.4	5-22	2	4.5	4.3-4.6
F	Pregnant	-	-	-	-	-	-	4	3.7	1.3-5.9
F	w/"coys"	4	1.0	0.3-1.7	-	-	-	3	10.8	8-15
F	w/yearlings	3	5.0	4.2-6.3	-	-	-	-	-	-

[a] 1 March-7 June.

[b] 8 June-21 October.

[c] 22 October-29 February.

subadult males were also distinctly larger in summer ($\bar{X}$ = 103 km^2) than in spring ($\bar{X}$ = 25 km^2) or fall ($\bar{X}$ = 26 km^2). Small sample sizes (N = 3) and large variances precluded statistical comparisons of the seasonal ranges within this cohort. Barren adult females utilized larger ranges in summer ($\bar{X}$ = 10.8 km^2, N = 4) than in spring ($\bar{X}$ = 3.1 km^2, N = 3) ($P<0.02$) or fall ($\bar{X}$ = 4.0 km^2, N =6) ($P<0.05$) as well. Relationships between seasonal ranges of subadult females were somewhat atypical. They used only slightly larger areas in summer ($\bar{X}$ = 5.9 km^2, N = 3) than in spring ($\bar{X}$ = 5.3 km^2, N = 3) and fall ($\bar{X}$ = 4.8 km^2, N = 3). The summer range of 1 yearling male (10.3 km^2) was much greater than his range the following fall (2.3 km^2), but the size of his summer range was influenced by dispersal from his natal range.

Seasonal range size of black bears on the Refuge appeared to be affected by both food availability and behaviors related to reproduction. In spring, foods were limited to herbaceous and green woody plant materials which were somewhat localized at higher elevations where understory cover was greatest. During this relatively short season, bears appeared to satisfy their nutritional requirements in small areas. In summer, as soft fruits of various species matured, and animal foods such as insects and fish became available, bears moved over larger areas to obtain these site-specific, widely dispersed foods.

Breeding behavior also was related to the larger size of summer ranges of certain population cohorts. Lindzey and Meslow (1977b) and Rogers (1977) found that adult males actively ranged over larger areas during summer, apparently to monitor estrous of adult females. Alt et al. (1980) reported that movements of adult males and breeding females peaked during summer. Ranges of immature males also may be indirectly affected by mating behavior due to social pressure from breeding adult males (Rogers 1977).

Given that all individuals in black bear populations utilize larger areas in summer than in other seasons, regardless of their reproductive status, it appears that the timing of mating has evolved to coincide with this period of increased movements and availability of protein- and carbohydrate-rich (i.e., nutritious) foods.

Overcup oak is abundant and widely distributed in the bottomland hardwood forest of the Refuge, and acorn production by this species is relatively consistent. In the falls of 1979 and 1980 when overcup oak mast was abundant, bears apparently were able to obtain adequate food within or adjacent to their summer ranges. However, when overcup oak mast failed in 1981, fall ranges were expanded, apparently due to movements in search of other foods.

Telemetry observations in December 1981 and January 1982 indicated that 6 adult males, 1 yearling male, and 3 adult females accompanied by cubs made long excursions outside their summer ranges to ridges where red oak (e.g., Nuttall and willow oaks) acorns and/or sweet pecans were abundant. Similar relationships between fall ranges and food availability, often expressed by long movements, have been made reported in Tennessee (Garshelis and Pelton 1981, Quigley 1982), Montana (Jonkel and Cowan 1971), Idaho (Reynolds and Beecham 1980), Minnesota (Rogers 1977), and California (Novick and Stewart 1982).

Seasonal ranges and movements of adult female black bears also may be dramatically affected in years when they raise cubs. On the Refuge, females with "coys" utilized very small areas in spring ($\bar{X} = 1.0$ km^2, N = 4). During summer, mobility of these families increased considerably (Figure 19), and by fall, females with "coys" were wide-ranging, utilizing significantly larger areas ($\bar{X} = 10.8$ km^2, N = 3) than solitary adult females ($\bar{X} = 4.0$ km^2, N = 6) ($P<0.005$) (Table 26). The relatively large spring ranges of females with yearlings ($\bar{X} = 5.0$ km^2, N = 3) indicate that activity and movements of these family units remain high until family break-up. This behavior of females with cubs to restrict movements following den emergence and expand ranges through summer and fall has been reported in other black bear populations (Lindzey and Meslow 1977b, Rogers 1977, Alt et al. 1980, Novick and Stewart 1982, Carr 1983).

Home range overlap. The degree to which home ranges of individual black bears overlap may be indicative of social heirarchy, reproductive status, or kinship. Studies by Rogers (1977) and Garshelis and Pelton (1981) have further demonstrated that home range overlap varies according to the dispersion and abundance of foods and that the social system in this opportunistic species alters to allow maximum utilization of available resources. Interpretations of home range overlap in most black bear studies have been tentative, however, because seldom have all (Lindzey and Meslow 1977b) or most (Rogers 1977)

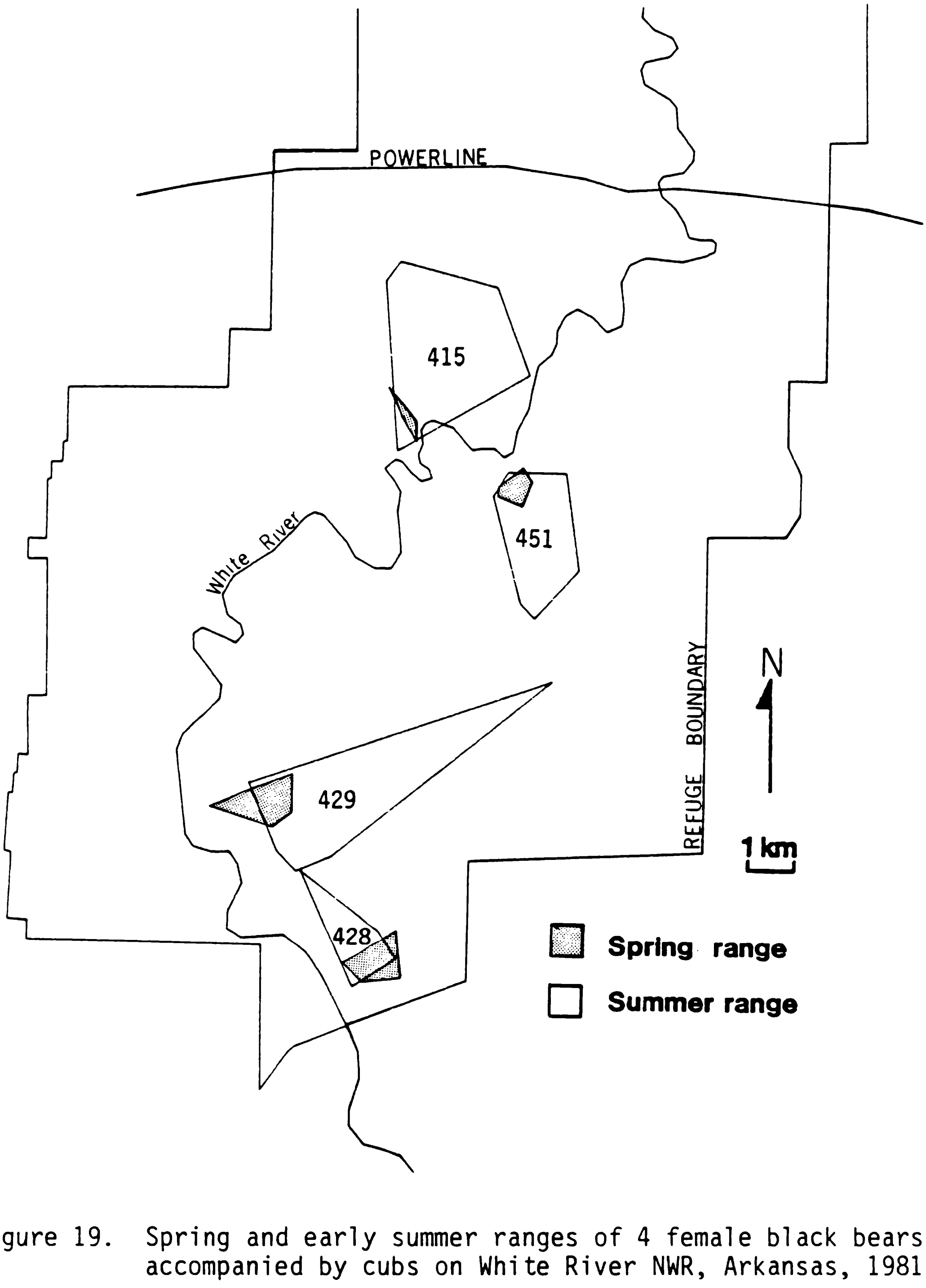

Figure 19. Spring and early summer ranges of 4 female black bears accompanied by cubs on White River NWR, Arkansas, 1981.

of the individuals in a population been simultaneously monitored. Generally, a small proportion of the population has been radio-telemetered, and the influence of uninstrumented bears is unknown. In these situations measures of overlap must be considered minimal and interpreted with caution. Such was the case in my study.

Despite the fact that a small proportion (possible 25 percent) of the bears resident to the study area core were radio-monitored, telemetry data indicated that annual home ranges of both males and females overlapped considerably on the Refuge. Three circumstances were particularly noteworthy. One has been mentioned previously (page 135) in which the annual ranges of 3 adult males overlapped by 39 to 72 percent. The annual home range of a 3-year-old subadult male also was encompassed by the composite range of these adult males (Figure 16, page 136). Overlap in the annual home ranges of these males was largely due to summer movements. In spring and fall, their ranges overlapped substantially less; in these seasons, areas utilized by at least 2 adults were exclusive of each other (Figure 20). The extent of overlap in the ranges of these males during the breeding season in summer indicates that adult male black bears on the Refuge do not defend territories. Rather, food availability or access to females probably determines the degree of overlap in males' ranges.

Adult males also exhibited social tolerance of each other during spring, and especially fall, when natural foods were locally abundant. On 8 radio-tracking occasions (3 in May and 5 in December), 2 radio-collared adult males were located less than 400 m apart. On one of

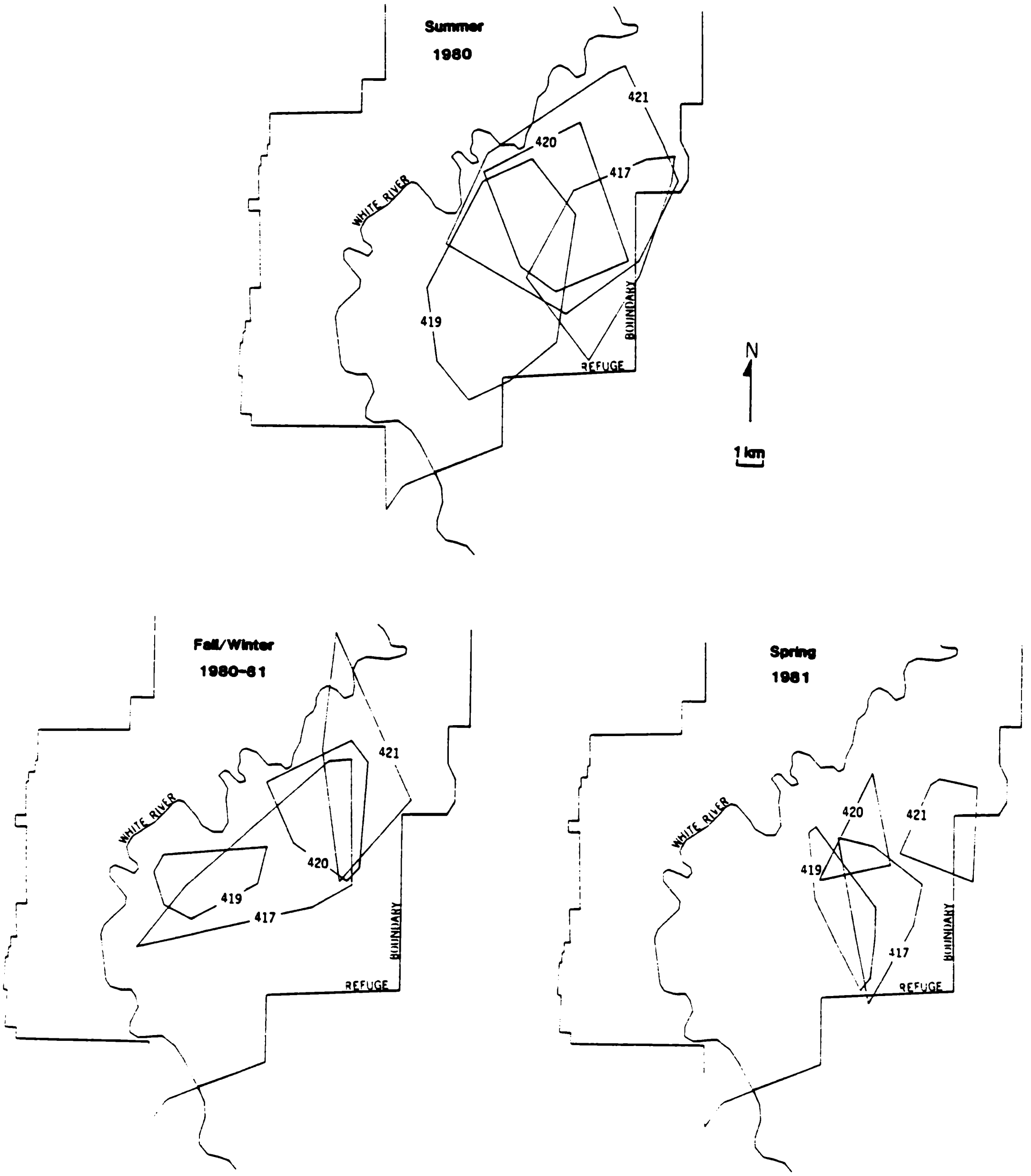

Figure 20. Spatial relationships of seasonal ranges of 3 adult and 1 subadult (420) male black bears on White River NWR, Arkansas, 1980-81.

these occasions, I observed 10 bears (2 adult males, 1 adult female, 1 subadult female, and 6 unidentified) in an overcup oak flat approximately 1 km^2 where acorns were particularly abundant.

Extensive overlap in home ranges of male black bears has been observed in most radio-telemetry studies of this species (Amstrup and Beecham 1976, Lindzey and Meslow 1977b, Rogers 1977, LeCount 1980, Reynolds and Beecham 1980, Garshelis and Pelton 1981, Young and Ruff 1982). An exception was the study of Poelker and Hartwell (1973) where ranges of 3 adult males did not overlap; the range of 1 of these individuals was widely separated (approximately 40 km) from those of the other 2 males, however, and reference to overlap in their ranges may not be appropriate. Jonkel and Cowan (1971) also reported minimal overlap in ranges of adult males, but they calculated home ranges from capture and reobservation rather than telemetry data. Garshelis and Pelton (1981) and Rogers (1977) also observed extensive range overlap and social tolerance between adult males at natural and artificial (i.e., garbage dumps) food sources, respectively.

Home ranges of radio-collared females also overlapped considerably on the Refuge. In two groups, each consisting of an older adult, a young adult which produced her first litter during the year of monitoring, and a subadult, overlap of annual ranges was 32 to 82 percent. In one case, when only the younger adult female produced cubs, no spatial or temporal exclusion in the ranges of these females was observed (Figure 21). In the other case, when both the older and younger adults produced litters in the same year, the two families

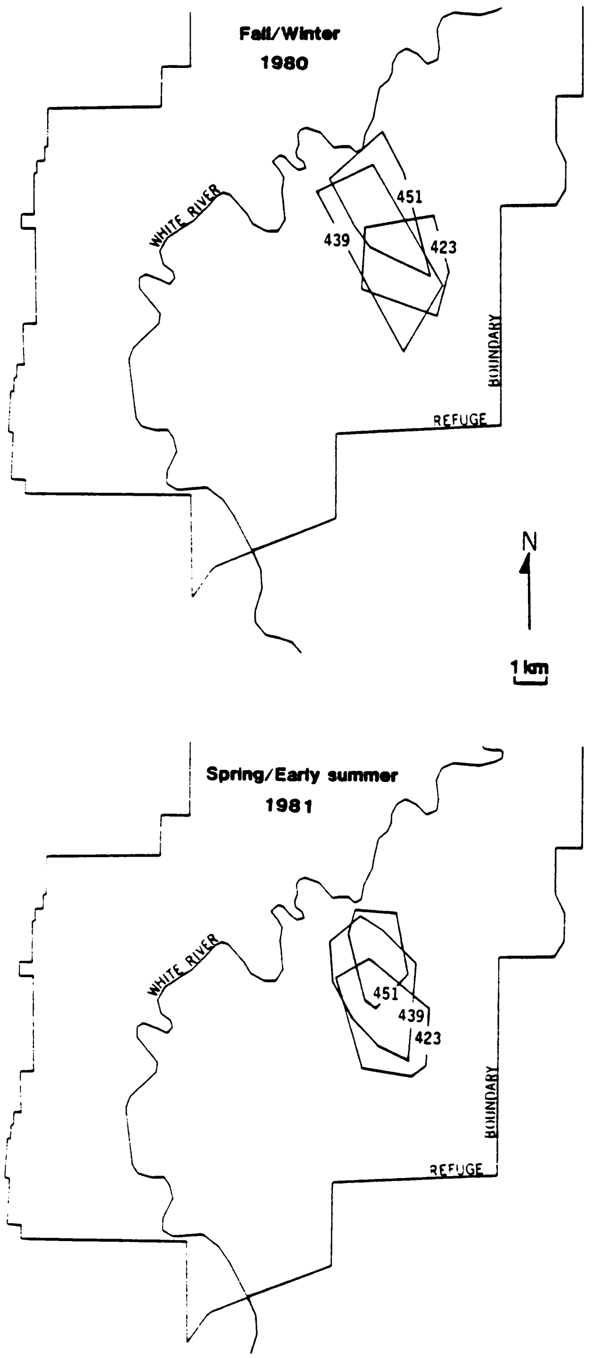

Figure 21. Overlap in seasonal ranges of a 9-year-old, a 3-year-old, and a 2-year-old female black bears on White River NWR, Arkansas, 1980-81. Bear 439, a 9-year-old, was barren in both 1980 and 1981. Bear 451, a 3-year-old, produced her first litter in February 1981 (i.e., was accompanied by cubs in spring/early summer 1981), and bear 423 was a 2-year-old subadult. Ages are for 1980.

used restricted and exclusive areas during spring and summer, while the immature female showed no avoidance of either family group (Figure 22). Limited observations in the following winter indicated that these 2 families utilized a common food source prior to denning. Additional evidence that territorial behavior of females with young diminished by fall was obtained when, in the same winter, I observed another radio-collared female and her cub feeding within 100 m of an uninstrumented female with 3 cubs. Amstrup and Beecham (1976) reported an instance where the cubs of 2 females rested in the same tree while their mothers fed below.

Rogers (1977) reported that adult females were highly territorial and excluded other unrelated females from their ranges. LeCount (1980) and Young and Ruff (1982) also observed that home ranges of females were exclusive of each other. Lindzey and Meslow (1977b), Reynolds and Beecham (1980), and Garshelis and Pelton (1981) reported considerable spatial overlap in the ranges of female black bears, but noted that common areas were separated temporally. The behavior of female black bears to avoid other females or exclude them from their ranges apparently occurs only during spring and summer when they are accompanied by young cubs or when they consort with males.

Kinship also may determine the degree of social tolerance between females. Rogers (1977) found that adult females were more tolerant of their female offspring than of other, unrelated females. This may explain the close association (i.e., range overlap) between the old and young adult females in one of the groups referred to

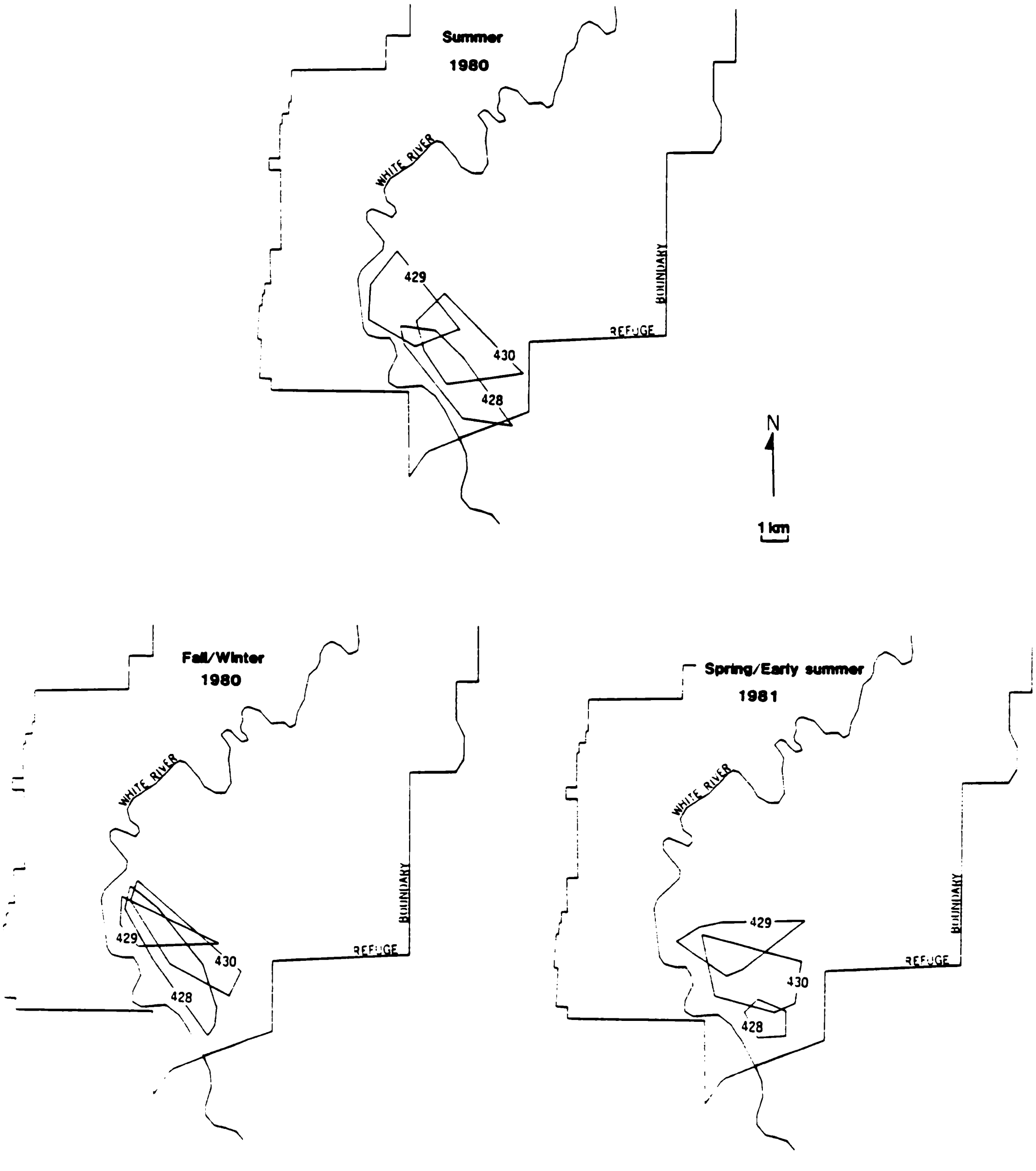

Figure 22. Overlap in seasonal ranges of female black bears on White River NWR, Arkansas, 1980-81. Bear 428, a 12-year-old, and bear 429, a 4-year-old, produced litters in the 1980-81 winter (i.e., both were accompanied by cubs in spring/early summer 1981). Bear 430 was a 3-year-old subadult. Ages are for 1980.

previously (Figure 22). Ranges of bears 439, a 9-year-old, and 451, a 3-year-old overlapped extensively in all seasons, even in the spring/ early summer of 1981 when 451 was accompanied by cubs and 439 was barren. These females were captured at the same trap site on consecutive days and used the same tree den in alternate years.

Dispersal. As yearlings (N = 2), 2-year-olds (N = 4), and 3-year-olds (N = 2) radio-monitored male black bears did not permanently disperse from the Refuge nor from their familiar ranges. One yearling male dispersed from his natal range following family break-up, but he utilized an area adjacent to (separated by the White River) his mother's range until radio contact was lost (apparently due to battery failure) when he was 2.5 years old. Another yearling male continued to reside in his natal range for 1 year after family separation, at which time the study was terminated. One male tagged as a 2-year-old was recaptured the following year 6 km from his original capture site. Another male marked as a 2-year-old was recaptured as an adult 2 years later only 5 km from his first capture location.

A 2-year-old male and a 3-year-old male exhibited sporadic, long-range movements during the early summer of 1980 (Figures 23 and 24), but by late summer, each had returned to the area where he was originally captured. These individuals then remained in their familiar ranges until summer 1981 when radio contact (again, presumably due to battery failure) was lost. Two radio-collared 4-year-old males utilized well-defined home ranges. One of these individuals had used the same area since being radio-instrumented as a 2-year-old.

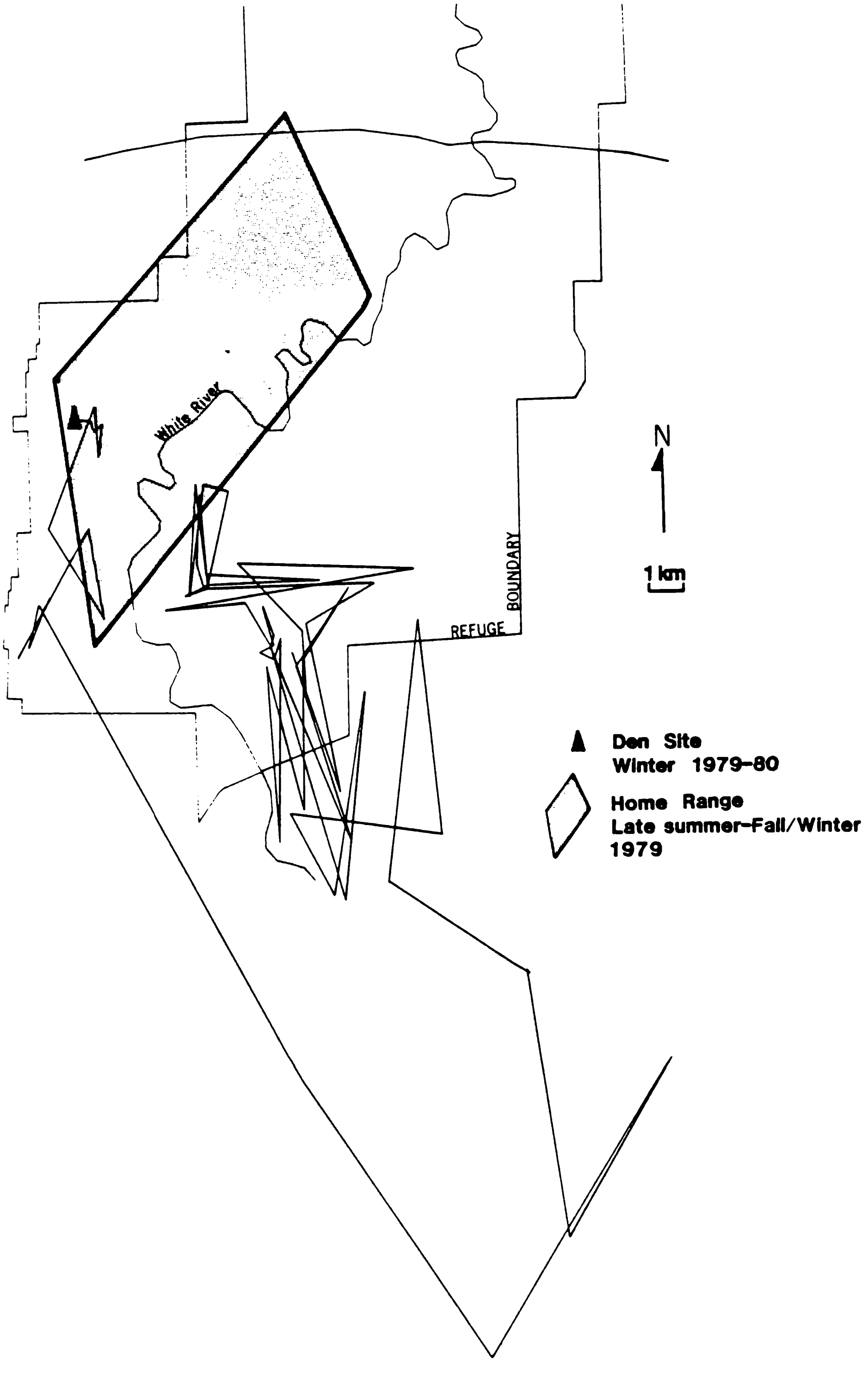

Figure 23. Sequential movements of a 3-year-old male black bear between 3 April 1980 and 25 October 1980, White River NWR, Arkansas.

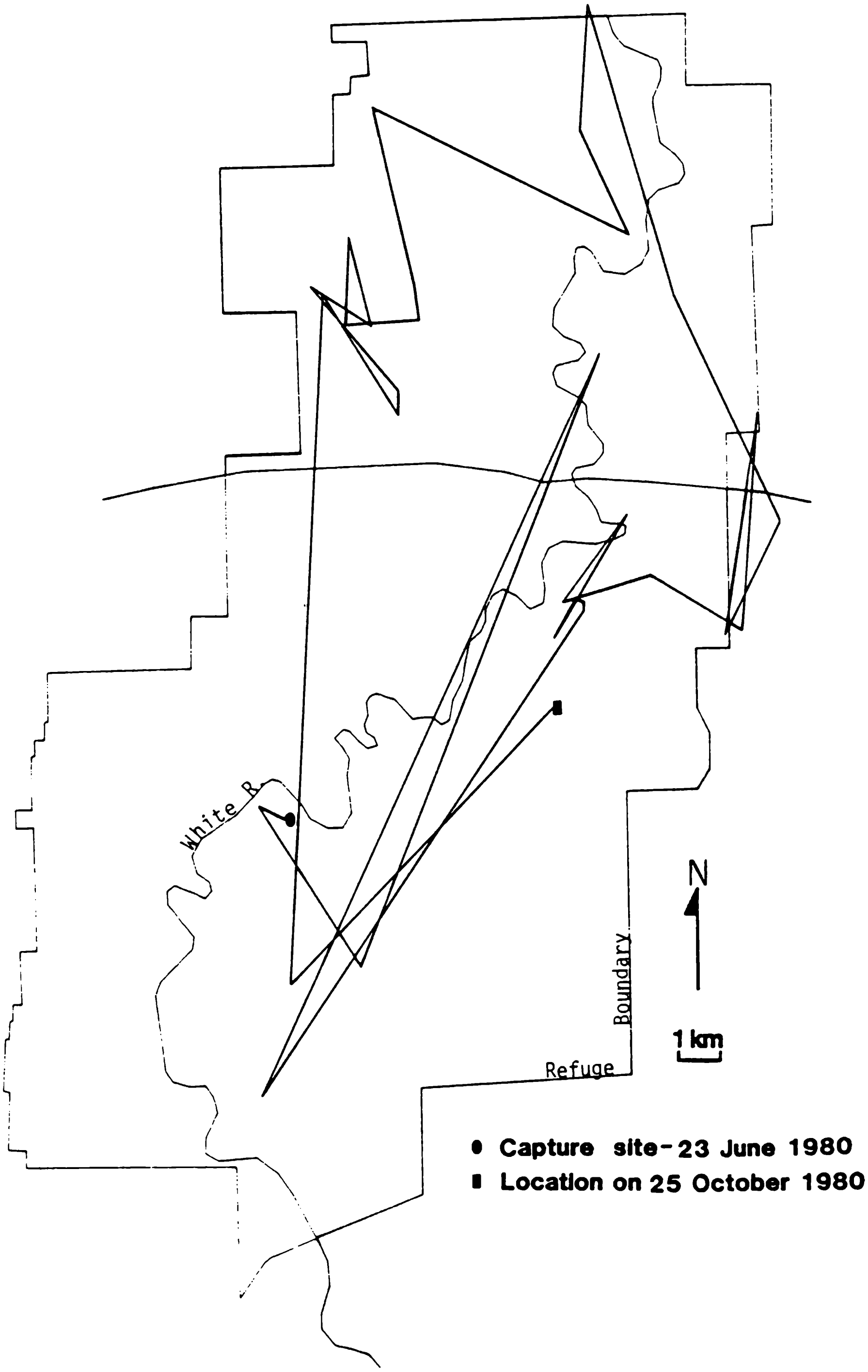

Figure 24. Sequential movements of a 2-year-old male black bear on White River NWR, Arkansas, June-October 1980.

Two females captured as 2-year-olds limited their movements to small ranges through the summer of their third year when their radio transmitters failed. Another female, which was radio-instrumented as a 3-year-old, did not move outside her well-defined home range during 2 years of monitoring. She subsequently raised cubs as a 5-year-old in that area.

In open black bear populations in Montana (Jonkel and Cowan 1971), Minnesota (Rogers 1977), Arizona (LeCount 1981), Idaho (Beecham 1983), and Maine (Hugie in press) dispersal was common in young males but rare or nonexistent in females. Rogers (1977) observed no dispersal by 10 yearling males; of these 6 dispersed as 2-year-olds and 4 as 3-year olds. Jonkel and Cowan (1971) and Beecham (1983) reported that dispersal was common in males 1.5 and 2.5 years old. In Washington (Lindzey and Meslow 1977b), males expanded their ranges as 2-year-olds, but dispersal from a coastal island occurred only in the 4-year-old male cohort. LeCount(1982) obtained limited evidence that males dispersed as 2-year-olds. Brody (1984) noted extensize movements and range expansions by yearling and 2-year-old males, and Hugie (in press) found that no males remained in their mother's ranges after they were 2 years old.

Rogers (1977) interpreted the exclusiveness of dispersal behavior in males as a selective advantage which increased inclusive fitness. by reducing inbreeding and competition among kin. Beecham (1983) hypothesized that young male black bears increase their chances of reproductive success by dispersing to new ranges rather than remaining on their natal ranges until they are large enough to compete with or replace resident adult males.

On the Refuge, subadult males may have dispersed from their natal ranges, but they likely established breeding ranges nearby. No dispersal corridors exist between the forested habitat of the lower White River basin and black bear populations to the west in Arkansas or to the south in Louisiana. These habitat restrictions apparently preclude long-range dispersal by young males and indicate that the Refuge black bear population is genetically closed.

Habitat Utilization

Seventeen habitat variables were quantified for 1106 25-ha quadrats (276.5 km^2) within and adjacent to the study area core. Of 2104 radio-telemetry locations made during the study, 1654 fell in this inventoried area and were used to analyze habitat utilization by black bears on the Refuge. Using a chi-square procedure, observed and expected frequencies of bear use of abundance categories of each variable were compared. All references to "less than" or "greater than" expected utilization are interpreted with respect to a significance level of 0.05.

Forest cover. With the exception of riparian forest, overall bear use of categories of each forest cover variable was disproportionate to availability (Table 27). Low forest (i.e., overcup oak-water hickory type) and transitional forest (i.e., sugarberry-American elm-green ash type) were preferred; considering all locations, bears

Table 27. Black bear utilization of habitat variables on White River NWR, Arkansas, 1979-1982.

Variable[a]	Abundance category	Overall[b] use	Spring 1981	Spring 1982	Spring 1980-82	Summer 1980	Summer 1981	Summer 1979-81	Fall/Winter 1979	Fall/Winter 1980	Fall/Winter 1981	Fall/Winter 1979-81
Low forest	low	-	o	o	o	o	+	o	-	-	+	-
	moderate	o	o	o	o	o	o	o	-	-	o	-
	high	+	o	o	o	o	-	-	+	+	-	+
Transitional forest	low	-	-	-	-	-	-	-	+	o	-	o
	moderate	+	+	+	+	+	+	+	-	o	+	o
	high	+	+	+	+	+	+	+	-	o	+	-
High forest	low	+	+	+	+	+	+	+	+	+	-	+
	moderate	o	o	+	o	o	+	o	-	-	+	-
	high	-	-	-	-	-	-	-	-	-	+	-
Riparian forest	low	o	o	o	+	o	o	o	o	o	o	o
	moderate	o	o	o	o	o	o	o	o	o	o	o
	high	o	o	o	-	o	o	o	o	o	o	o
Forest diversity	low	-	o	-	o	-	-	-	+	+	-	o
	moderate	+	+	o	o	+	+	+	-	-	o	o
	high	+	+	+	+	+	+	+	-	-	+	o
Elevational diversity	low	+	o	o	o	o	o	o	+	+	o	+
	moderate	-	o	o	o	o	o	o	-	-	o	-
	high	o	o	o	o	o	o	o	-	-	o	-

Table 27 (Continued)

Variable	Abundance category	Overall use	Spring			Summer			Fall/Winter			
			1981	1982	1980-82	1980	1981	1979-81	1979	1980	1981	1979-81
Miscellaneous	low	+	o	o	+	o	o	o	+	+	o	+
	moderate	o	o	o	o	+	o	o	-	-	o	-
	high	-	o	o	-	-	o	-	-	-	o	-
Swamps	low	-	-	o	-	-	-	-	+	-	o	-
	moderate	+	+	o	+	+	+	+	o	+	o	+
	high	+	+	o	+	+	+	+	-	o	o	o
Lakes and bayous	low	o	o	+	o	-	+	o	-	o	o	-
	moderate	+	o	-	o	+	o	o	+	+	o	+
	high	-	-	-	-	o	o	o	o	-	o	-
Streams	low	-	o	o	o	o	o	o	+	-	-	-
	moderate	+	o	o	o	o	o	o	-	+	+	+
	high	o	o	o	o	o	o	o	o	o	+	o
Habitat diversity	low	-	-	o	o	-	-	-	+	o	o	o
	moderate	+	+	o	o	+	+	+	o	o	o	o
	high	o	o	o	o	o	o	o	-	o	o	-
Logging roads	low	+	o	o	o	o	o	o	+	+	o	+
	moderate	-	o	o	o	-	o	-	-	-	o	-
	high	o	o	o	o	+	o	o	o	o	o	o

Table 27 (Continued)

Variable	Abundance category	Overall use	Spring 1981	Spring 1982	Spring 1980-82	Summer 1980	Summer 1981	Summer 1979-81	Fall/Winter 1979	Fall/Winter 1980	Fall/Winter 1981	Fall/Winter 1979-81
Maintained	absent	+	o	o	o	o	o	o	+	+	o	+
roads	present	-	o	o	o	o	o	o	-	-	o	-
Total	low	-	-	o	o	-	-	-	+	o	o	o
edge	moderate	o	o	o	o	o	o	o	o	o	o	o
	high	+	+	o	o	+	+	+	-	o	o	o
Total	low	o	o	o	o	o	o	o	o	+	-	+
contour	moderate	-	o	o	o	o	o	o	o	o	o	o
	high	o	o	o	o	o	o	o	o	-	+	-
Refuge	absent	+	+	+	+	+	+	+	+	+	o	+
boundary	present	-	-	-	-	-	-	-	-	-	o	-
White	absent	o	o	+	o	o	o	o	o	o	o	o
River	present	o	o	-	o	o	o	o	o	-	o	-

[a] Definitions of variables are given in Table 2, page 39.

[b] - = used less than expected by chance ($P<0.05$)

o = used in proportion to availability

+ = used more than expected by chance

used habitats with moderate and/or high abundance of these types more than expected by chance. Conversely, overall utilization of habitats with high proportions of high forest (i.e., sum of sweetgum-Nuttall oak-willow oak, sycamore-pecan-American elm, and white oak-red oak-hickory types and their variants) was less then expected.

Given results of food habits and home range analyses, which indicated that behaviors of black bears on the Refuge were related to seasonal availability of foods, I repeated the chi-square test, sorting bear locations by season over years and within years. This analysis demonstrated that most overall disproportionate use of forest cover was attributable to seasonal preferences. The overall greater than expected use of low forest was primarily due to the affinity of bears for this type in fall/winter. During summer, bears used homogeneous areas of low forest less than expected. In spring, utilization of low forest was proportional to availability. Concomitantly, homogeneous habitats of transitional forest were used more than expected in spring and summer and less than expected in fall/winter. Homogeneous areas of high forest were used less than expected in all seasons. Riparian forest was used in proportion to its availability in summer and fall/winter and less than expected during spring.

Patterns of forest cover utilization in spring and summer were relatively consistent between years, especially the preference for transitional forest and less than expected use of high forest. In fall/winter, bear use of forest cover contrasted between years, apparently due to variations in hard mast availability. In fall/winters of 1979 and 1980, homogeneous areas of low forest were used more than expected, while areas with high proportions of transitional forest and high forest were used less than expected. Conversely, during late fall/winter of 1981, bears used areas with an abundance of low forest less than expected and exhibited preferences for habitats with high proportions of transitional forest ($P<0.005$) and high forest ($P<0.1$). In the fall/winters of 1979 and 1980, overcup oak mast was abundant, but in 1981, overcup oak mast failed and the production of willow and Nuttall oak acorns, as well as sweet pecans, was good.

Forest diversity. The diversity of forest cover also was related to the seasonal distribution of black bears on the Refuge. Overall bear use of habitats with moderate and high forest diversity was greater than expected (Table 27). This could be reduced, however, to preferences for these areas in spring, and especially in summer. This pattern was consistent for all years of the study and appeared to be related to food availability. Diets of black bears on the Refuge are more diverse in summer than in other seasons. Phenological development and the availability of soft fruits, the staple food of the summer diet, vary between forest cover types, primarily due to the duration of flooding (and soil characteristics) at different elevations. Hence, areas with high forest diversity provide bears with the most diverse and consistent food supply during summer.

The utilization-availability analysis indicated that overall use of categories of forest diversity in fall/winter was proportional to availability. However, this apparently uniform indifference to forest diversity actually represented a balance of contrasting preferences in different years. In 1979, habitats with low forest diversity were used more than expected, in 1980 use was proportional to availability, and in 1981, habitats with high forest diversity were used more than expected. These contrasting results apparently were more related to preferences of bears for forest cover than for forest diversity *per se*. Transitional and high forest are associated with linear topographic features (e.g., ridges and/or waterways) and generally do not cover large continuous tracts in the study area core. On the other hand, low forest dominates on the broad flats and terraces in this area and may uniformly cover tracts of 300-1000 ha or more. Hence, a 25-ha quadrat with $\geq$ 60 percent cover (i.e., high abundance category) of low forest is less likely to contain other forest types (i.e., more likely to have lower forest diversity) than a quadrat with $\geq$ 60 percent cover of transitional forest. Furthermore, despite the abundance of possumhaw holly and sugarberry fruits in the fall/winter of 1980, bears focused their attention on fat-rich acorns in low forest. Apparently, the greater than expected use of diverse forest cover in the fall/winter of 1981 was due to the abundance of hard mast in transitional and high forest types rather than the diversity of food in these habitats.

Elevational diversity. The fall/winter distribution of black bears on the Refuge was further related to elevational diversity, but this parameter also appeared to be correlated with forest cover. In the fall/winters of 1979 and 1980, when low forest was preferred, utilization of habitats with low elevational diversity was greater than expected. In 1981, when transitional and high forest were preferred, utilization of categories of elevational diversity was proportional to availability. Elevational diversity is inversely related to homogeneity of low forest, and greater than expected use of habitats with low elevational diversity in fall/winter further demonstrates the preference of bears for overcup oak acorns during that season. In spring and summer of all years, no disproportionate use of habitats based on their degree of elevational diversity was observed.

Water resources. Overall disproportionate use of all water-related habitat variables was observed (Table 27, page 158). Of these, however, only swamps (i.e., wooded swamp/marsh, mostly beaver impoundments and dead timber reservoirs) appeared to consistently affect the seasonal distribution of black bears on the Refuge.

In all seasons habitats with moderate or high proportions of swamps were used more frequently then expected, while those with low proportions were used less than expected. A strong preference ($P<0.005$) for swamp habitats was exhibited in each summer of the study. In spring, the importance of swamps was somewhat reduced. In spring of 1982, abundance categories of swamp were utilized in porportion to availability. Preferences for swamps in fall/winter varied between years of the study. In 1979, areas with low proportions of swamps were preferred and those with high proportions of swamp were used less than expected. In 1980, habitats with a moderate abundance of swamps were used more than expected, and those with low proportions of swamps were used less than expected.

Despite the variations between fall/winters of different years, the overall preference for areas with an abundance of swamps was outstanding and indicated that this habitat component is very important to black bears on the Refuge. I believe that swamps were preferred primarily for their value as cover rather than as a source of food. Scat analysis did not indicate that aquatic plants common to swamps (e.g., American lotus and naiad) were frequently utilized for food. Landers et al. (1979) found that secluded hardwood swamps were important as refuges for black bears in coastal North Carolina. In northern Wisconsin, escape routes of black bears being chased by dogs always included swamp habitats (Massopust and Anderson 1984), and Alt et al. (1980) suggested that swamps were an important component of black bear habitat in northeastern Pennsylvania.

The overall use of categories of open water (i.e., lakes, large open bayous, and the White River) was disproportionate. Again, however, the relationship between this habitat component and the distribution of black bears on the Refuge varied between seasons. In spring, habitats with low and moderate amounts of open water were used in proportion to availability, while those with high amounts of open water were used less than expected. In summer, bear use of open water was proportional to availability. However, the lack of less-than-expected utilization of habitats with high proportions of open water in that season, suggest a stronger affinity to open water in summer than in other seasons. In fall/winter, it appeared that bears preferred habitats with moderate amounts of open water at the expense of those with high or low proportions of open water.

Since bears were rarely located in open water (5 of 2104 telemetry locations), it is reasonable to assume that preferences for this habitat feature represent utilization of banks or shallow water at the margins of lakes, bayous, and the White River. The increased use of these habitats during summer is likely related to food availability. Dead fish accumulate along the edges of lakes and bayous and in log drifts on the White River. Soft mast-producing species such as swamp privet also may be common along the margins of lakes and bayous.

The abundance of streams appeared to have little effect on the seasonal distribution of black bears on the Refuge. In spring and summer, each abundance category for this habitat variable was utilized in proportion to availability. In fall/winter, overall disproportionate use of categories occurred, but preferences varied between years and were likely due to factors other than the abundance of streams; most streams on the Refuge are seasonal and become dry by the fall/winter season.

Habitat diversity. Variables used to define habitat diversity include first bottom forest (i.e., low forest), second bottom forest (i.e., transitional and high forest), riparian forest, swamps, open water, and miscellaneous areas (i.e., levees, rights-of-way, and dredge spoils). These variables were considered discrete habitat components.

Preferences of black bears for diversity in habitats varied between seasons, however, seasonal patterns were relatively consistent between years. Over all spring seasons of the study, categories of habitat diversity were used in proportion to availability. In spring of 1981, bears exhibited a slight preference for increased diversity, using habitats with low diversity less than expected and those with moderate diversity more than expected. In all summers, areas with low diversity were used less than expected, those with moderate diversity were used more than expected, and those with high diversity were used in proportion to availability. These utilization patterns are similar to those for forest diversity and probably relate to the use of transitional forest by bears during summer. In fall/winter, bears either utilize highly diverse habitats less than expected (1979) or exhibited an indifference to habitat diversity (1980 and 1981).

Roads. Overall, habitats with few logging roads were used more than expected, those with a moderate number were used more than expected, and those with an abundance were used in proportion to availability (Table 27, page 158). This pattern of use applied only to fall/winter data, however. In spring, the abundance of logging roads was not related to bear distribution. In summer, specifically in 1980, bears preferred areas with an abundance of logging roads and used those with a moderate amount less than expected. The only overall disproportionate summer use was a less than expected utilization of the moderate abundance category.

It is difficult to interpret disproportionate use of categories when it does not follow a gradient. I believe that these relationships between logging roads and distributions of bears are part of a broad model of seasonal habitat utilization. Logging roads are more abundant at higher elevations on the Refuge where transitional and high forest dominate. Summer preferences for these types of forest cover may be due, in part, to understory foods in the forest gaps associated with logging roads. However, in fall/winter, preferences for these habitats are apparently due to mast availability, and an abundance of logging roads in preferred habitats may be incidental. This argument is reinforced by the greater than expected use of habitats with a low abundance of logging roads in the fall/winters of 1979 and 1980. In those years, bears preferred the overcup oak-water hickory forest cover at lower elevations where logging roads are less abundant.

The use of habitats in relation to maintained roads further clarified this broad model of habitat utilization. In fall/winters of 1979 and 1980, bears used habitats containing maintained roads less than expected. In those years, they also preferred overcup oak stands in low-elevation flats. Roads are seldom, if ever, maintained in these low areas which are susceptible to frequent and prolonged flooding. Rather, maintained roads generally are constructed along ridges where transitional and high forest cover types occur. The proportional utilization (i.e., no avoidance) of habitat quadrats containing maintained roads in fall/winter of 1981 coincided with a preference for transitional and high forest cover types in that season.

Edge. Edge was defined as the sum of open water/forest edge, swamp/forest edge, streams, logging roads and maintained roads. Bears exhibited an overall preference for habitats with a high amount of edge and used those with little edge less than expected (Table 27, page 158). This pattern of utilization was consistent only in summer and was probably related to the use of swamps and especially transitional forest (where roads and streams are abundant). Greater than expected use of habitats with an abundance of edge also occurred in spring of 1981, when flooding persisted into May. Bears moved to higher elevations (i.e., transitional forest) after emerging from dens in that year. In fall/winter of 1979, habitats with an abundance of edge were used less than expected. This corresponded to the use of homogeneous stands of overcup oak-water hickory, which contain few roads and streams.

Contour. Disproportionate use of habitats based on their amount of contour (i.e., contour lines) was slight and occurred only in fall/winter. Quadrats with high proportions of contour were used less than expected and those with low amounts were used more than expected.

Again, this was apparently due to the distribution of bears in relation to mast availability in that season. In 1979, overcup oak mast production was very high and uniform throughout the low forest. In the fall of that year, no preferences were exhibited for habitats based on contour. Overcup oak acorns also were abundant in the fall/winter of 1980, but they were restricted to mesic flats. In that year, habitat quadrats with low proportions of contour were used more than expected. Conversely in 1981, when overcup oak mast failed, and pecans and acorns were abundant in high forest and transitional forest, habitats with high proportions of contour (primarily due to distinct ridges) were used more than expected.

Refuge boundary. With one exception, black bears used quadrats along the boundary of the Refuge less than expected in all seasons of all years of the study (Table 27, page 157). Again, the exception was the fall/winter of 1981. In that year, quadrats on the boundary of the Refuge were used in proportion to availability (i.e., not avoided). This was apparently related to the availability of willow oak acorns along Honey Locust Bayou in the western extremity of the study area core. The lower than expected use of quadrats along the boundary of the Refuge may have been due, in part, to an avoidance of human activity and unforested habitats. However, it was not uncommon to observe or capture black bears near ($\leq$ 1 km) the Refuge boundary.

White River. Overall, black bears did not appear to avoid the White River. In certain seasons, however, disproportionate use was observed. In the spring of 1982, habitat quadrats along the river were used less than expected. This was apparently due to flooding in that year when bears moved to higher elevations away from the river and toward the periphery of the Refuge. For all fall/winter observations, but specifically for the fall/winter of 1980, bear use of habitats along the White River also was less than expected. I believe that this applied only to river margins, however. In December 1980, several radio-collared bears utilized an overcup oak flat along the river (page 148).

The chi-square analysis of individual variables delineated several distinct patterns of habitat utilization. The seasonal distribution of bears appears to be fundamentally related to forest cover due to the availability of foods in these habitats. Swamps may be the singularly most important constituent of black bear habitat on the Refuge in all seasons. Other habitat components (e.g., lakes and bayous, edge, forest diversity, roads) may influence bear distribution in certain seasons but in many cases, are apparently incidental to preferences for forest cover and swamps. To verify correlative effects and identify those variables which had an important (i.e., despite the simultaneous effects of other variables) influence on distributions of black bears on the Refuge required a multivariate approach.

Multiple regression models. Based on results of the utilization-availability analysis, I selected 10 variables which appeared to be most related to habitat utilization by black bears on the Refuge. Employing the SAS (1982b) GLM procedure for classification (i.e., categorical) variables, these independent habitat variables were simultaneously regressed against the number of bear observations in individual habitat quadrats. Models were constructed for seasons over all years and by years. I relaxed the significance level to 0.1 for interpretations of results of this analysis.

Regression coefficients for seasonal models ranged from .082 to .136 (Table 28), indicating that they explained little of the seasonal variation in habitat utilization. Sorting observations by year reduced the efficiency of seasonal regression models even further (R^2 = .031 - .10). Despite these low regression coefficients, the multivariate models were useful to clarify results and strengthen interpretations of the chi-square analysis.

Variables which independently contributed significantly ($P \leq 0.1$) to seasonal models generally coincided with those which the utilization-availability analyses had delineated as important. In the spring model, Type III (i.e., partial) sums of squares results indicated significant effects for swamps, forest diversity, transitional forest, roads, and lakes and bayous (open water). All of these habitat features except open water were positively correlated with bear use. Goodness-of-fit tests also had indicated that habitats with an abundance of swamps, transitional forest, and roads, and high forest diversity were used more than expected in spring. They further demonstrated that habitats with high proportions of open water were used less than expected in that season.

Table 28. Type III sums of squares results for multiple regression models of seasonal habitat utilization by black bears on White River NWR, Arkansas, 1979-1982

	Spring, R^2= .082			Summer, R^2= .136			Fall/Winter, R^2=.096		
Variable	F[b]	P>F[c]		F	P>F		F	P>F	
Low forest	0.40	0.67		0.06	0.95		2.56	0.08	+
Transitional forest	3.23	0.04	+[d]	1.68	0.19		0.33	0.72	
High forest	0.62	0.54		1.72	0.18		1.09	0.34	
Swamps	4.11	0.02	+	13.78	0.0001	+	5.44	0.005	+
Lakes and bayous	6.55	0.002	-	4.63	0.01	-	2.43	0.09	-
Streams	0.31	0.73		1.85	0.16		1.90	0.15	
Roads	2.39	0.09	-	3.00	0.05	-	1.41	0.24	
Edge	0.07	0.94		1.88	0.15		1.86	0.16	
Forest diversity	4.35	0.01	+	0.57	0.56		2.37	0.09	-
Habitat diversity	0.57	0.56		3.00	0.05	+	2.99	0.05	-

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[a] Definitions of variables given in Table 2, page 39.

[b] F-value for Type III sums of squares.

[c] Probability of a greater F-value.

[d] Direction of significant ($P \leq 0.1$) correlation.

In the summer model, swamps and habitat diversity exhibited significant effects and were positively correlated with bear use. Swamps were distinctly the most important component of bear habitat in that season (F = 13.8, $P<0.0001$) (Table 28). Lakes and bayous (i.e., open water) and roads also contributed significantly to the summer model ($P<0.005$). For both of these variables, the correlation was negative and represented reduced use of habitats with large proportions of open water and roads. Interestingly, transitional forest ($P>0.18$), forest diversity ($P>0.56$), and edge ($P>0.16$) did not have significant effects. Utilization-availability analyses had indicated that each of these variables were related to the summer distribution of black bears on the Refuge, apparently due to food (i.e., soft mast) availability. The effects of transitional forest and edge approached significance (Table 28), but it is possible that a bias favoring swamps was present in my telemetry sampling and influenced these results. Radio-locations were always made during daylight hours, generally between 0800 and 1800 hrs. If bears were less active at those times during summer, and as I suspect, utilized swamps primarily for cover, the effect of swamps may have been accentuated, or conversely, the importance of transitional forest obscured.

In fall/winter, low forest, swamps, lakes and bayous, forest diversity, and habitat diversity contributed significantly to the habitat utilization model (Table 28). Swamps and low forest were positively correlated with bear use. Open water and the two diversity indices were negatively correlated with bear use. These results mirror those of the utilization-availability analysis, demonstrating an overall preference for low forest. However, the

Since the utilization-availability analysis indicated that the fall/winter distribution of bears on the Refuge varied in different years according to the type of forest cover in which mast production was high, I constructed fall/winter models for individual years of the study. In 1979, when overcup oak mast was abundant and uniformly distributed, no variables exhibited significant effects ($P>0.1$) in the fall/winter model. In 1980, when overcup oak acorns were plentiful, but only in low flats, low forest contributed significantly ($P<0.07$) to the model. The effect of forest diversity was also significant ($P<0.04$), but it correlated negatively with bear use. In 1981, when overcup oak mast failed and red oak acorns and sweet pecans were abundant, transitional forest contributed significantly ($P<0.03$) to the model. The effect of streams also was significant ($\underline{P}<0.04$) in that fall/winter, but it was likely an artifact of the topography associated with the distribution of transitional forest.

Results of these analyses indicate that the seasonal distribution of black bears on the Refuge is dictated by food availability. Similar relationships between black bear habitat utilization and food availability have been reported in a variety of habitats (Jonkel and Cowan 1971, Amstrup and Beecham 1976, Rogers 1976, Lindzey and Meslow 1977b, Landers et al. 1979, Kelleyhouse 1980, Garshelis and Pelton 1981, Novick and Stewart 1982). Cover, primarily swamps, also appears to have a large influence on the distribution of black bears on the Refuge. Lindzey and Meslow (1977b) and Landers et al. (1979) concluded that cover was a critical component of black bear habitat in coastal Washington and coastal North Carolina, respectively.

The opportunistic strategy of black bears is apparently best adapted to heterogeneous habitats which offer a diversity of patchy food sources. Existing habitat conditions on the refuge meet this criterion, and black bears appear to be efficiently exploiting the available resources of this area. Continued maintenance of the relatively natural conditions in this bottomland hardwood forest should allow this relationship to persist.

CHAPTER V

SUMMARY AND CONCLUSIONS

Due to habitat modifications, primarily deforestation, black bears currently occupy only 5-10 percent of their former range in the southeastern United States. Losses of forested habitats have been especially high in the rich alluvial plain of the Mississippi River where bottomland hardwood forest acreage was reduced from 4.8 to 2.1 million ha between 1937 and 1977. Concomitantly, black bears have been nearly extirpated from this vast river valley. One, possibly the only native population which has survived occurs in the bottomland hardwood forest within and adjacent to the White River National Wildlife Refuge in the lower White River basin of eastern Arkansas. Between June 1979 and June 1982 an ecological investigation of this remnant black bear population was conducted.

A 212 km^2 section in the southern half of the 457 km^2 Refuge was chosen as a study area core. Capture-mark-recapture and radiotelemetry procedures were employed to obtain data on population characteristics, growth patterns, reproduction, mortality, food habits, denning, home range and movements, and habitat utilization.

Trapping was preceded by prebaiting to identify areas with relatively high bear activity and enhance capture success. Capture success was higher (6.2 percent) at sites where bear visitation had occurred 1-5 days after prebait establishment than at those visited 6-10 days or 11-15 days after prebait establishment (4.9 percent and

0 percent, respectively). In 1453 trapnights over 3 summers, 63 captures of 51 individual black bears were made. The majority (92 percent) of the trapping effort was accomplished with spring-activated foot snares. Barrel traps were utilized only sparingly, but capture success was similar for both trap types (4.4 percent and 3.4 percent, respectively). Capture success varied considerably between years on each trap line, however, total capture success did not vary significantly ($P>0.05$) between years of the study.

Motion sensitive radio transmitters affixed to collars were fitted to 28 black bears during the study. These individuals were radio-monitored for periods of 17 to 1001 days; 19 bears were monitored for 1 year or longer. A total of 2104 telemetry locations were made between 23 July 1979 and 26 May 1982. Flat topography and dense vegetation hinder ground radio-tracking in bottomland hardwood forest, and the majority (85 percent) of radio-locations were made from aircraft. The mean interval between radio-locations outside the denning period was 4.2 days in 1979, 4.4 days in 1980, and 6.1 days in 1981 and 1982.

Estimates of the number of bears resident on the study area core in 1980 were made applying the Petersen method to mark-recapture (all marks) and mark-recapture-reobserve (radio-collar marks only) data. These estimates applied only to bears $\geq$ 1-year-old; independent estimates of the cub cohort were made from information on population structure, mean breeding interval of radio-collared females, and cub survival.

The estimate based on mark-recapture-reobserve data (87 bears) appeared to be less biased and more precise than that derived from mark-recapture data only (92 bears). Available information indicated that the density of black bears is greater on the study area core than elsewhere on the Refuge. Extrapolation of the estimate for the study area core to the total acreage of the Refuge was adjusted accordingly, producing an estimate of 130 bears for the entire Refuge population. Based on these estimates, black bear density on the Refuge ranges from 1 bear/ 2.4 km^2 to 1 bear/5.7 km^2 ($\bar{X}$ = 1 bear/4.5 km^2).

Population estimates for the Refuge were used to extend the extrapolation and define broad limits of the actual number of bears occupying the lower White River basin. Using these numbers, assuming a 1:1 sex ratio, and applying estimates of age structure and age of sexual maturity of bears on the study area core, conservative and liberal estimates of the genetically effective size of this closed population were 75 and 130 bears, respectively. Relaxing these assumptions, and assuming that (1) the 1.56:1 sex ratio in the capture sample was representative of the entire population and (2) that only 50 percent of the males $\geq$ 4 years old and 25 percent of the 3-year-old males actually contributed to reproduction, the effective number of the population was estimated at 53 to 92.

Regardless of the approach, effective population sizes in this range are dangerously low due to the potential loss of genetic variation within the population. This situation is compounded by the "bottleneck" event which occurred during the early 1900's and apparently reduced the population to a size lower than that which presently exists. This event also geographically (and genetically) isolated the population from other black bear populations in west-central Arkansas and northern Louisiana. The low effective size and apparently eminent reduction in genetic variation of the black bear population in the lower White River basin indicate that its long-term fitness is precariously low. Maintenance of an effective number equal to or greater than that which presently exists appears critical to the survival of this remnant population.

Two indices of relative density were generated in this study, prebait visitation rate and the number of bear observations per hunter-day during managed deer hunts. Prebait visitation rate varied within year and area samples, but overall, did not vary significantly between years or areas. The index of relative density based on bear observations during managed hunts appeared to have several sources of bias and is not as accurate as the prebait visitation index for monitoring long-term population trends. Observations by deer hunters are valuable, however, for obtaining data on the fall distribution and litter sizes of black bears on the Refuge.

More males (N = 39) than females (N = 25) were captured during the study; the deviation of this 1.56:1 composite sex ratio from the theoretical 1:1 was not significant ($0.1>P>0.05$). Male:female ratios of the 1979 and 1980 capture samples (1.2:1 and 1.1:1, respectively) approximated the expected 1:1. In 1981, significantly more males than females (2.4:1) were captured ($P<0.05$). Due to their mobility and aggressive behavior, males may have a higher probability of capture than females, however, the high proportion of males in the capture sample may represent a bias in favor of males in this unexploited population.

Bears ranging from 1 to 12 years of age were captured during the study. Females appear to be longer-lived than males; 7 (28 percent) females were between 9 and 12 years of age, while no males were older than 9 years. Subsequent radio-monitoring proved, however, that bears of both sexes reach greater ages than the capture sample indicated. Two radio-collared females attained 14 years of age, and 1 radio-instrumented male was 11 years old when the study was terminated. Annual capture samples were too small to delineate population trends based on age structure, but it appears that the population may have attained a stable age structure.

Growth was curvilinear in both sexes. For males, measures of length and girth were strongly related to age. For females, relationships between body size and age were less distinct and limited to measures of girth. Males reached maximum weight by 5 years of age. Females attained adult stature (i.e., height and length) earlier than males, possibly by 2 or 3 years of age, but apparently continue to add body weight until they are 9 or 10 years of age. Mean weight of adult males (102.1 kg) was approximately twice that of adult females (52.2 kg).

Age of sexual maturity in females was determined from teat condition or the presence of cubs at the time of capture and from reproductive histories of radio-collared individuals. Sexually mature males were identified by signs (i.e., scars) of fighting and testicular measurements. It appeared that approximately one-third of the female black bears on the Refuge successfully bred at 3 years of age, producing cubs as 4-year-olds. All females whose reproductive histories were known or could be construed had bred by 5 years of age. Males may become sexually mature at 3 years of age but probably do not successfully compete for females at that age due to their smaller size (i.e., $\bar{X}$ = 70 kg versus $\bar{X}$ = 95 kg for older males) and the high proportion of adult males in the population.

Limited evidence indicated that black bears may breed on the Refuge from mid-June to mid-August. No estrous females were captured, but radio-telemetry observations of male/female bonds (N = 4) were made between 18 July and 13 August. Also, a yearling male permanently separated from his mother on 11 July, and fresh fighting scars were observed on adult males between 27 June and 27 August.

Breeding frequency (i.e., interval between litter production) of adult females was estimated at 2.4 years. One female produced litters in 1979, 1981, and 1983, and 2 others bore cubs in 1980 and 1982. Three females skipped at least 1 year (i.e., $\geq$ 3-year interval) between litters.

Nine litters were born to radio-collared females during the study. Seven litters were whelped between 30 January and 29 February. One litter was born prior to den inspection on 21 January and another between den inspections on 8 January and 19 February. These findings suggest that parturition in black bears may vary geographically, occurring later in southern regions.

The observed mean litter size at birth (N = 10) was 2.3 cubs. Estimates of litter size at 9-12 months post-partum based on my observations ($\bar{X} = 1.5$, N = 22) and those of hunters ($\bar{X} = 1.58$, N = 106) were similar. This reduced to a mean minimum mortality rate for the cub cohort of 32 percent. Most cub mortality appeared to occur within 6 months of den emergence. Two cubs which drowned in a flooded tree den represented 13 percent of the observed cub mortality. Such events probably do not account for the high cub mortality which I observed. Flooding may indirectly cause cub mortality by delaying phenological development (i.e., food availability) and restricting movements of females with young cubs in late spring and early summer.

Mortality rate of radio-collared bears $\geq$ 1 year old was approximately 5 percent; in 39 "bear-years" of monitoring, 2 bears died. An 11-year-old female was illegally shot in late September or early October 1979 near the periphery of the Refuge. At about the same time, a 9-year-old female also died, but the cause of her death was unknown. U.S. Fish and Wildlife records since 1935 indicate that black bears are occasionally killed illegally on the Refuge, most commonly during managed hunts. This may represent a significant source of mortality among subadult and adult bears. The combined effects of illegal and natural mortality of subadults and adults and high cub mortality may balance the high reproductive rate currently exhibited by black bears on the Refuge.

Food habits of black bears were determined from scat analysis and observations of feeding behavior of radio-collared individuals. Twenty-six food items were identified in 195 scats. These were assigned to broad categories for descriptive purposes; herbage, soft fruits, hard mast, insects, fish, and mammals. Four forms of debris also were treated as a category.

Examination of mean monthly percentage volumes of these categories delineated three distinct seasonal diets. In spring (1 March-7 June), herbage predominated in the diet; grasses and unidentified green stems and leaves were most commonly utilized. Oak flowers and winter wheat also were represented in spring scats, the latter item being available in cultivated fields adjacent to the Refuge. Debris and nuts of American lotus constituted 11 and 10 percent of the mean volume of spring scats.

In summer (8 June-21 October), the diet of bears on the Refuge is relatively diverse. Soft fruits (e.g., Rubus spp., red mulberry, swamp privet, greenbrier, dogwood, peppervine, and muscadine grape) composed 49 percent of the mean volume of summer scats. These fruits mature at different times through the summer and provide bears with a consistent source of protein. Persimmon predominated in the diet during late September and October. The importance of insects (primarily carpenter ants) increased from spring to summer when they represented 8 percent of the mean scat volume (plus 25 percent associated debris). White-tailed deer and to less extent, muskrat and rabbit appeared in summer scats; these animals apparently were scavenged. Fish composed

2 percent of the mean volume of summer scats, but was likely underrepresented in scat contents. Bears often concentrated their activities around drying lake and stream beds during summer when stranded fish were abundant.

Late in October bears began to utilize immature oak acorns, and by November this food predominated in the diet. Acorns constituted 88 percent of the mean volume of fall/winter (22 October-29 February) scats. Overcup oak is the most abundant and consistent hard mast-producing species in the study area core, and bears generally concentrated their fall/winter activities in homogeneous overcup oak stands where acorn production was high. When overcup oak mast failed in 1981, bears utilized red oak acorns and sweet pecans which were abundant on ridges and second bottom terraces. Animal foods were utilized less frequently during fall/winter. White-tailed deer were scavenged during managed hunts and beetles and yellow-jackets occasionally were consumed.

Percentage activity of radio-collared bears declined from 47 to 29 percent between late October and the initiation of the denning period in mid-December. After entering dens, bears reduced activity to a mean level of 5 percent. Meanwhile, bears which were not denned maintained a mean activity level of 42 percent. Limited radio-monitoring of bears in dens indicated that periods of activity occurred at a mean rate of 1.7 bouts per hour and lasted an average of 6.6 minutes; activity periods as long as 57 minutes were recorded for denned bears, but no movements from dens occurred. Numerous inspections of occupied dens also indicated that bears did not intermittently leave and return to dens during dormancy.

Forty-two bear-winters were monitored during the study. With two exceptions, all bears entered dens. Two subadult males did not den during the 1980-81 winter. Pregnant females denned earliest ($\bar{X}$ = 15 Dec) followed by barren adult females ($\bar{X}$ = 22 Dec), subadult females ($\bar{X}$ = 3 Jan), adult males ($\bar{X}$ = 17 Jan), and adult females with "coys" ($\bar{X}$ = 19 Jan). One 2-year-old male entered his den on 29 January, and a yearling male did not den until 29 February.

The sequence of den emergence by different population cohorts was generally the reverse of den entry. Two subadult females emerged distinctly earlier ($\bar{X}$ = 3 March) than other groups. Yearling males, adult males, barren adult females, and 1 2-year-old male emerged from dens during late March or early April. Females with yearlings and "coys" were last to leave their dens ($\bar{X}$ = 15 April and $\bar{X}$ = 27 April, respectively). Parturient females denned for significantly longer periods ($\bar{X}$ = 134 days) than barren adult females ($\bar{X}$ = 107 days), adult females with yearlings ($\bar{X}$ = 81 days), adult males ($\bar{X}$ = 76 days), subadult females ($\bar{X}$ = 59 days), and yearling males ($\bar{X}$ = 41 days).

Occasionally bears were forced from their dens due to flooding. They moved to alternate dens and did not appear to be adversely affected by this disturbance. When flooding extended into April and May, most bears, especially females with young cubs, remained in their dens until floodwaters receded. Occasionally bears swam through floodwater to other trees or relocated to higher ground on ridges.

Denning chronology of black bears on the Refuge was similar to that reported for other populations in relatively mild climates. Dormancy behaviors (i.e., den entry, fidelity to den, depressed activity, lethargy, and reaction to human disturbance) also were consistent with those reported in other studies. These results indicate that the degree of dormancy in black bears is relatively uniform across the species' range and that denning behavior (i.e., dormancy) is more likely a response to food availability than to climatic conditions _per_ _se_.

Two types of dens were utilized by black bears on the Refuge, elevated tree cavities and ground nests. Females used tree dens exclusively, while males used both den types at similar frequencies. Tree species most often used for dens were overcup oak (61 percent) and baldcypress (27 percent). Use of individual tree species for denning appeared to be proportional to their availability on the study area. Males and females utilized trees of equal size (i.e., dbh and bechamber width), but entrances to dens of females were significantly smaller ($\bar{X}$ = 39 cm) than those to dens of males ($\bar{X}$ = 59 cm) ($P<0.05$). Females may reduce competition for dens by utilizing cavities with small entrances. Females also used trees with deeper cavities and exhibited a preference for tree cavities with side entrances. These properties increase the thermoregulatory capacities of females' dens as well as provide greater protection from disturbances. However, deeper cavities may increase the susceptibility of bedchambers to flooding in bottomland hardwood forest.

Ground dens or nests were located in forest gaps with little or no canopy cover. This exposed occupants of these dens to precipitation but also increased solar radiation to the den. Secondary beds were often found under dense vine mats in close proximity (<10 m) to ground nests; these may have been used during periods of heavy precipitation. Nests were associated with dense understory cover such as vines, tree tops, and logs. They were constructed by digging a shallow depression and pulling debris from around the depression to form a wall and line the oval nest. Dimensions of nests were proportional to the size of the occupant. Bears denned in ground nests were much more susceptible to disturbance than those denned in tree cavities.

The frequency of reuse of tree dens was 26 percent (9 of 36 potential cases). No reuse of ground dens was observed. This behavior occurred in both consecutive and alternate years, by the same and different individuals, and by all age and sex classes. The relatively high percentage of den reuse was apparently not due to a lack of available dens.

The exclusive use of tree dens by female black bears on the Refuge indicates that tree cavities maximize protection and survival of parturient females and young cubs in bottomland hardwood forest. Protection and perpetuation of an abundance of den trees on the Refuge appears to be important to the long-term fitness of the black bear population.

Estimates of annual and seasonal home ranges were made by the convex polygon method; polygons were modified to exclude unsuitable habitat and minimize the size of areas between disjunct cluster of locations. Substantial variation occurred in home range estimates within population cohorts, especially for subadult and adult males. Despite the variation, annual ranges of males ($\bar{X}$ = 128 km^2, range = 26-266 km^2) were significantly larger than those of females ($\bar{X}$ = 11 km^2, range = 6.6-21.6 km^2) ($P<0.03$). Mean annual ranges of adult males ($\bar{X}$ = 116 km^2, range = 39 to 266 km^2) and subadult males ($\bar{X}$ = 148 km^2, range = 26-226 km^2) were not statistically different ($P> 0.5$); nor were those for adult females ($\bar{X}$ = 12 km^2, range 6.6-21.6 km^2) and subadult females ($\bar{X}$ = 9 km^2, range = 8.2-10.3 km^2) ($P>0.5$).

Variations in home range size within cohorts may have reflected disparities in habitat quality between different areas of the Refuge; bears occupying the southeastern portion of the study area core had relatively small home ranges. This area appeared to have a higher diversity of habitat components, particularly swamps, and was more secluded; a higher proportion of large adult males also was captured in this area.

Seasonal ranges and movements of black bears was related to food availability and reproductive status and behaviors. Seasonal range sizes varied considerably within age and sex classes, but general trends of seasonal distribution were relatively consistent between cohorts. With the exception of subadult females, which ranged over equal-sized areas in all seasons, all cohorts utilized significantly larger areas in summer than in spring or fall. Sizes of spring and fall ranges were commensurate within all groups except adult females with cubs, which had smaller ranges in spring than in fall.

Following den emergence and during the transition from dormancy, bears restricted their movements to small areas, generally at higher elevations, where understory foods (i.e., herbaceous and green woody plants) were abundant. Bears increased their ranges in summer, apparently in response to widely dispersed foods; soft fruits of various species matured, insects became available, and fish were occasionally abundant in lakes and bayous that "turned-over" or dried up. Mating also occurred during summer, and the increased movements of adult males and barren adult females during that season were likely influenced by breeding behavior.

By late October and early November, the fruiting season of soft mast-producing species had passed, and bears shifted their diet to hart mast. In 1979 and 1980 production of overcup oak acorns was high, and bears often restricted their activities to very small "flats" where acorns were especially abundant. In 1981, overcup oak mast failed, but production of Nuttall oak and willow oak acorns, as well as sweet pecans was good. Apparently bears ranged over larger areas (i.e., outside their spring/summer ranges) to locate these sources of food, but then concentrated their activities in small areas along ridges and at higher elevations where these foods were available.

Females accompanied by cubs of the year utilized very small areas during spring and early summer. By late summer, however, movements of these family units had increased considerably, and during fall/winter, females with "coys" used significantly larger ranges than barren adult females.

Annual home ranges of both males and females overlapped considerably. Interpretation of the extent of overlap between individuals or within cohorts is tentative, however, because only a portion (possible 25 percent) of the bears resident to the study area core were simultaneously radio-monitored. Adult males did not appear to defend territories nor maintain long-term bonds with one or more females. Range size and overlap of adult males in summer indicated that they may maintain contact with several females intermittently during the breeding season. Consequently, selection would be for efficiency in timing the reproductive readiness of females and dominance over other males in competition for individual females during their estrous.

Two adult females, whose summer and fall/winter ranges overlapped when they were barren, maintained exclusive ranges in the following spring and summer when both were accompanied by cubs. The ranges of two other adult females overlapped considerably in all seasons, including the spring and summer when one was accompanied by cubs and the other was not.

During fall, black bears on the Refuge, including females with cubs, were socially tolerant of each other. As many as 10 bears of various age and sex classes were known to utilize the same small area where food (i.e., acorns) were especially abundant.

None of the 2 yearling, 4 2-year-old, or 2 3-year-old radio-collared males dispersed from, or long distances within the Refuge during the study. One 2-year-old male which I did not radio-collar was recaptured as a 3-year-old 6 km from his original capture site. Another 2-year-old male was recaptured as a 4-year-old just 5 km from the location of his first capture. A 3-year-old radio-collared male made a long (∿25 km) exploratory excursion south of the Refuge along the Mississippi River during spring and early summer of 1980. By mid-summer he had returned to his familiar range, however, where he remained until the following spring when his radio transmitter failed. In the same summer, a 2-year-old male exhibited long-range sporadic movements within the Refuge but remained in a defined area until he was 3 years old and his radio-transmitter also failed. None of the three subadult females moved outside their small well-defined home ranges.

These findings indicate that black bears do not disperse from the Refuge. Furthermore, it appears that subadult males may disperse only short distances from their natal ranges. No dispersal corridors exist between the Refuge population and populations in west-central Arkansas and northern Louisiana, and the black bear population on the Refuge appears to be genetically closed.

The abundance of 17 habitat variables was determined for approximately 1100 25-ha quadrats within and adjacent to the study area core. A chi-square goodness-of-fit procedure was used to compare observed frequencies of categorically values of each variable in quadrats utilized by bears with frequencies for these values over the entire study area core. None of the 17 variables were used by bears in proportion to availability; overall disproportionate utilization was generally attributable, however, to seasonal preferences for particular types of habitats.

Based on the results of the utilization-availability analysis, 10 variables were selected for constructing multiple regression models of seasonal habitat utilization. These models explained only a small amount of the variation in bear distributions, but were useful, nonetheless, to clarify results of the utilization-availability analysis and evaluate the independent significance of individual habitat components.

In spring, bears restrict their movements to moderate and high elevations where transitional and high forest occur. This often may be a response to flooding, especially during early spring. The understory at these elevations is more diverse and develops relatively early, providing bears with the herbaceous and green woody plant foods which predominate in the spring diet. Overstory trees at high elevations also green-up earlier than those (e.g., overcup oak) at lower elevations. The flowers and new leaves of these canopy trees may be a source of food for bears in spring.

During summer, bears increase their utilization of transitional and high forest cover. Forest and habitat diversity are higher in these habitats. Roads and streams (i.e., edge) are abundant, as well, and swamp impoundments often occur within the ridges on which forest types occur. Swamp is a particularly important habitat component during the summer, apparently for cover. In summer, bears also exhibit an affinity to lakes and bayous where fish and soft mast may be abundant.

In fall/winter, the distribution of bears coincides with the availability of hard mast. Acorns of overcup oak appear to be preferred, possibly due to the wide distribution and consistent mast production by this species. In years when overcup oak mast is abundant, bears may concentrate their activities in small homogeneous areas where acorn production is especially high. In such cases, fall/winter habitats are characterized by low forest, elevational, and habitat diversities and a paucity of streams, roads, and open water. When overcup oak mast fails, bears may utilize red oak (e.g., willow oak and Nuttall oak) acorns and sweet pecans at higher elevations. Correlated with, yet incidental to this, fall/winter habitats may be relatively heterogeneous. Regardless of the type of forest cover in which hard mast is available in fall/winter, bears continue to maintain an affinity to swamps.

These analyses demonstrate that habitat utilization by black bears in bottomland hardwood forest is strongly tied to food availability. Seasonal distribution of bears on the Refuge generally follows phenological development of plant foods. Less consistent, but abundant sources of animal food, especially fish, also periodically dominate habitat utilization patterns. Swamps are a particularly important component of black bear habitat on the Refuge, apparently for their value as cover.

Existing conditions on the Refuge provide an abundance of food and cover for black bears. Current forest management, i.e., limited selective cutting, appears to promote an uneven-aged forest and ensure a diversity of foods. Similar conditions may result, however, from natural dynamics in bottomland hardwood forest if hydrologic regimes are not impaired. On the Refuge, protection and perpetuation of mature homogeneous stands of overcup oak at lower elevations appears to be critical to black bears. The relatively few mature stands of willow oak and pecan in the southern portion of the Refuge also are important as an alternate source of hard mast when overcup oak mast fails. The affinity which bears exhibit for swamps, particularly beaver impoundments, warrants special concern for the maintenance of this habitat component on the Refuge.

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