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**Douglas A. Wassmer, Del D. Guenther,
and James N. Layne**



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ECOLOGY OF THE BOBCAT IN SOUTH-CENTRAL FLORIDA

Douglas A. Wassmer, Del D. Guenther, and James N. Layne*

ABSTRACT

The ecology and life history of the bobcat (*Felis rufus*) were studied on the protected Archbold Biological Station and surrounding semi-developed land in south-central Florida from 1979 to 1982. Mean densities were 5 adult males, 8 adult females, and 13 juveniles/100 km². Overall adult sex and age ratios were 0.64 male/female and 1.00 juvenile/adult, respectively. Breeding occurred from August to March, with a peak in February and March. The mean size of 13 mobile litters was 2.6. Of 17 radio-collared cats, 9 died during the study, and 9 unmarked individuals were found dead or reported killed in the study area. A higher proportion of mortality (73%) was due to natural (feline panleucopenia and Notoedric mange) than to man-related causes. Cottontail rabbits (*Sylvilagus floridanus*), marsh rabbits (*S. palustris*), and cotton rats (*Sigmodon hispidus*) were the primary prey species, comprising 73% of the occurrences of food items in scats and 86% of estimated prey biomass. Overall home ranges of 5 adult males and 7 adult females averaged 25.5 km² and 14.5 km², respectively. Short-term home ranges during 12 intervals of 3 to 16 weeks averaged 14.5 km² for males and 9.3 km² for females. Females tended to use their home ranges more intensively than did males, but males moved farther from day to day than females. One adult female and one male adult were known to abandon their ranges, the female's range apparently being acquired by her male and female young. Adults of the same sex had non-overlapping home ranges, but ranges of males and females overlapped extensively. Adult males and females with shared home range areas occasionally travelled or rested together in all seasons. Activity was primarily crepuscular and nocturnal. Seasonal variation in activity of males appeared to be related to temperature and in females to care of young. Both sexes used natural vegetation types more than man-modified habitats, with males using man-modified habitats relatively more than females. Marking behavior varied seasonally and appeared to play a significant role in maintenance of home range boundaries of adult males and adult females. Compared with data from other parts of the range, the south-central Florida population had an average density comparable to values reported from

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elsewhere in the southern U.S. and somewhat higher than levels recorded in northern areas; relatively low litter size; comparatively small home range size; and a possibly higher frequency of cases of a single adult female range contained entirely within an adult male range suggestive of a facultative monogamous relationship. Implications of the study to conservation and management of bobcats are discussed.

RESUMEN

Se estudiaron la ecología y historia natural del gato montés (*Felis rufa*) en la protegida Estación Biológica de Archbold y en áreas adyacentes semidesarrolladas en el centro-sur de Florida, de 1979 a 1982. Densidades medianas eran de 5 machos adultos, 8 hembras adultas, y 13 juveniles por 100 km². Las relaciones de sexo adulto y de edad eran 0.64 macho/hembra y 1.00 juvenil/adulto, respectivamente. Había reproducción de agosto a marzo, con el máximo en febrero y marzo. El tamaño mediano de 13 crías móviles era 2.6. De 17 gatos marcados con radio-collares, murieron 9 durante el estudio, y se encontraron o se informaron de otros 9 individuos muertos en el área. La mayor parte de la mortandad (73%) se debía a causas naturales (panleucopenia felina a sarna notoédrica), y no a actividades humanas. Conejos (*Sylvilagus floridanus* y *S. palustris*) y ratas de algodón (*Sigmodon hispidus*) son las presas principales, formando 73% de las ocurrencias en heces, y 86% de la biomasa calculada. A base de 5 machos adultos y 7 hembras adultas, los promedios de territorios totales eran de 25.5 km² para machos y de 14.5 km² para hembras. A corto plazo, durante 12 periodos de 3 a 16 semanas, los territorios promedios eran de 14.5 km² para machos y de 9.3 km² para hembras. Las hembras suelen usar sus territorios mas intensivamente, mientras que los machos viajan más de día a día. Una hembra adulta y un macho adulto abandonaron sus territorios durante el estudio, el territorio de la hembra aparentemente pasando a sus hijos. Los territorios de adultos del mismo sexo no traslapan, pero los territorios de machos y hembras traslapan extensivamente. Machos y hembras adultos con territorios compartidos viajan o descansan juntos de vez en cuando en todas las estaciones. La actividad es principalmente crepuscular y nocturna. Variación estacional en actividad se relaciona con la temperatura en los machos y con el cuidado de la cría en las hembras. Ambos sexos usan ambientes de vegetación natural más que ambientes modificados por el hombre, con los machos usando ambientes modificados relativamente más que las hembras. El comportamiento de demarcar territorio varía con las estaciones y parece jugar un papel signficante en mantener los limites territoriales de machos y hembras adultos. Comparada con datos de otras áreas, la población del centro-sur de Florida tiene una densidad mediana comparable con otras áreas del sur de los EE.UU. y algo más alta que las densidades encontradas en áreas norteañas; cría relativamente pequeña; territorio relativamente pequeño; y posiblemente mayor frecuencia de tener el territorio de una hembra adulta enteramente dentro del territorio de un macho adulto, sugiriendo una relación monógama facultativa. Se discuten las implicaciones del estudio para la conservación y el manejo de la especie.

TABLE OF CONTENTS

Introduction.....	161
Acknowledgements.....	162
Study Area.....	163
Methods.....	167
Capture and Handling.....	167
Subjects.....	167
Study Techniques.....	169
Data Analysis.....	170
Results and Discussion.....	171

Capture Success.....	171
Demographic Characteristics.....	173
Density.....	173
Sex and Age Ratios.....	173
Breeding Season.....	175
Natality.....	175
Mortality and Injuries.....	176
Longevity.....	181
Food Habits.....	181
Home Range and Social Organization.....	184
Home Range Size.....	184
Use of Area Within Home Ranges.....	189
Relationships Between Adult Home Ranges.....	189
Female-Young Behavior and Home Range Use.....	198
Daily Travel.....	205
Activity.....	208
Habitat Use.....	212
Marking Behavior.....	217
Frequency of Types of Marking Behavior.....	217
Seasonal and Yearly Variation in Marking.....	217
Spatial Patterns of Marking Behavior.....	220
Conservation and Management Implications.....	223
Literature Cited.....	225

INTRODUCTION

Previous studies of the bobcat (*Felis rufus*) in the southeastern United States (e.g. Buie et al. 1979, Hall 1973, Kitchings and Story 1979, 1984, Marshall 1969, Miller 1980) and in other parts of North America (e.g. Bailey 1972, 1974, 1979, Lawhead 1978, Zedulak and Schwab 1979) have revealed considerable geographic variation in habitat relationships, movement patterns, population levels, and other aspects of the species' ecology and behavior. Such variability emphasizes the need for basic ecological and life history data from many populations throughout the bobcat's range in order to gain a more complete understanding of the basic biology of the species and its role in natural and man-modified ecosystems. Increasing pressure on the bobcat by the fur trade (National Wildlife Federation 1977) together with habitat loss in many parts of the range also have created a need for more detailed information on population dynamics, habitat requirements, and other ecological and life history parameters of regional populations to provide the basis for more effective management.

Although numerous references to local distribution and general habits of the bobcat appear in the published literature on Florida mammals, there have been few detailed studies of specific aspects of its biology in the state. The principal objective of this study was to obtain baseline data on demographic

characteristics, home range, movements, activity patterns, habitat use, food habits, social organization, and marking behavior of the bobcat in south-central Florida. The study area consisted of a core area of completely protected natural habitat surrounded by a semi-developed area typical of many parts of Florida. This configuration allowed comparison of mortality rates and certain other life history parameters in natural versus variously man-modified habitats. Although bobcats in the part of the study area outside the protected core area were at risk of being casually shot, they were not purposely hunted or trapped for sport or the fur trade. Thus, for comparative purposes, the population can be considered as unexploited. In addition, the core area was dominated by relatively xeric vegetative associations that differ considerably from habitats in northern Florida and elsewhere in the eastern United States in which bobcats previously have been studied. A feline panleucopenia virus (FPLV) outbreak during the course of the study also provided an unexpected opportunity to observe the effects of disease on the ecology and social organization of a wild carnivore population.

The study area of approximately 200 km² was located in Highlands County. The protected core area was the 16 km² Archbold Biological Station, 10 km south of the town of Lake Placid (27°11'N, 81°21'W). The main period of the study extended from January 1979 through March 1982, with incidental observations made on marked animals through 1984.

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STUDY AREA

The study area (Fig. 1) is located near the southern end of the Lake Wales Ridge, a southward extension of the state's Central Highlands region and the most prominent topographic feature of peninsular Florida. The Ridge is characterized by relict sand dunes, scarps, and other features indicative of former higher sea levels (White 1970). In the vicinity of the study area the Ridge ranges from about 6 to 12 km in width and from 30 to 68 m in elevation.

The climate of the region is characterized by hot, wet summers and cooler, drier winters. Mean annual rainfall and temperature are 1370 mm and 22.2°C, respectively. Relative humidity usually ranges from about 75-85% at dawn to about 20-45% at midday throughout the year (Douglass and Layne 1978). During the study, mean annual temperature was 21.9°C, and the extreme high and low temperatures were 37.2°C and -7.2°C, respectively. Daily maximum and minimum temperatures for the warmer months (May-October) averaged 33.2°C and 25.9°C, respectively, while corresponding averages for the cooler months (November-April) were 19.0°C and 9.9°C. Mean annual rainfall was 1201 mm, with 73% occurring from May through October. Standing water was present in drainage canals, creeks, and seasonal ponds throughout 1979 and early 1980. During summer 1980, most of these sources dried up and open water was limited to two large and three small permanent lakes or ponds, scattered livestock watering troughs, and an irrigation ditch system. Dry conditions prevailed during the rest of the study despite normal rainfall in 1981.

Seven major natural vegetation associations (southern ridge sandhill, sand pine scrub, scrubby flatwoods, flatwoods, swale, bayhead, seasonal ponds) are found in the protected core area (Abrahamson et al. 1984). Similar associations and various man-modified habitats occur on the remainder of the study site. For purposes of this investigation, the following eight general habitat types were recognized (percentage of each type in parentheses): closed canopy xeric pine-oak (4), open canopy xeric pine-oak (28), flatwoods (21), bayhead (7), citrus grove and tree nursery (16), oldfield (10), improved pasture (12), and man-occupied (2). Figure 2 shows the distribution of these habitat types in the study area.

The xeric pine-oak category includes the vegetative associations recognized by Abrahamson et al. (1984) as southern ridge sandhill, sand pine scrub, and scrubby flatwoods. These associations are characteristic of the deep sandy, well-drained soils of the Lake Wales Ridge. South Florida slash pine (*Pinus elliotii* var. *densa*) and sand pine (*P. clausa*) are the dominant overstory species. Common understory and shrub layer species include turkey oak (*Quercus laevis*), inopina oak (*Q. inopina*), Chapman's oak (*Q.*

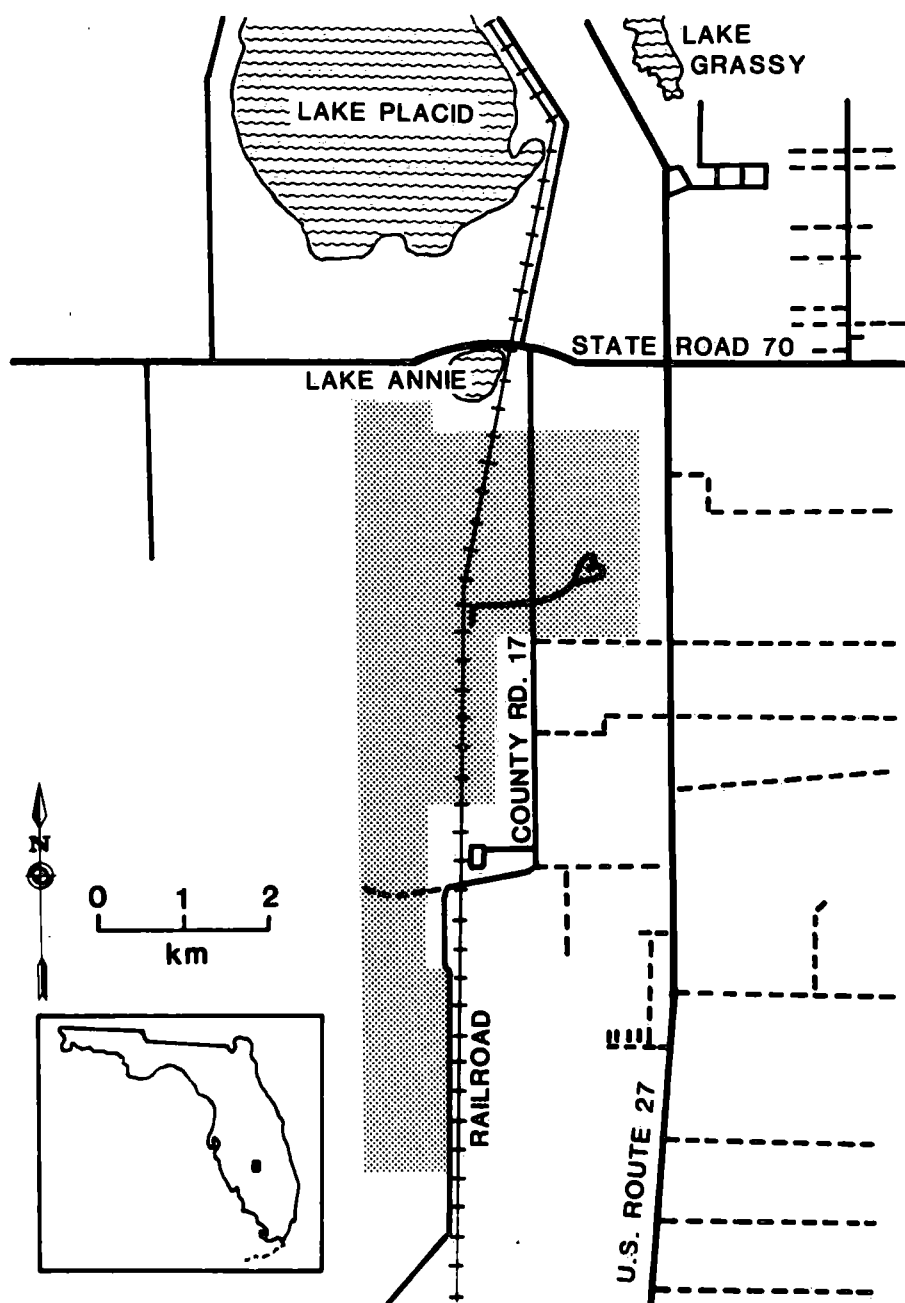


Figure 1. Study area showing Archbold Biological Station core area (stippled). Paved roads indicated by solid lines, graded roads by dashed lines.

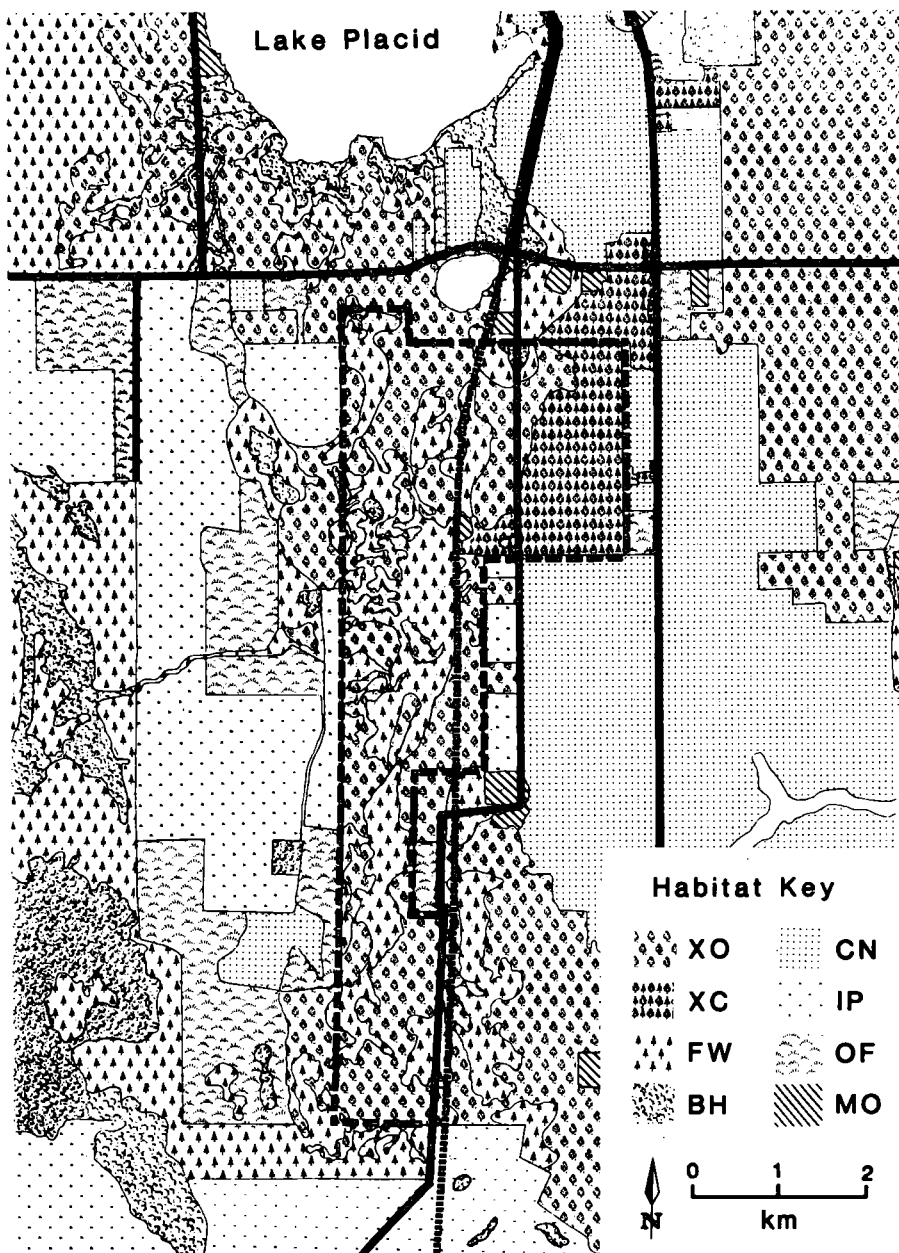


Figure 2. Habitats of the study area. XO = xeric pine-oak, open canopy; XC = xeric pine-oak, closed canopy; FW = flatwoods; BH = bayhead; CN = citrus grove and tree nursery; IP = improved pasture; OF = old field; MO = man-occupied; paved roads indicated by solid lines; railroad indicated by short dashed line; boundary of core area indicated by long dashed line.

chapmanii), sand live oak (*Q. geminata*), myrtle oak (*Q. myrtifolia*), scrub hickory (*Carya floridana*), rusty lyonia (*Lyonia ferruginea*), scrub palmetto ?(*Sabal etonia*), saw palmetto (*Serenoa repens*) and rosemary (*Ceratiola ericoides*). Ground cover is generally sparse, consisting of grasses, forbs, lichens, and shrub and tree sprouts. Xeric pine-oak habitats with canopy coverage less than 50% were classed as "open canopy" and those with canopy coverage greater than 50% as "closed canopy." The majority of open canopy areas had less than 25% canopy coverage. The most extensive blocks of closed canopy habitat were in a portion of the core area that had not been burned for over 50 years.

Flatwoods occur on generally level, sandy soils with a relatively high water table. South Florida slash pine is the dominant overstory species. Typical shrub and ground cover components are gallberry (*Ilex glabra*), fetterbush (*Lyonia lucida*), wiregrass (*Aristida stricta*), cutthroat grass (*Panicum abscissum*), and saw palmetto. Grassy seasonal ponds and swales are included in this category. Most flatwoods in the study area are relatively open, with widely-spaced pines. However, small patches of flatwoods with dense pines and heavy saw palmetto undergrowth often occur at the edges of ponds, lakes, and bayheads and in parts of the core area where fire has been long excluded.

Bayheads, characterized by broad-leaved evergreen trees that form a dense, closed canopy, occur along creeks, at lake edges, and in shallow depressions with muck soils in flatwoods. The typical overstory species include loblolly bay (*Gordonia lasianthus*), red bay (*Persea borbonia*), sweet bay (*Magnolia virginiana*) and slash pine. Characteristic shrub layer components are young bay trees, wax myrtle (*Myrica cerifera*), gallberry, and saw palmetto. Mosses and ferns are often abundant components of the ground cover, and muscadine grape (*Vitis rotundifolia*) is common along edges.

Citrus groves and tree nurseries are found principally on land that formerly supported xeric pine-oak communities. As the groves are periodically disced, ground cover between rows is generally sparse or absent. However, grasses and forbs may become extensive in groves that have not been disced for some time. The oldfield category includes vacant lots, fallow agricultural fields, decadent citrus groves with sparse dead trees and rank grass and weedy ground cover, pastures overgrown with weeds and brush, and railroad and road right-of-ways. Improved pastures are open areas of dense, short-cropped natural or exotic grasses with widely scattered shrubs, clumps of palmettos, or pines. A golf course in the study area also is included in this category. Man-occupied areas consisted of three light industrial complexes of about 3 ha each, an extensive housing development with scattered houses and much open land, a mobile home park, a recreational vehicle park, several areas containing clumped rural residences, and a few gardens or agricultural fields. The study area was traversed by a railroad and two major highways and contained a

number of secondary paved and unpaved roads. The core area contained a network of 4-wheel drive roads, foot trails, and firelanes.

METHODS

Capture and Handling

Bobcats were captured with National live traps (104 x 50 x 40 cm). From 1 to 10 traps were deployed at any given time. Trapping was concentrated in the core area in an attempt to capture all bobcats utilizing that area. Of a total of 109 trap sites, 107 were distributed throughout the core area, 1 was located adjacent to the boundary of the core area, and another 0.5 km from the core area. The number of trapnights (TN) per site ranged from 1 to 61, with a total of 2013 for all sites. Baits included live animals (cotton rats, *Sigmodon hispidus*; adult domestic rabbits; young and adult chickens) and pieces of meat (chicken; cottontail rabbit, *Sylvilagus floridanus*; gray squirrel, *Sciurus carolinensis*). Meat baits were suspended by a string just behind the trap treadle and live animals were housed with food and water in separate wire-mesh enclosures attached either inside the trap above and behind the treadle (cotton rats) or to the back of the trap (rabbits, chickens).

Captured bobcats were sedated with intramuscular injection of ketamine hydrochloride ("Ketaset," Bristol Laboratories, Syracuse, New York) at doses ranging from 5 to 36 mg/kg of body weight. Low doses were given when changing collars and higher doses when more thorough examination was necessary. Data recorded for each animal included body measurements (total length, tail length, hind foot, ear from notch, neck circumference) and weight; length and diameter of the upper right canine; pelage condition and markings; ectoparasites; reproductive condition; presence and nature of injuries or scars; and length and width of foot pads and notes on their shape and symmetry. Weight; dental condition, including amount of wear, coloration, and stage of replacement (Crowe 1975); and appearance of teats of females and the scrotum of males were used to classify cats as adults or juveniles. Plaster casts of the right fore and hind feet were made to aid in identifying individual bobcats by tracks in the field. The animals were marked with an ear tag in one ear and an alphanumeric tattoo in the inside of the other ear. Radio collars were color coded with reflective paint or with colored tape to facilitate visual identification.

Subjects

Seventeen bobcats were radio-collared (Table 1), including 13 adults (6 males, 7 females) and 4 juveniles (2 males, 2 females). Two additional individuals handled during the study included an emaciated 5.3 kg adult female (F2) with a severe infestation of mange mites (*Notoedres cati*) that died after being darted and a 2.4 kg juvenile female (F7) captured twice and released without radio-tagging due to her small size. Mean and extreme weights of adult males and females were 9.5 kg (8.1-10.5) and 7.9 kg (5.8-10.1), respectively. Weights of individuals classified as juveniles ranged from 5.3 to 7.9 kg ($X = 6.1$).

One of the females (F1) included in the study was a semi-tame individual. She was captured outside the study area in spring 1974 and kept in a cottage on the Archbold Biological Station from mid-September 1974 until May 1975 when about a year old, then released at the site (Winegarner and Winegarner 1982). She reappeared at the cottage 16 days later and continued to return periodically. She was often fed when visiting the cottage. No effort was made to tame the cat during captivity, and she was not handled after release, except when captured and sedated for a series of treatments for mange in 1978 and for attachment of a radio-collar in the present study. She was tolerant of, but not friendly to, humans; and, except for her visits to the cottage,

Table 1. Weights and measurements of radio-collared bobcats.

Individual	Date of Original Capture	Weight (kg)	Body Measurements (mm)				Upper Canine (mm)	
			Total Length	Tail	Hind Foot	Ear from Notch	Maximum Diameter at Gum Line	Length from Gum Line to Tip
ADULT MALES								
M1	28 Apr 79	9.4	895	139	163	85	8.7	16.9
M2	5 May 79	9.5	931	167	168	71	9.2	15.6
M3	9 Aug 79	9.0	908	155	173	70	7.5	15.8
M6	19 Apr 80	9.1	978	160	183	67	7.0	16.5
M7	26 Apr 80	9.5	986	181	191	65	6.8	16.2
M8	11 Sep 80	10.5	901	148	173	71	7.1	16.9
ADULT FEMALES								
F1	8 Dec 79	8.8	913	182	170	63	6.1	13.4
F3	1 Jun 79	5.8	845	160	160	62	6.1	11.9
F4	25 Jul 79	7.8	845	138	163	61	8.4	12.7
F8	31 Jan 80	6.5	837	158	160	71	5.6	13.3
F9	1 Feb 80	7.8	865	150	154	70	5.6	15.0
F10	13 Feb 80	9.9	894	146	163	65	6.4	13.9
F11	9 Mar 80	9.4	910	168	172	65	6.6	14.2
JUVENILE MALES								
M4	11 Oct 79	5.3	770	155	160	71	6.7	14.0
M5	11 Feb 80	7.9	954	174	188	61	7.2	16.0
JUVENILE FEMALES								
F5	27 Nov 79	5.7	795	170	170	70	5.6	12.5
F6	7 Dec 79	5.4	806	156	159	65	6.5	12.9

her behavior appeared not to differ significantly from that of wild bobcats. Various aspects of the behavior of this individual were reported by Winegarner (1985a).

Study Techniques

The principal study method was radiotelemetry, but additional data were obtained from tracking, sightings, and observations of sign. The mean number of records (including trap captures, radio fixes, and sightings) for individual bobcats was 320, with a range of 7 to 1248. The mean interval between the first and last records of marked cats was 327 days, with a range of 9 to 1143 days.

Most of the radiotracking was done from a 4-wheel drive vehicle equipped with a marine compass mounted on the dash and an 8-element, dual-Yagi null peak antenna system mounted through the roof so that it could be rotated from within. A hand-held, collapsible, 4-element Yagi antenna also occasionally was used to approach a stationary bobcat during the day in a rest site away from a road. Radio collars, manufactured by AVM Instrument Company or Davidson Electronics, weighed 127-185 g, had a pulse rate of 60-121 beats/minute, and transmitted in the 150-151 MHz range. Collar antennas were either external whip-type or copper alloy bands incorporated into the collar material. Most of the positions of radio-collared bobcats were determined by triangulation at distances less than 1 km. Guenther (1980) found that at a distance of 1 km triangulation was accurate to within an area of about 4 ha. Data recorded for each radio fix included date, time, weather, and activity state (moving or inactive) based on the nature of the signal.

Intensive radiotracking was conducted from April 1979 through December 1981. A total of 5344 radio locations was obtained on the 17 instrumented bobcats over the 32-month period. Tracking was conducted at all hours of the day and night. Emphasis was placed on monitoring significant events such as male-female interactions or movements of a female with newborn young rather than on locating each individual at some fixed time schedule. Individuals were monitored for periods ranging from 15 minutes to 24 hours for 1 to 35 consecutive days separated by intervals of usually less than a week. Following the termination of major field work at the end of December 1981, we continued to monitor on a less regular basis the movements of several individuals by radiotracking until March 1981, and by sightings and tracks until December 1984.

Trailing bobcats on foot provided additional information on movements and activities of particular individuals; marking behavior; litter size; adult male-adult female and female-young interactions; and the presence, sex, and age of unmarked cats. The probable presence of unmarked bobcats on the study area was assumed from the occurrence of tracks that did not match those of known individuals. If tracks believed to be of the same unmarked individual were repeatedly found on the study area, that individual was considered a resident. When such tracks consistently occurred at the periphery of an instrumented bobcat's home range, the unknown cat was assumed to be of the same sex as the marked individual. If the unknown tracks were within the interior of the range of a collared cat, the unknown individual was assumed to be of the opposite sex. This interpretation is based on the findings of Lawhead (1978), Miller (1980) and other investigators that same-sexed bobcats exhibit very little range overlap while opposite-sexed individuals may exhibit substantial overlap. On the basis of this assumption portions of the range boundaries of several bobcats were determined prior to their capture. Lembeck (1978) also used this method to identify the sex and to estimate the range of an unmarked bobcat on his study area and later confirmed the sex and range estimate by capturing and radiotracking the individual.

Three types of marking behavior recognized in this study included:

- 1) Scrapes: Distinctive elongate ruts or "ploughed" areas in the soil or litter made by alternating rearward thrusts of the hind feet with the body in a semi-squatting position and usually containing either feces or urine.
- 2) Urine marking: Deposition of urine onto the substrate or objects on the ground from a squatting position (squat-urination) or spraying it on above-ground objects from an upright posture (spray-urination).

3) **Scat marking:** Deposition of scats which are left exposed.

Exposed scat deposition sites were counted along a 10-km route of primitive roads, firelanes, and footpaths through various habitats in the core study area during February, March, July, and August 1979 (Guenther 1980), and more intensive censuses of scrapes and scats were conducted from October 1979 through April 1981 (Wassmer 1982). Foot trails and railroad tracks were walked and primitive roads or firelanes were surveyed from a vehicle at a speed of 1-5 km/hr. All scats were collected, and scrapes were usually marked with a toothpick to prevent their being recounted in a subsequent census. In the October 1979-April 1981 period, regular censuses were made along 37 km of routes, which included the 10-km route used by Guenther (1980). Most routes were censused once or twice a month; a few regularly-driven roads were inspected more frequently; and some trails that were infrequently marked were searched every 1 to 3 months. Other parts of the study area were searched irregularly. As it was not possible to census all routes on the first day of each month, several types of evidence were used to estimate the age of a mark so that it could be assigned to a particular month. These included time since the route was last searched, whether or not the mark was made before or after a recent rain, amount of vehicle tracks or other disturbance in the vicinity of the site, and the condition of the scat or scrape. Totals of 2220 exposed scats and 5291 scrapes (including scrapes containing scats) were recorded. Of these, 1461 (66%) scats and 3326 (63%) scrapes were located along the regular census routes.

A total of 349 sightings of bobcats were made by us or reported by others during the study. Sixteen of the collared cats and 10 unmarked but recognizable (e.g. kittens accompanying a collared female) individuals were observed. In addition, unidentified bobcats were seen on 30 occasions.

Information on food habits was obtained from analysis of 146 scats; 69 were collected in the core study area on a random basis from 1967 to 1978, and 77 were collected from January to September 1979. Each scat was soaked in detergent for 3 or 4 days, then rinsed in a sieve with fine wire mesh until all fine debris was removed and the remaining material oven dried for examination. The minimum number of individuals of a given prey species represented in a scat was based on the number of the most frequent element occurring singly in a skeleton (e.g., left third upper molar). Weights of mammals and other vertebrate species used to convert prey frequency of occurrence to biomass values were obtained from specimens collected in or near the study area.

Data Analysis

Density estimates were based on the cluster of individuals centered on the core area that was most intensively and continuously monitored. Estimates were computed for 12 unequal time intervals during the period from April 1979 through August 1981 for which the most complete data on the number and sexes of individuals and sizes of home ranges were available. Five of the intervals were delimited by known deaths or disappearance of individuals. Break-points for the remaining intervals were more subjective, involving times of collar failures which prevented further detailed monitoring of individuals or prolonged (about 1 month) gaps in radiotracking. For each period, the area used for calculating density was that of the minimum convex polygon formed by the outermost boundaries of the cluster of contiguous or overlapping home ranges of the individuals present during that interval. Individuals known or assumed to be present on the study area during a given interval on the basis of tracks or other evidence, but for which there was no, or insufficient, data on home range, were treated in 1 of 2 ways. If they were located on the periphery of the cluster of known home ranges, they were excluded from the calculations. If they were within the cluster and data on their home range from a prior or subsequent time period indicated that the range was most likely included within the cluster during the current period, they were included in the density estimate. Estimates of juvenile density were based on the total number of juveniles known or believed to be present within female ranges. As number of young in a litter usually could not be determined until the young were approximately 2 months or older and moving with the mother, juvenile density estimates apply to mobile young prior to dispersal.

The validity of this method of density estimation rests on the assumptions that (1) male home ranges do not overlap appreciably, (2) male home ranges are essentially contiguous, with little or no unoccupied areas between them, and (3) female ranges are included within male ranges. Although these assumptions were probably not fully met, the available data suggest they generally applied on the core area. Any bias in the method is probably in the direction of an overestimate of density, particularly for the entire study area. On the other hand, using the alternative method of dividing the total study area (as determined by maximum movements of individuals captured and marked on the core area) by the number of bobcats believed to be present would probably significantly underestimate density because of the increasing probability of not detecting the presence of bobcats at increasing distances from the core area.

Locations of marked individuals obtained by radiotracking, capture, or visual observations were plotted on a large scale (1:4800) map of the study area gridded at 200 m intervals into 4-ha quadrats. The 4-ha quadrat size was selected as the minimum area of resolution based on the accuracy of radio fixes at distances of 1 km or less. Home range areas were estimated by the minimum convex polygon method (Mohr 1947). For purposes of this study, the area used by an individual based on all locations over the entire period it was monitored is termed the "overall" home range, and areas used by individuals during one of the 12 time periods mentioned above are designated as "short-term" home ranges. The distribution of fixes among the 4-ha quadrats enclosed by home range boundaries was used as a measure of the intensity of utilization of home range areas (Siniff and Tester 1965).

Estimates of daily movements were based on straight-line distances between the first radio locations on consecutive days of monitoring.

Whether a bobcat was moving ("active") or stationary ("inactive") was determined by the nature of the signal and the animal's location on successive fixes. When more than one fix was available for a bobcat in a given hour, the first record was arbitrarily selected to indicate the animal's activity state during that hour. The period between 2400 and 0600 hours was relatively poorly sampled, with only 325 (7%) of the total of 4966 hourly records included within this interval.

The amounts of different habitats contained within home ranges of individual bobcats were determined by counting the number of 4-ha quadrats containing each type. When more than one habitat occurred within a quadrat, each was assigned a fractional value corresponding to the number of habitat types represented, regardless of the actual coverage of the habitats in the quadrat. Habitat preferences were assessed by comparing the observed frequencies of locations in quadrats representing different habitats with expected frequencies based on the relative areas of those habitats within the home range. Fixes within quadrats containing more than one habitat were arbitrarily assigned fractional values for use of each habitat corresponding to the number of habitats represented within the quadrat.

Statistical tests used include Mann-Whitney U (U), Spearman rank correlation (Rho), and Chi-square (X^2) as described in Siegel (1956) and the Log-likelihood ratio (G) given in Zar (1984).

RESULTS AND DISCUSSION

Capture Success

Overall capture success (18 original captures, 19 recaptures) was 1.8 captures/100 TN. The number of TN in different seasons ranged from 609 to 660, and capture success (per 100 TN) was as follows: December through February, 3.1; March through May, 1.1; June through August, 0.7; September through November, 1.1.

Meat baits were more effective than live baits or live and meat baits combined. All captures with live baits were in traps baited with chickens. Capture rates per 100 TN were meat baits 2.5, live baits 1.1, and mixed baits 0.4. The difference in capture frequencies between live and meat baits was significant ($X^2 = 6.59$, 1 df, $p < 0.05$). Bobcats also tended to be captured sooner with meat baits than with live baits ($X = 1.8$ days vs. 7.9 days).

The overall capture rate in this study was relatively high compared with that (0.26/100 TN) reported from northeastern Florida by Progulske (1982) and elsewhere in the southeast. Trapping success with steel traps, live traps, and mixed steel and live traps in studies in Alabama, Louisiana, South Carolina, and Tennessee ranged from 0.10 to 4.8/100 TN, with a mean of 1.5/100 TN (Hall 1973, Kight 1962, Kitchings and Story 1979, Lueth 1962, Miller 1980). Trap success rates in the southeast are generally comparable to those in other parts of the bobcat's range. Capture rates with steel traps at two sites in Arizona were 0.72 and 1.33/100 TN (Jones 1977, Lawhead 1978); and Lembeck (1978) and Gould (1980) reported rates of 1.02 and 1.04/100 TN with mixed steel and box traps in two areas in California.

Critical comparison of trapping efficiency in different studies is difficult because of the great variety of types of bait, traps, and techniques used by different workers. One of the factors that may potentially influence capture success in mark-and-release studies is a change in susceptibility to capture of a given individual as a result of previous experience with traps. In the present study, trap success generally was high when new, unmarked bobcats were targeted for capture. In contrast, previously captured bobcats often appeared to avoid traps. Tracks showed that marked individuals walked past open traps on numerous occasions. Behavior of females (especially those previously trapped) with young may reduce chances of capturing the young. For example, despite intensive efforts the two kittens of an adult female in 1980 could not be trapped, although her three offspring the previous year were captured two or more times each using similar traps, baits, techniques, and approximately the same level of effort. However, in 1980 the mother urinated on traps or made fecal or urine scrapes in front of them on a number of occasions, most frequently after she had been captured. This behavior, which may have served to inhibit the kittens from entering, was not observed the previous year. Berrie (1973) reported what seems to be similar behavior of an adult male lynx (*Felis lynx*) which deposited very small amounts of feces (= "tokens," Schaller 1967) in front of 6 traps on 1 night without being captured.

Demographic Characteristics

Density.— Estimated overall mean density of bobcats for the period April 1979 to August 1981 was 26 individuals/100 km². Mean densities of adult males, adult females, and juveniles during this period were 5, 8, and 13/100 km², respectively. Overall densities in different periods of the study ranged from a maximum of 42/100 km² in the 1 July-25 October 1979 interval to a low of 14 in the 29 February-30 April 1980 interval (Table 2). Numbers of adult males ranged from a high of 7/100 km² in summer-fall 1979 to 0 in late winter 1980. Maximum and minimum densities of adult females were 12/100 km² in spring-early summer 1979 and 6 in fall 1980. Male density estimates for the different time periods ranked significantly lower ($U_{12,12} = 7.5$, $p < 0.01$, 2-tailed) than those of females, with males showing a more pronounced decline in late fall and winter 1979-80. Male density was still below the original level at the end of the study. Highest (26/100 km²) juvenile density was attained in summer-fall 1979; no mobile juveniles with resident females were recorded on the study area during the 29 February-30 April 1980 interval. Numbers of juveniles were relatively high in 1979, declined through 1980, and increased again in 1981.

The overall mean density of bobcats in this study was half of that (52/100 km²) estimated by radioisotope marking in northeastern Florida by Conner (1982). Density estimates based on radiotracking elsewhere in the southeast include 77-116/100 km² in Alabama (Miller and Speake 1978), 13-19/100 km² (Kight 1962), and 58/100 km² (Provost et al. 1973) on the Savannah River Plant in South Carolina, and 9-18/100 km² in Virginia (Progulsk 1952). Densities of bobcats in the southeastern United States tend to be higher than values reported for northern populations and are broadly comparable to those from the western United States (McCord and Cardoza 1982). However, detailed comparisons between most published population data are not possible because of the variety of techniques and assumptions involved in density estimates by different workers.

Sex and Age Ratios.— The overall mean age ratio based on the bobcats known or assumed to be present during the 12 time intervals was 1.00 juvenile/adult (Table 2) compared with a 0.42 juvenile/adult capture ratio. The difference reflects the difficulty of trapping juveniles still in the company of their mother. Juvenile/adult ratios closely tracked the population trend, being high from July 1979 to early February 1980, low during most of 1980, and increasing from March to August 1981. Adult sex ratios over the 12 time intervals ranged from 0 to 1 male/female ($X = 0.64$ male/female, Table 2). The proportion of adult males to females declined sharply from late October 1979 to early February 1980 then increased to a fairly stable level by the

Table 2. Estimated numbers of individuals, densities (individuals/100km²), adult sex ratios (males/female) and age ratios (juveniles/adult) of bobcats on the study area during 12 time periods (see text for methods).

	1979				1980				1981			
	28 Apr to 30 Jun	1 Jul to 25 Oct	26 Oct to 16 Jan	17 Jan to 5 Feb	6 Feb to 28 Feb	29 Feb to 30 Apr	1 May to 19 Jul	20 Jul to 7 Oct	8 Oct to 30 Nov	1 Dec to 8 Mar	9 Mar to 30 Jun	1 Jul to 12 Aug
NUMBER												
Ad. males	3	3	2	1	0	3	4	4	4	4	4	3
Ad. females	5	4	4	4	5	5	5	5	5	5	4	4
Juveniles	2	11	11	9	6	0	7	7	7	7	9	9
Total	10	18	17	14	11	8	16	16	16	16	17	16
DENSITY												
Ad. males	7	7	5	3	0	5	6	6	5	5	6	4
Ad. females	12	9	9	10	10	9	8	7	6	7	7	7
Total adults	19	16	14	13	10	14	14	13	11	12	13	11
Juveniles	5	26	26	24	12	0	11	10	8	9	15	15
Overall	24	42	40	37	22	14	25	23	19	21	28	26
SEX RATIO	0.60	0.75	0.50	0.25	0	0.60	0.80	0.80	0.80	0.80	1.00	0.80
AGE RATIO	0.25	1.38	1.83	1.80	1.20	0	0.78	0.78	0.78	0.78	1.13	1.29

following summer. A similar trend in sex ratio during a "crash" and recovery of a California bobcat population was observed by Lembeck (1986). Thirteen juveniles whose sex was known included 7 males and 6 females (1.17 males/female). Adult and juvenile sex ratios of the bobcats trapped were 0.86 and 1.00 male/female, respectively.

Breeding Season.— Eight litters whose birth dates could be determined to within a week were born in April (4), May (2), October (1), and January (1). Births of four other litters of radio-collared cats were estimated to have occurred in February (1), April (1), and May (2); and an unmarked female on the periphery of the study area apparently produced a litter in April. Based on a gestation period of about two months (McCord and Cardoza 1982), the breeding season extended from August through March, with 10 of the 13 known or estimated mating dates occurring in February and March and 1 each in August, November, and December.

Various derived estimates of the breeding season in other parts of the range include February to April in 11 western states (Duke 1954); January to July or later in Utah (Gashwiler et al. 1961); January to July or later in Wyoming (Crowe 1975); December to March in Arkansas (Fritts and Sealander 1978); February to July with peaks in March and April in Alabama (Miller 1980); February to mid-March in South Carolina (Griffith and Fendley 1986); and November to July in Texas (Blankenship and Swank 1979). Comparison with these data suggests that there may be more fall and early winter breeding in southern Florida than elsewhere in the range.

Natality.— Mean litter size of 1 unmarked and 12 radio-collared females was 2.6 (range = 1-5). As all litters observed were over 2 months of age and may have experienced some mortality, mean litter size at birth was probably higher. Four litters of the semi-tame female (F1) during the study averaged 3.5 with a range of 2-5 compared with a mean of 2.2 and range of 1-3 for 9 litters of other females. This suggests higher litter size at birth for F1 or better survival of her young, possibly as a result of the supplemental feeding she and her kittens received at the cottage they visited. Mean litter size in this study was lower, particularly if litters of the semi-tame individual are omitted from the sample, than values (2.8-3.5) based on observations of kittens in three studies in the western United States (Bailey 1972, Gashwiler et al. 1961, Zezulak and Schwab 1979).

Two females (F8, F9) gave birth to litters when about 1 year old. The low number of young (1 and 2) in these litters suggest that young primiparous females produce smaller litters than older females. The first litter of the semi-tame female (F1) was also smaller than the average of succeeding litters (Winegarner and Winegarner 1982). Breeding between the first and second years of life has been recorded in other bobcat populations (e.g. Crowe 1975;

Brittall et al. 1979; Fritts and Sealander 1978; Johnson and Holloran 1985), but available data are insufficient to provide an adequate basis for interpopulation comparisons in frequency of early breeding in females.

The semi-tame female (F1) had 4 litters (April 1979, May 1980, April 1981, October 1981) over a 31-month period. She also produced a litter during each year from 1976 to 1978 (Winegarner and Winegarner 1982). Thus, she typically bore only one litter per year, although two were produced in 1981. The second 1981 litter was not the result of recycling following the loss of a recently-born litter, as young of the first litter were seen with her until September, and there was circumstantial evidence that at least 1 of them remained in her range until December. Although the female was occasionally artificially provisioned and thus may have been in a better nutritional state than the typical wild female, this case suggests that bobcats in the southern part of the range occasionally may be capable of producing two litters in a year, although one is the norm. Estimated birth intervals for two other females (F8, F9) that produced two litters while being monitored were 8 months in both cases (April-January and May-estimated February).

Mortality and Injuries.— Of the 17 instrumented bobcats, 9 were known to have died between April 1979 and August 1982, including 5 of 6 adult males, 2 of 7 adult females, and 2 of 4 juveniles. The other juveniles of a litter of three disappeared at the same time one died, suggesting that all three perished. Including these two individuals, the mortality rate during the 40-month period was 54% for adults, 80% for juveniles, and 56% for all marked cats. In addition, nine unmarked bobcats (4 adult males, 2 adult females, one juvenile male, one juvenile female, and one unsexed juvenile) died or were found in a moribund condition in or adjacent to the study area between January 1979 and August 1982.

Including both known and probable deaths and causes, 8 of the 17 instrumented bobcats were killed by feline panleucopenia infections and 3 by vehicles. Of the 9 unmarked individuals, 5 (2 adult males, 1 adult female, 1 juvenile male, 1 juvenile female) were killed on roads, 2 adult males were shot, 1 unmarked juvenile (sex unknown) was killed by dogs, and 1 adult female with a severe case of Notoedric mange died within a few minutes of capture. The last individual was weak and extremely emaciated (5.3 kg vs. mean adult female weight of 7.9 kg) and undoubtedly would have soon died if she had not been captured. She had been periodically observed in the study area over a 5-week period before capture, during which time she became progressively thinner and weaker. Three females (F4, F10, F11) among the animals live-trapped and radio-collared from July 1979 to March 1980 also had scabby areas with sparse hair or bare patches on the head, neck, or shoulders, suggesting a current or former mild mange infestation. The partially decomposed carcass of an adult male (M2) found in November 1979 also had similar bare patches on the inside

of the forelegs. In 1978, prior to this study, the semi-tame female (F1) developed a severe case of mange and probably would have died if she had not been captured and treated; and her four kittens that year also apparently died from mange (C. E. Winegarner, pers. comm.). These data suggest that there was a relatively high incidence of mange in the bobcat population of the study area during 1978 and 1979.

Direct and circumstantial evidence indicated that a feline panleucopenia epizootic occurred among the bobcats of the study area during the fall and winter of 1979-1980. The deaths of 4 marked individuals (adult males M1, M3; adult female F10; juvenile male M5) whose fresh carcasses were recovered in January and February 1980 were diagnosed as being due to the disease. Circumstantial evidence also suggested that four other individuals, including an adult male (M2) and a marked juvenile female (F6) and her two siblings (M4, F5), also died from the disease. In addition two adult females (F1, F4) were suspected to have had sublethal infections based on their behavior (see below). Whether only necropsied animals or all possible cases are included, mortality from FPLV from October 1979 through February 1980 accounted for a significant proportion of the known bobcat population, including 3 or 4 of 8 adults and from 1 to 4 of 11 juveniles. Sexes of bobcats known or suspected to have died from FPLV included 2 or 3 of 3 males and 1 of 5 females among adults and 1 or 2 of 3 males and 0-2 of 3 females among known-sex juveniles.

Data on the symptoms of the disease and its effect on behavior were obtained for several of the instrumented bobcats. All known or suspected FPLV victims exhibited a progressive reduction in movements from 2 to 4 days prior to death. A juvenile male was glassy-eyed and lethargic when recaptured 4 days prior to his death and was slow to move away from the observer when released. Disturbance of the ground around the body, which was found soon after death, indicated that the animal had struggled. A large amount of greenish, apparently bile-tinted, fluid exuded from the mouth while the carcass was being transported to the laboratory. An adult male observed near a pond shortly before death was unable to get on his feet or hold his uncontrollably bobbing head erect. Greenish fluid was dripping from his mouth. When checked 2 hours later, he was dead, perhaps drowned, in the pond in water about 10 cm deep. The surrounding vegetation was matted down, indicating the animal had struggled before dying. Four other bobcats known or believed to have died from FPLV also were found near water.

Circumstantial evidence suggests that adult female F4 was principally responsible for the spread of the disease through the population. The first death attributable to FPLV was that of an adult male (M2) in late October 1979. M2 and F4 had overlapping home ranges and probably were in occasional contact outside the breeding season. Therefore, F4 may have transmitted the disease to M2 or received it from him. On 14 January 1980 from 2000 to 2100, F4 and adult male M3 were in close proximity based on

radio fixes. Tracks at the site the next morning also indicated they had been together. M3 was found dead on 16 January and had a FPLV infection based on laboratory diagnosis. Radio locations indicated that F4 and adult male M1 had associated together between midnight 31 January and 0200 on 1 February. The following night M1 was in the vicinity of, if not in actual contact with, F6, one of three juveniles of F1, whose home range was contained within his. As these young were still closely associated, the other two juveniles (M4, F5) probably were also in the area, but their radio-collars were not functioning. Both M1 and F6 apparently died on or about 5 February. F6's carcass, recovered in the area where she and M1 had been located 4 days before, was too decomposed for necropsy. No sightings or tracks believed to be of her litter mates were recorded after this date, suggesting that they also died from the disease.

During the period of apparent contact between M1 and one or more of F1's young, F1 was in another part of her range and did not return to the site until after the male had left the area. Over the next two weeks, she spent an unusual amount of time in that area and in another remote portion of her range with canals and a pond containing water. C. E. Winegarner (pers. comm.) also reported that she stayed away from the cottage where she was occasionally fed for 18 days from late-January to mid-February, her longest period of absence on record. Her apparent attraction to water and prolonged absence from the cottage area suggest that she may have had a sublethal FPLV infection (Bittle 1970), which she could have acquired either from M1 or her young. F4 may also have had a sublethal infection during the winter-early spring period. This could have contributed to her effectiveness in transmitting the disease to other bobcats, as Bittle (1970) stated that an animal recovering from an infection could remain a carrier for a long period. F4's behavior during this period was abnormal. Following the death of M2, her movements became more restricted, and she was observed on three occasions (once near water for about an hour) in February and March 1980 walking slowly or lying down in the open and could be easily approached to within a few meters.

The two remaining bobcats (juvenile male M5, adult female F10) believed to have died of FPLV in late February occupied home ranges adjacent to F4's and thus could have been infected by her. M5 and F4 were recorded visiting the same sites along their common range boundaries during this period.

Only 1 of the 17 bobcats live-trapped in this study showed signs of current or past injury. This was the semi-tame female (F1). A small cloudy area in the lower portion of the left cornea with a tiny wound in the center was noted during laboratory examination of the animal in October 1980. On occasions when she was observed at close range in the field during the previous 2 weeks, the eye was watering profusely and was kept closed almost continuously. The eye appeared normal when she was seen 2 weeks later (C. E. Winegarner, pers. comm.). In October 1982 she was observed limping badly, a forefoot dangling

helplessly. She was nursing a litter of two kittens at the time. She also appeared to recover fully from this injury.

Of the known and probable causes of deaths of radio-collared bobcats in this study, a substantially higher proportion of mortality was due to natural than to man-related causes (73% vs. 27%). In generally comparable studies of radio-collared bobcats in exploited or unexploited populations in other parts of the range (Alabama, California, Idaho, Minnesota, Oklahoma), natural causes accounted for an average of about 38% of deaths, with a range from 0 to 100% (Bailey 1972, Fuller et al. 1985, Gould 1980, Lembeck 1978, 1986, Miller 1980, Rolley 1985). The present study, in which over half (4 of 7) of the resident adults were killed by feline panleucopenia in a 4-month period, demonstrates that the proportion of deaths due to natural causes as well as the actual rate of natural mortality can be high. Thus, Crowe's (1975) model of the annual cycle of bobcat numbers which assumes adult mortality from factors other than trapping to be negligible is clearly not applicable to all populations. It is difficult to assess the relative importance of various mortality factors for other than radio-collared bobcats because of a serious sampling bias; there is a greater probability of recovering animals that have died from man-related causes, such as shooting or being killed on roads, than animals that have died from natural mortality agents. In the present study, for example, it is highly unlikely that the carcasses of any of the bobcats known or suspected to have died from FPLV would have been recovered if they had not been radio-collared.

McCord and Cardoza (1982) noted that documentation of diseases in wild populations of bobcats was sparse and stated that "...bobcat populations have not succumbed to epizootics or die-offs due to heavy parasitic infections...", citing the commonly reported solitary nature and habits of the species as an explanation for the apparent lack of infectious diseases in bobcats. In contrast, our findings suggest that parasites and disease can be important mortality agents in bobcat populations. The relatively high incidence (24%) of current or apparent former Notoedric mange infestations in bobcats that were captured, including F1 who undoubtedly would have died from mange prior to the study if she had not been treated; the capture of one individual (F2) near death from a heavy mange infestation; and the probable death of F1's 1978 litter of four young from mange suggests that heavy parasitic infections can be a significant cause of bobcat mortality in Florida. Deaths of bobcats from mange also have been reported in other geographic regions (Pence et al. 1982, Penner and Parke 1954, Pollack 1949).

Our study also indicates that feline panleucopenia may be an important mortality agent in Florida bobcat populations. Progulske (1982) also documented an apparent die-off of bobcats in northeastern Florida during summer 1980, which may have been due to a FPLV outbreak. Mortality from FPLV also has been reported in bobcats in other widely-separated parts of the

range. Lembeck (1978, 1986) and Gould (1980) recorded confirmed deaths of bobcats from FPLV in California. In an unharvested population studied by Lembeck (1986) from 1976 to 1982, 11 of 22 deaths from known, non study-related causes resulted from natural causes, and five of these were attributable to panleucopenia. FPLV was the probable cause of death of two of five radio-collared bobcats in a study on the Savannah River Plant, South Carolina (Griffith and Fendley 1986). Fox (1983) concluded that feline panleukopenia was probably an important cause of bobcat mortality in New York based upon diagnosed cases of the disease in the Adirondack and Catskill mountains and a relatively high (21%) prevalence of FPLV antibodies in a statewide sample of bobcats.

Our data suggest that FPLV could have been transmitted indirectly through contaminated feces or urine (Csiza et al. 1971), as well as by actual contact between animals. Bobcat marking with exposed scats was most frequent during winter, and bobcats were known to visit each other's marking sites. Bouillant and Hanson (1965) found that healthy mink (*Mustela vison*) who received stomach inoculations of 20% suspended feces passed by animals experimentally infected with mink enteritis virus (MEV) developed clinical symptoms of MEV, even when carrier feces were half-buried for several months during cold, damp weather, which favored survival of the virus. The winter of 1979-1980 in south-central Florida was relatively cool and wet. These facts suggest that bobcats might become infected through investigating contaminated feces and that weather conditions could influence the probability of an outbreak by affecting survival of the virus. The higher incidence of FPLV mortality in males than females suggested by our data may reflect the larger home range size of males (see below), which might increase their probability of contacting infected animals and/or feces. Further, FPLV infections occurred during the peak period of marking, which might also have increased chances of virus transmission.

In addition to being a cause of death of young or adult bobcats, FPLV may also kill embryos or fetuses of pregnant females with a sublethal infection (Povey and Davis 1977). It may be significant in this connection that female F1, believed to have had a sublethal infection during winter 1979-80, produced only two young in her first litter following this period, whereas her two previous litters and subsequent two litters numbered three, four, and five, four, respectively. In addition, F4, also suspected of having a sublethal infection, was the only collared female in the population who did not rear a litter in the year following the epizootic.

Although FPLV was probably spread through the bobcat population by contact with infected individuals or contaminated feces, other potential vectors, including free-ranging domestic cats (*Felis catus*) and raccoons (*Procyon lotor*), were present in the study area. Feline panleukopenia is common in domestic cats throughout the United States, and Goss (1948) reported that raccoons are

susceptible to FPLV. Feral domestic cats were seen regularly in the study area prior to the epizootic but not for several months afterwards, and a local veterinarian (J. Causey pers. comm.) reported that a relatively high number of cats with feline distemper were brought to his small animal clinic in Lake Placid during the bobcat epizootic. Young (1958) noted that bobcats are known to kill domestic cats. In addition, an unusual number of sick or dead raccoons was observed within and in the vicinity of the study area from March to May 1980, and bobcats were known to feed on raccoons in the study area (see **Food Habits** section).

Although its reported incidence in wild felids in the United States is low (Burridge et al. 1986), rabies also may be a significant mortality factor in bobcat populations. In Florida, 11.1% (7 of 63) bobcats submitted for rabies testing from 1975 to 1983 were positive for the disease, compared with 3.1-9.7% for raccoons, foxes, and bats which are the principal vectors in the state (Burridge et al. 1986). The actual prevalence of rabies in bobcat populations may be higher than the available data suggest, as rabid bobcats may be less likely to come to the attention of the public than rabid raccoons or foxes.

Longevity.— Radio-collared animals known to have survived beyond the end of the study included females F1 and F8. F1 was last observed in May 1984 at an age of approximately 9 years, 10 months, and F8 was last observed in December 1984 at an age of about 5.5 years.

Food Habits

Fourteen species of mammals and four species of birds were identified in scats collected on the core portion of the study area (Table 3). Cottontail, marsh rabbit, and cotton rat were the principal prey species, comprising 73% of total prey items and 86% of estimated prey biomass. Although seasonal differences in the frequency of these three species were not statistically significant (X^2 tests, $p > 0.05$), there were suggestive trends. The lowest frequency (26%) of cottontail was in summer (June-August), compared with 38-42% in winter (December-February), spring (March-May), and fall (September-November). Cotton rat showed a similar trend, with a frequency of 16% in summer versus 21-29% in other seasons. Marsh rabbit was lower in both summer (5%) and fall (0%) than in winter (8%) and spring (8%). The reduced frequency of the three major prey species in summer was reflected in an increased frequency (26% vs. 4-11% in other seasons) of other small mammals (*Glaucomys*, *Rattus*, *Peromyscus*, *Podomys*, *Oryzomys*). The number of mammal species represented in scats in different seasons was lowest in fall (4 vs. 8-10 in other seasons). Separate and combined frequencies of cottontail,

Table 3. Animal food items in 146 bobcat scats collected on the core study area, 1967-1979.

Scientific Name	Common Name	Minimum Number of Individuals	% of Total Prey Items	% of Scats Containing Prey Item	% Biomass of All Prey Items
MAMMALS		250	89.9	100.0	99.9
<i>Sylvilagus floridanus</i>	Eastern cottontail	110	39.6	75.3	74.0
<i>Sigmodon hispidus</i>	Hispid cotton rat	72	25.9	49.3	4.0
<i>S. palustris</i>	Marsh rabbit	20	7.2	13.7	8.5
<i>Peromyscus floridanus</i>	Florida mouse	11	4.0	7.5	0.2
<i>Sciurus carolinensis</i>	Gray squirrel	10	3.6	6.8	1.8
<i>Didelphis virginiana</i>	Opossum	5	1.8	3.4	6.2
<i>Rattus rattus</i>	Black rat	4	1.4	2.7	0.2
<i>Peromyscus polionotus</i>	Oldfield mouse	4	1.4	2.7	<0.1
<i>Glaucomys volans</i>	Southern flying squirrel	3	1.1	2.1	0.1
<i>Oryzomys palustris</i>	Marsh rice rat	3	1.1	2.1	0.1
<i>Neofiber alleni</i>	Round-tailed muskrat	2	0.7	1.4	0.3
<i>Procyon lotor</i>	Raccoon	2	0.7	1.4	3.6
<i>Bos taurus</i>	Cow	1	0.4	0.7	*
<i>Sus scrofa</i>	Pig	1	0.4	0.7	*
Unidentified Mammals		2	0.7	1.4	
BIRDS		28	10.1	16.4	1.0
<i>Colinus virginianus</i>	Northern bobwhite	2	0.7	1.4	0.2
<i>Cyanocitta cristata</i>	Blue jay	1	0.4	0.7	<0.1
<i>Gallus gallus</i>	Chicken	1	0.4	0.7	0.8
<i>Sturnella magna</i>	Eastern meadowlark	1	0.4	0.7	<0.1
Unidentified Birds		23	8.3	15.8	

* Assumed to be carrion

marsh rabbit, and cotton rat did not differ significantly (X^2 tests, $p > 0.05$) between years for years with adequate samples of scats (1971-1975, 1979).

Of the scats analyzed, 40% contained grass or other vegetation. In 9.6% of the scats, vegetation comprised from 10 to 40% of the volume of the scat. The high frequency and quantity of plant material in scats suggest that it was intentionally consumed in some cases. Plant material had a frequency of occurrence of 11% and comprised 4.4% of the volume of bobcat stomach contents from other Florida localities (Maehr and Brady 1986). Young (1958) noted that wild fruits, principally of cactus (*Opuntia*), occurred (5%) in a Florida bobcat stomach collected in April. Kight (1962) reported that grass made up 11.2% of the diet of bobcats in South Carolina and suggested that it was deliberately rather than accidentally eaten.

In addition to the scat analysis, occasional observations were made on foods and feeding behavior on the core study area. Bobcats were seen carrying a cotton rat on one occasion and a black rat on another. The semi-tame individual was once seen springing out of hiding in a palmetto thicket in an unsuccessful attempt to catch a cottontail, and twice individuals were observed chasing gray squirrels, once in a tree and once on the ground. On two days in November 1979, Hope Ryden (pers. comm.) followed the semi-tame female (F1) in the field to observe her hunting methods. The cat tended to walk along trails and would stop and listen intently when she heard a sound off the trail, then stalk slowly in that direction. She once stalked an armadillo (*Dasypus novemcinctus*) by sound, but lost interest when she saw what it was. On another occasion, Ryden (1981) watched the bobcat kill a raccoon and take it to her young. Another instance of predation on raccoons in the core area by a different bobcat was observed by C. E. Winegarner (pers. comm.) in March 1982. A juvenile raccoon released from a live trap was caught by the bobcat as it entered the woods a short distance away. The bobcat held the raccoon by the throat as it squalled and struggled violently. The bobcat dropped the raccoon when it saw the observer, but apparently returned and recaptured the raccoon after the observer left the area, as he heard the raccoon squalling again. In April 1982, a deer (*Odocoileus virginianus*) that had been hit by a car was fed upon and sparsely covered with dry grass by a bobcat. The only record of non-mammalian or avian prey of bobcats on the study area, was an observation in July 1981 of the semi-tame female killing a large adult southeastern five-lined skink (*Eumeces inexpectatus*). She slowly stalked the lizard, which was moving around at the edge of a clump of palmettos, from about 6 m away then rushed it from about 1.5 m. It ran under a pile of dry grass and the bobcat spent 3-4 minutes chasing the lizard before she caught it. She would stand still, listening intently, then pounce on a spot with her feet and push her snout into the grass. After catching and killing the lizard she carried it to a nearby shady spot, then abandoned it and moved on.

The food habits data suggest that the diet of bobcats on the study area was influenced both by prey availability and selection for certain species, based on knowledge of habitat relationships and populations of vertebrates of the core area (Layne unpubl. data). The predominant prey species, cottontail, was common in drier habitats throughout the study area and frequently foraged in the open on road shoulders and along trails. In contrast, marsh rabbits were apparently less abundant than cottontails and largely restricted to dense grass or palmetto thickets of seasonal ponds. They seldom foraged in the open and when they did so rarely moved more than 1 m from the edge of dense cover. In view of the lower numbers, more restricted habitat distribution, and presumably less vulnerability to capture of this species, its high rank order in the diet suggests it was hunted selectively by bobcats. Although generally distributed throughout the study area and relatively abundant in habitats with well-developed ground cover, the cotton rat was overall less abundant and widespread on the study area than such smaller rodents as *Peromyscus gossypinus*, *P. polionotus*, and *Podomys floridanus*, suggesting that its larger size made it a more favored prey item. A number of potential prey species were conspicuous for their absence in scats. The cotton mouse, *P. gossypinus*, the most abundant and habitat-tolerant species on the study area was not recorded in scats. Armadillos (*Dasypus novemcinctus*), also abundant in the study area, did not appear in scats, and the observation cited above suggests they were ignored when encountered. Also noteworthy was the absence in scats of such ground-frequenting birds as common ground dove (*Columbina passerina*), scrub jay (*Aphelocoma coerulescens*), rufous-sided towhee (*Pipilo erythrophthalmus*), brown thrasher (*Toxostoma rufum*), and gray catbird (*Dumetella carolinensis*) that are common seasonally or year-round in habitats used by bobcats.

The data from this study agree with those from elsewhere in the range that indicate the bobcat concentrates on medium-sized prey with some species of lagomorph being a major food item (Rosenzweig 1966, McCord and Cardoza 1982). Cottontail, marsh rabbit, and cotton rat also predominated in previous food habits studies of bobcats in other parts of Florida (Fickett 1971, Maehr and Brady 1986). Data summarized by Maehr and Brady (1986) indicated that bobcats in Florida and elsewhere in southeastern U.S. utilize deer less frequently than in northeastern U.S.

Home Range and Social Organization

Home Range Size.— Mean overall home range size of 12 adult bobcats was 19.1 km² (Table 4). Means and ranges of five male and seven female adults were 25.5 km² (14.8-31.1) and 14.5 km² (8.9-21.6), respectively. Adult male

ranges were significantly larger ($U_{5,7} = 3, p < 0.05$, 2-tailed) than those of adult females. The individuals were monitored from 16 to 1143 days ($X = 465$) and located on 26%-94% ($X = 44$) of the days during the total period they were tracked. The mean number of fixes per cat was 333 (range = 21-1248). The shape of home ranges tended to be elliptical. Mean maximum range length and width were 7.3 km (range = 5.3-9.0) and 5.1 km (range = 4.3-5.8), respectively, for adult males and 5.2 km (range = 4.2-7.0) and 4.0 km (range = 2.6-6.6) for adult females (Table 4). Adult male ranges were significantly longer ($U_{5,7} = 4, p < 0.05$, 2-tailed) than those of adult females, but there was no sex difference in width ($U_{5,7} = 7, p > 0.05$, 2-tailed). The mean ratio of length to width was 1.5 (range = 1.0-2.1) for adult males and 1.4 (range = 1.1-1.8) for adult females. The difference was not significant ($U_{5,7} = 15.5, p > 0.05$, 2-tailed).

Home range boundaries tended to coincide with such features as railroad tracks, firelanes, roads, footpaths, and well-defined edges between natural and man-modified habitats. When portions of the vacated range of a deceased bobcat were occupied by surviving same-sexed neighbors or when a range boundary shift occurred between two same-sexed bobcats, the new boundaries were usually established along such distinctive habitat features. No "exploratory" movements were detected. It is possible that with the relatively intense tracking effort in this study visits to peripheral areas were regularly recorded and thus the areas were recognized as part of the range, whereas with less frequent monitoring movements to such outlying points might have been regarded as "exploratory."

Observed short-term home ranges of adults with an adequate number of locations in any of the 12 time periods to provide a reliable indication of movements are given in Table 5. As in the case of overall home ranges, male short-term ranges averaged larger ($X = 15.5 \text{ km}^2$, range = 11.8-22.0) than those of females ($X = 8.8 \text{ km}^2$, range = 5.9-12.4). The difference was significant ($U_{5,7} = 2, p < 0.01$, 2-tailed). Short-term ranges of males in different time intervals were from 15 to 84% ($X = 56$) of their respective overall home ranges, as compared with 32-87% ($X = 60$) for females). Ratios of maximum to minimum short-term home ranges for individuals with estimates in two or more time intervals averaged 0.61 (range = 0.24-0.91) for five males and 0.62 (range = 0.39-0.84) for five females. The difference in ranks of ratios for males and females was not significant ($U_{5,5} = 12, p > 0.05$, 2-tailed), indicating that there was no sex difference in relative variability of the home range over time.

Short-term home range estimates did not exhibit any obvious seasonal trends. Two young individuals (M6, F8) showed expansion of their home ranges following independence from the mother. Observed home range size of other individuals frequently changed abruptly from one time period to another. A major cause of such changes was the death or disappearance of a neighbor.

Table 4. Overall home range areas and range axes of adult bobcats.

Individual	Length of Record (days)	Number of Days Located	Number of Locations	Home Range Area (km ²)	Home Range Axes (km)		
					Maximum Length (A)	Maximum Width (B)	Ratio (A/B)
MALES							
M1	284	145	490	24.9	6.0	5.8	1.0
M2	184	64	196	14.8	5.3	4.6	1.2
M3	161	59	196	25.8	9.0	4.3	2.1
M6	690	231	517	31.0	8.4	5.0	1.7
M8	606	156	510	31.1	7.8	5.7	1.4
FEMALES							
F1	1,143	426	1,248	18.2	5.2	4.5	1.2
F3	168	56	199	8.9	4.6	2.6	1.8
F4	497	257	600	19.4	7.0	6.6	1.1
F8	519	232	531	12.7	4.6	3.4	1.4
F9	699	251	466	21.6	6.8	4.2	1.6
F10	16	15	53	9.4	4.2	3.3	1.3
F11	258	121	171	11.6	4.2	3.6	1.2

Table 5. Home ranges (km^2) of adult bobcats during 12 time intervals between April 1979 and August 1981. Values indicated by an asterisk are for juveniles during the first period they were considered to occupy their own home range. Estimates in parentheses are considered too low as a result of behavior of females with young litters (see text) and were not used in statistical calculations.

Individual	1979				1980				1981			
	28 Apr to 30 Jun	1 Jul to 25 Oct	26 Oct to 16 Jan	17 Jan to 5 Feb	6 Feb to 28 Feb	29 Feb to 30 Apr	1 May to 19 Jul	20 Jul to 7 Oct	8 Oct to 30 Nov	1 Dec to 8 Mar	9 Mar to 30 Jun	1 Jul to 12 Aug
MALES												
M1	12.2	10.2	15.1	18.2	-	-	-	-	-	-	-	-
M2	12.4	11.3	-	-	-	-	-	-	-	-	-	-
M3	-	12.3	17.1	-	-	-	-	-	-	-	-	-
M6	-	-	-	-	-	4.8*	5.8	16.0	18.2	19.8	19.2	20.3
M8	-	-	-	-	-	-	-	21.3	25.2	23.3	24.8	15.6
FEMALES												
F1	-	-	11.0	11.5	10.6	14.0	(10.3)	13.8	12.9	12.4	12.9	12.9
F3	-	5.9	-	-	-	-	-	-	-	-	-	-
F4	-	10.9	10.4	7.0	6.8	11.7	(8.9)	11.0	8.6	-	-	-
F8	-	-	-	-	4.1*	4.8	5.2	7.9	9.8	10.4	-	-
F9	-	-	-	-	11.1	11.3	8.1	12.6	13.1	14.7	13.5	15.0
F10	-	-	-	-	8.2	-	-	-	-	-	-	-
F11	-	-	-	-	-	7.1	(2.3)	8.4	-	-	-	-

Such a case was that of adult male M6 who expanded his range approximately 175% within two weeks following the death of a presumed adjoining male. Females with recently-born young in the period 1 May-19 July 1980 (F1, F9, F11) showed an apparent sharp decrease in home range size. However, as described more fully in the following section, intensive monitoring of selected females with small young indicated that they did not significantly reduce their home range but rather visited their range boundaries for shorter periods of time, resulting in a lower probability of detecting such longer movements.

Overall home ranges of adult males in this study averaged about 73% larger than those of females, agreeing with data from throughout the species' range indicating that adult male bobcats consistently have larger home ranges than females (e.g. Bailey 1972, Berg 1979, Brittell et al. 1979, Buie et al. 1979, Erickson and Hamilton 1980, Fuller et al. 1984, Gould 1980, Hall 1973, Kitchings and Story 1984, Lancia et al. 1986, Lawhead 1978, 1984, Lembeck 1978, Miller 1980). From observations of tracks independent of this study, Winegarner (1985a) obtained home range estimates for the semi-tame female (F1) of 4.68-6.45 km² from about May 1980 to May 1981. In contrast, our estimates of home range of this individual during five time intervals over the same year ranged from 10.3 to 13.8 km² ($X = 12.4$ km²). The marked discrepancy in the home range estimates of the two studies apparently reflects the increased resolution of movements provided by radiotracking supplemented by trailing and perhaps also a difference in the intensity of monitoring. Mean range size of males in this study was considerably smaller than that (44.4 km²) reported for two males in northeastern Florida (Progulskie 1982), the only other available data on home range size of bobcats elsewhere in the state. Mean home ranges of adult bobcats determined by radiotelemetry and calculated by the minimum home range method from other geographic regions (Alabama, Arizona, California, Louisiana, Minnesota, Nevada, South Carolina, Tennessee) ranged from 2.6 to 50.4 km² for males and from 1.1 to 77.0 km² for females (Berg 1979, Buie et al. 1979, Fuller et al. 1984, Golden 1982, Hall 1973, Kitchings and Story 1984, Lawhead 1984, Miller 1980). The great variability in bobcat home range size in different parts of the range undoubtedly reflects both variation in methods of study, as well as environmental factors. On the basis of present data, little can be concluded concerning general trends in bobcat home range size related to habitat or geographic region, although the largest reported home range sizes tend to be in northern and western populations.

The influence of habitat features on movements of bobcats and hence on home range size and use seen in this study also has been observed by other workers. Buie et al. (1979) found that home ranges generally interfaced along roads, railroads, and water ways. Most fixes obtained by Hall (1973) were within a few hundred meters of a road or trail, and Miller (1980) stated that bobcats rapidly accepted and utilized logging roads, firelanes, and farm roads

as avenues of travel. High levels of use of unpaved roads and similar features may be related to higher abundance of prey along their edges coupled with a better opportunity for a stealthier approach as compared to stalking in more dense areas (see **Food Habits** section).

In south-central Florida, Alabama (Miller 1980), and presumably elsewhere in the southeast, an abundance of suitable rest sites provided by dense thickets, vine-covered areas, patches of palmettos, etc. may allow less restricted movements than some other regions. For example, McCord (1974) stated that in an area in Massachusetts ledges were important to bobcats and their location was a factor influencing bobcat movements; and in relatively sparsely-vegetated areas in Idaho (Bailey 1972) and California (Zezulak and Schwab 1979) bobcats tended to occur in areas with rock falls, caves, and other such features. In severe weather, movements were even more restricted to these areas, which were in high demand and were frequently shared among several cats.

Use of Area Within Home Ranges.—Based on the distribution of radio fixes in 4-ha quadrats, adults visited from 10 to 62% of the area in their overall home ranges. Males appeared to use their home ranges less thoroughly than did females. Five males were recorded in from 14 to 34% ($X = 27$) of their home range quadrats compared with 10-62% ($X = 40$) for seven females, although the difference was not significant ($U_{5,7} = 7, p > 0.05$, 2-tailed). About 47% of the quadrats visited by females contained more than one fix, as compared with only 29% for males. As in the case of the proportion of quadrats used, this difference points to more intensive utilization of the home range by females. The highest number of locations in a single quadrat recorded for any individual was 59 for the semi-tame female F1 in the quadrat including the dwelling at which she was occasionally fed and often rested. The distribution of her locations outside of this area was not obviously different from that of other females in the population.

Comparison of the distributions of active and inactive (= rest sites) locations, indicates that, although inactive locations occurred throughout the range, there was a tendency for them to be clumped into 2-6 vaguely defined areas near the periphery of the home range. An average of 42% (range = 32-51) of the home range quadrats used by females contained rest sites, compared with 27% (range = 17-36) for males, indicating that females used relatively more areas within the home range for resting. Of quadrats with fixes, an average of 17% of those in both male and female home ranges contained only rest sites. Thus there appeared to be no sex difference in the relative proportion of the home range area used only for resting.

Relationships Between Adult Home Ranges.—Figures 3-5 show the spatial relationships of bobcats in the core area during the 12 time intervals from 28

April 1979 to 12 August 1981 as determined by radiotracking, trailing, and visual observations. The general locations of all presumed resident bobcats are indicated. These include individuals radiotracked during the interval as well as marked cats whose collars had stopped transmitting and unmarked animals known or believed to be present on the basis of tracks or sightings.

Configuration of home ranges varied continuously throughout the study but tended to be relatively more stable during the initial (April-October 1979) and final (March-August 1981) periods than during the interval from winter 1979-80 to spring 1981. Although the shape and size of home ranges of individual resident bobcats varied over time, the cats exhibited a strong tendency to remain in the same general area. Two females occupied the same overall home range for periods of about 5.5 years (F8) and 9 years (F1). Of the 13 adults monitored during the study, one exhibited a local home range shift and one made a long-distance movement. In the first case, an adult female (F3) apparently moved to an area adjacent to her original home range. In August 1982 she was killed on a highway about 1.5 km N of the nearest boundary of the home range she had occupied from June through November 1979, when her collar failed. She continued to use the area at least through December, based on tracking. Sightings believed to be of this individual were made at the edge of her previously known range in February and August 1980. The male (M6) and female (F8) juveniles of this female remained in the natal range, and the daughter produced her first litter in May 1980. On the assumption that two breeding females would not occupy the same area, the old adult must have vacated her former range by spring 1980 or before. The long-distance movement involved a male (M7). He was trapped and marked in late April 1980 and radiotracked for 3 days following release, after which the transmitter failed. He was sighted 20 August 1980 and 3 June 1981 within 2 km of the area in which he was tracked in April 1980, indicating he was still in the study area after 14 months but may have shifted his home range. In July 1982, he was found dead on a highway 70 km from the study area. The distance moved by this individual exceeds values previously reported from the southeast (Griffith et al. 1980, Kitchings and Story 1984). Knick and Bailey (1986) noted that the longest documented bobcat movements (158 and 182 km) were from a region with a cyclic prey base and that in areas, including the southeast, characterized by a stable prey base movements have been < 50 km.

Neither resident adult males nor females showed appreciable home range overlap with adjacent bobcats of the same sex. The overlap of adjacent adult male home ranges believed to be relatively accurately delimited averaged 5%, with a range of 1-11%. Mean and extremes of home range overlap of adult females were 3 and 0-17%, respectively. These values indicate that in both males and females adults of the same sex tended to have exclusive home ranges. Tracking of neighbors, radio fixes, and sightings suggested that, in

general, mutual use of areas by adult bobcats of the same sex was confined to a narrow zone along the line of contact of their current home range boundaries.

Bobcats apparently only rarely came into close contact with neighbors of the same sex. Only four cases of two adult males or two adult females being in close proximity were recorded during the study. Daytime rest sites of females F4 and F1 were within 200 m of each other on one occasion in December 1979, and F4 rested near F8 on one day in October 1980. These two females also walked within 100 m of each other one night in August 1980. The only instance of two adult males being close together was recorded in October 1980, when M8 followed M6 about 2 minutes behind along a stretch of railroad track, then each veered off in a different direction.

Death or disappearance of a resident bobcat resulted in major changes in the size and shape of home ranges of adjacent animals of the same sex. In contrast, opposite-sexed survivors did not exhibit such a response to the loss of a neighbor. Thus spacing mechanisms may operate independently in males and females. Three clear-cut examples and a probable fourth case of this phenomenon were documented. After the death of M2 in late October 1979, adjoining males M1 and M3 expanded their home ranges into the area of M2's former range, whereas the boundaries of the female (F1, F3, F4) ranges remained stable (Fig. 3B, C). The apparent expansion of F1's range reflects better sampling in the subsequent time period and not an actual change in movements. M3 died in mid-January 1980, and his death was followed by further expansion of M1's range but no obvious changes in those of females (Fig. 3C, D). Female ranges also remained stable following the death of M1 in early February 1980 (Fig. 3D, Fig. 4A). The most dramatic male range expansion documented was that of M6 in late July 1980, following the death of an unmarked adult male on the north boundary of his range (Fig. 4C, D). Female ranges also showed an apparent slight increase during this period, which is believed to reflect changes in their movements related to age of their young rather than an actual expansion in response to the increase of M6's range. In the single case of a confirmed death of a female (F10, late February 1980), one (F4) of two neighboring females markedly expanded her range into the vacated area (Fig. 4A, B). The other female (F1) was also subsequently located in the former area of F10, but data available on F10 up to the time of her death were not complete enough to definitely establish the boundary between the home ranges of these individuals.

Range expansion of adjoining same-sexed bobcats began a short time after the death of a resident. In six cases, such shifts were first detected within 5-14 days, with a mean of 9 days. There was no significant difference ($U_{24} = 4, p > 0.05$, 2-tailed) between sexes in the time before the first recorded incursion into the new area. Home range boundaries in the invaded area appeared to be realigned within several weeks with no evidence of "jockeying" for position.

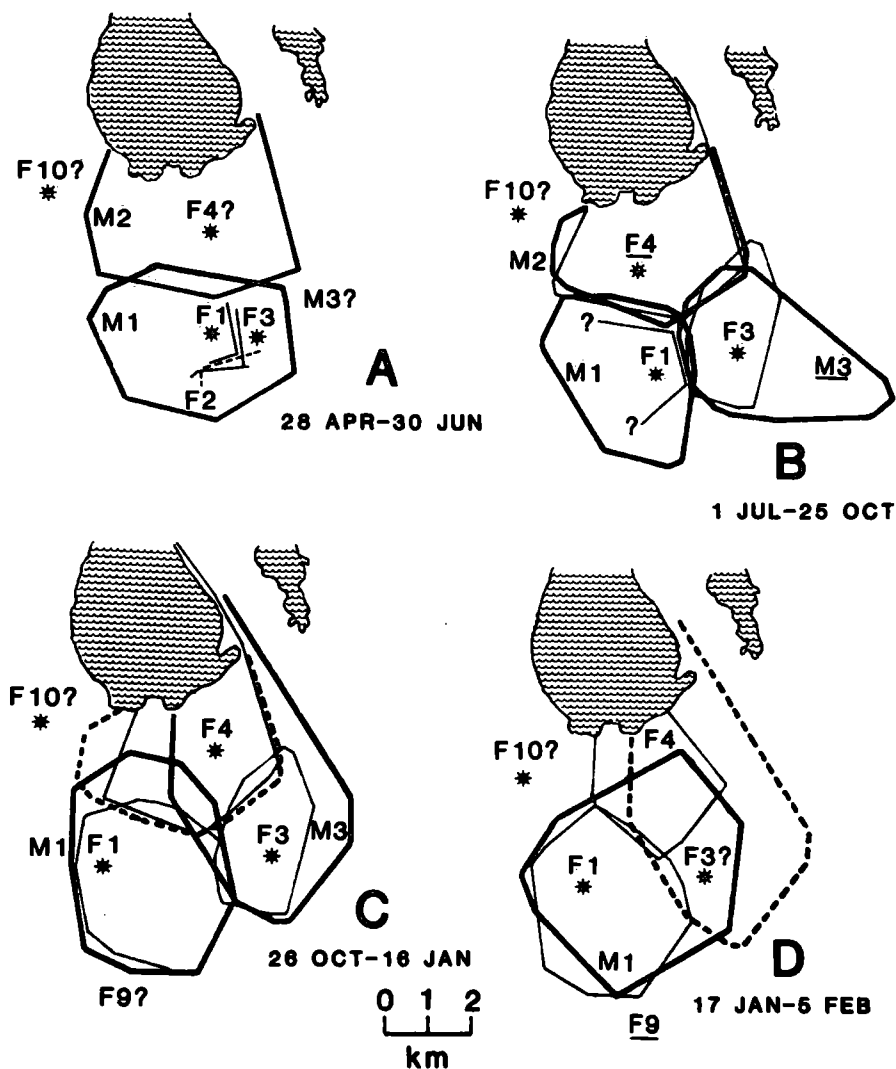


Figure 3. Bobcat home ranges during four time intervals between 28 April 1979 and 5 February 1980. (A) 28 April-30 June 1979; (B) 1 July-25 October 1979; (C) 26 October 1979-16 January 1980; (D) 17 January-5 February 1980. Observed boundaries of home ranges of adult males and females alive during a given period are shown in heavy and light solid lines, respectively. Ranges of adult males and females that died or vacated their range in the period just preceding a given interval are shown by heavy and light broken lines. Females with young during the interval are indicated with an asterisk. Other individuals known or assumed to be present on the basis of circumstantial evidence, but whose ranges could not be estimated, are included without indication of home range boundaries. Individuals first captured during a given period are underlined. Individuals believed to have been seen after radio collars failed are overlined. Two lakes in the northern end of the study area are also shown.

In contrast to the intrasexual exclusiveness of home ranges, adult male ranges were typically superimposed on those of adult females (Figs. 3-5). In the majority of cases, a single smaller female range was largely or entirely contained within the larger home range of a male, with the relationship persisting until one of the individuals died. Of nine combinations of male/female home range overlap (Figs. 3-5), six involved a male and a single female (M1/F1, M2/F4, M3/F3 during the period 1 July-25 October 1979, M7/F1 from 29 February to 30 April 1980, M6/F8 from 29 February 1980 to 8 March 1981, and M8/F1 from 20 July 1981 to 12 August 1981). One of these pairs involved probable siblings (M6, F8). The remaining combinations consisted of a male and two or three females (M1/F1,F4 and M3/F3,F4 from 26 October 1979 to 16 January 1980 and M1/F1,F3,F4 from 17 January to 5 February 1980). In addition to containing the range of his probable sister, M6's range may also have overlapped that of his mother (F3) during the period 20 July 1980-12 August 1981 (Figs. 4D, 5). The number of different males with which a given female was known to associate during the study ranged from 1 to 3.

Three pair relationships (M1/F1, M2/F4, M3/F3) existed on the core region of the study area during the early period of the study after a sufficient number of radio fixes had been accumulated to give a reasonably reliable picture of home range configurations (Fig. 3B). The range shown for F1 in Fig. 3B was based on relatively few fixes. Prior to being equipped with a radio-collar she was tracked farther to the west than shown by the telemetry data and probably used a major part of the range of M1 during the 1 July-25 October 1979 interval. Although the M7/F1 pair (Fig. 4B) appears to be the reverse of the usual case of a larger male range with a contained smaller female range, the range shown for M7 is based on only seven radio locations and is undoubtedly less than his actual range. Because of collar failure, this animal could not be tracked in subsequent periods. Following the collar failure and apparent disappearance of M7 from the range of F1 in late spring 1980, adult male M8 aligned his range boundary with that of F1 (Fig. 4D) such that about 97% of F1's area was contained within about 49% of M8's range. This configuration persisted until early March 1981 (Fig. 5A, B), after which the male gradually ceased movements in the western portion of his range. As a result, all of F1's observed range was contained within about 83% of the male's range by summer 1981 (Fig. 5D).

Two male-female associations involving more than one female, were established following the death of M2 on 25 October (Fig. 3C). Male M1, initially associated only with female F1, extended his range to also overlap a portion of that of female F4, who had been associated only with M2 prior to his death. During the same period, M3 also extended his range to encompass part of F4's. M3's previous female associate (F3) could not be radiotracked after 15 November 1979 because of collar failure. However, tracks, sightings, and the

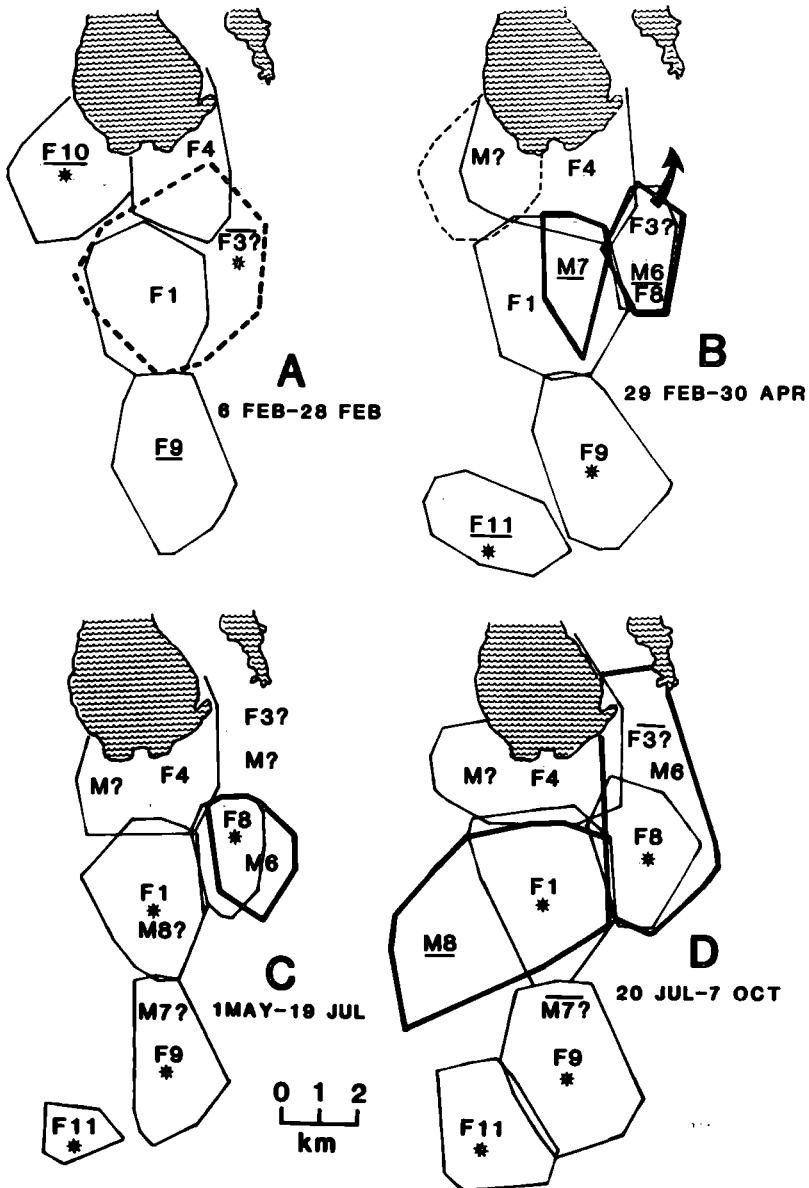


Figure 4. Bobcat home ranges during four time intervals from 6 February to 7 October 1980. (A) 6-28 February; (B) 29 February-30 April; (C) 1 May-19 July; (D) 20 July-7 October. Arrow indicates home range shift. See Figure 3 for description of other symbols. M6 and F8 (captured in January 1980), presumed to be young of F3 and present since beginning of study, first considered as adults in the 29 February-30 April interval.

pattern of movements of her radio-collared young (M5, M6, F8) indicated that she was probably still in the area through February 1980. Her range is shown in Figure 3C as similar to that of the previous period based on radio locations through mid-November, and she is shown as present in the same general area in Figures 3D and 4A. Following the death of M3, M1 expanded his range, probably to overlap or include that of F3 (Fig. 3D), as F3 is assumed to have remained in her former range until February 1980. Thus, during 17 January-5 February 1980 M1's range probably overlapped all or major portions of the ranges of three adult females (F1, F3, F4), two of which (F1, F3) had young. It may be significant that while the range of male M1 was superimposed on those of more than one female, the greatest overlap was with the female F1, with which he was originally associated.

Although the ranges of given males and females overlapped and both individuals were known to use the same places within the common area, observations indicated that for the most part they did not visit the same sites at the same time, i.e. they were spatially associated but tended to be temporally isolated. However, males and females were occasionally located in close proximity, if not actually together. Instances of such close association were recorded in every month of the year except June and July, during which time less radiotracking was done and fewer marked male/female combinations were present in the population. These data indicate that adult males and females with overlapping ranges did associate, if only infrequently, outside of the breeding season.

Observations suggested that the male of a pair may keep other males from a female with small young. During the night of 5 April 1981, an adult male (M6) adjacent to the M8/F1 range (Fig. 5C) was located less than 200 m from the den of F1 with her recently-born litter. After spending about 2 hours in the area of the den, he moved about 1 km SSE, passing through the area near the cottage where F1 was occasionally fed and which was one of her preferred rest areas. During the night of 8-9 April, he also passed within 0.5 km of the den. Immediately following M6's appearance in the vicinity of the den and cottage, M8 began to concentrate his activity in these areas, moving through and resting in them during the day and night. Although no actual contact between the two males was documented, it is possible that M8's behavior was a response to the presence of M6 in the vicinity of the den and may have served to discourage further visits by M6 to the den area. Lembeck (1986) reported several cases where males (sometimes more than one) were in close proximity to a female for a few days following parturition.

The adult male also may promote the dispersal of older juveniles. When not in the area of the den or cottage, M8 could usually be found moving along the periphery of other portions of his and F1's shared range, particularly in the area apparently used by an older kitten of F1 that was still in the natal range. On four of five days during the first two weeks of April that the juvenile was

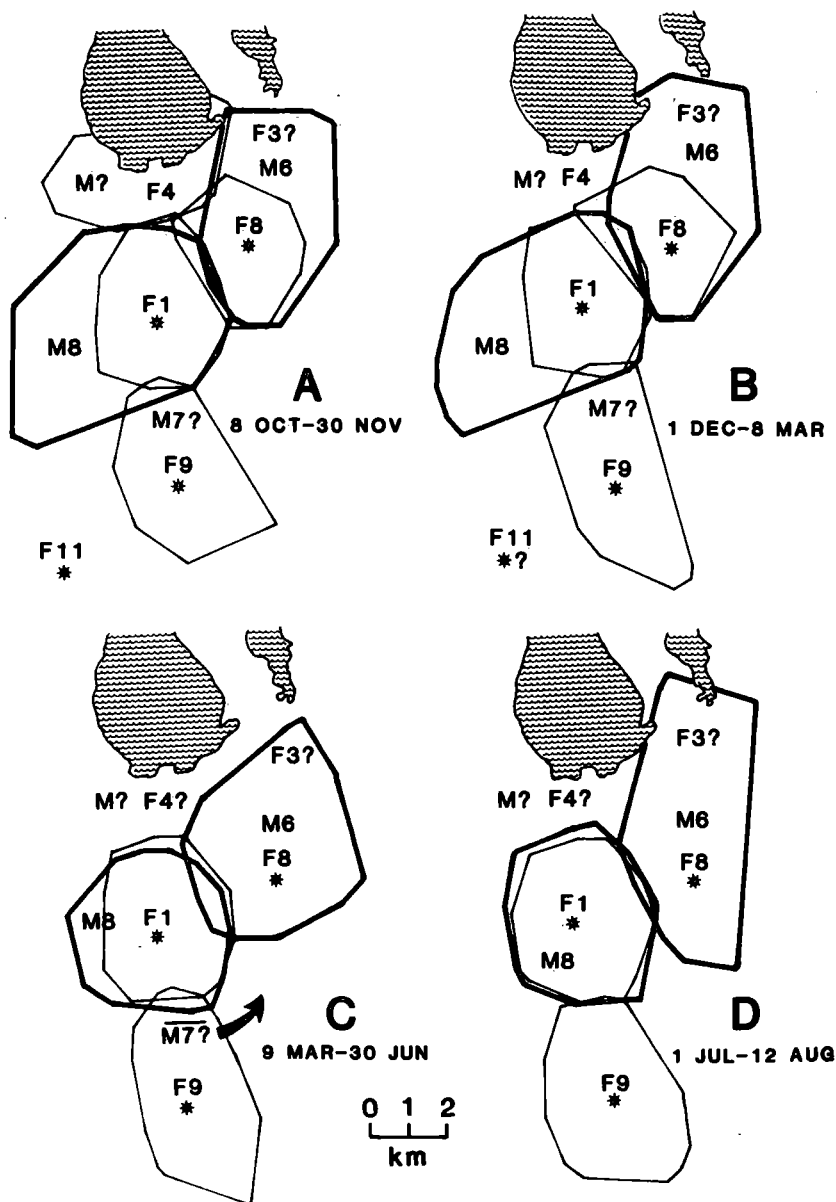


Figure 5. Bobcat home ranges during four time intervals from 8 October 1980 to 12 August 1981. (A) 8 October-30 November; (B) 1 December 1980-8 March 1981; (C) 9 March-30 June; (D) 1 July-12 August. Arrow indicates long-distance movement. See Figure 3 for description of other symbols.

trailed or seen along or close to the edge of the home range, tracks were found that suggested that it had been in contact with M8. No signs of fighting were noted, but on all occasions of apparent contact between these individuals there were many, frequently overlapping, tracks scattered over a wide area. Tracks of the juvenile were not seen in the area following the last of the apparent contacts with M8, suggesting that it may have dispersed. If this interpretation is correct, its dispersal may have been hastened by the contacts with the adult male.

The number and complexity of social and ecological factors that may potentially affect home range size and configuration, the small number of bobcats studied, and the relatively high turn-over of adults leading to considerable instability of the population during a major part of the study make it difficult to partition the causes of the observed variation in home range size and spatial relationships. However, death of individuals, relationships between adult males and females, and the mother-young relationship appeared to be important factors affecting the spatial organization of the population. Death of a resident influenced home range size of adjacent individuals of the same sex. Bailey (1972) and Miller (1980) also observed marked expansion of home ranges of neighboring bobcats of the same sex upon the death or disappearance of a resident. In contrast, however, Anderson (1986) reported that a male that shifted his home range into the area previously occupied by an experimentally removed male exhibited decreased home range size following the shift. Seasonal changes in range size of individual bobcats also have been reported by Buie et al. (1979), Kitchings and Story (1979), Lembeck (1978), and Zezulak and Schwab (1979).

The low degree of male-male and female-female home range overlap observed in this study indicates that residents of the same sex occupied mutually exclusive ranges. Similar range separation of adjacent same-sexed individuals also has been reported elsewhere in the range (Bailey 1972 in Idaho, Brittell et al. 1979 in Washington, Buie et al. 1979 in South Carolina). Erickson and Hamilton (1980) in Missouri, Lawhead (1978) in Arizona, and Lembeck (1978) in California reported that males showed substantial range overlap while females did not, whereas in another California study both males and females showed substantial range overlap (Zezulak and Schwab 1979). In contrast, male and female ranges usually exhibit extensive overlap (Berg 1979, Brittell et al. 1979, Buie et al. 1979, Erickson and Hamilton 1980, Karpowitz and Flinders 1979, Kitchings and Story 1979, Marshall 1969, Miller 1980). In this study the home range of a female usually was contained within a larger male range. This configuration apparently reflected a persistent, loose pair bond, the individuals not only associating together for mating but also maintaining social integration during the nonbreeding season. Such a relationship appears to fit Kleiman's (1977) definition of facultative monogamy. In the cases in which a single male home range overlapped the

ranges of more than one female, it tended to include a greater share of the range of one female than of the others, suggesting a closer relationship with some females than others. Male-female associations involving more than one female occurred during the period of increased mortality, particularly among males, and may have reflected the shortage of males and instability of the population at that time.

In addition to increased accessibility of a mate, the observed tendency of association between a single male and female could have other adaptive advantages. The male may serve to protect food and other resources for the female and young within his range by inhibiting encroachment by other males. The male may also aid in protecting young from predation, including cannibalism by other males (Crowe 1974, Erickson 1955). In this study, the increased presence of an adult male (M8) in the areas frequented by the female (F1) and her young litter within his home range following visits by the male (M6) from an adjacent territory may be an example of a resident male attempting to prevent an outsider from disturbing the young litter of his mate. As suggested above, the male also may encourage dispersal of older juveniles from their natal range thus reducing possible competition for food for the next litter and contributing to the dispersion of the population. Marshall's (1969) observation of an adult and a juvenile male bobcat growling and spitting at each other (possibly over food), with the larger male pursuing the smaller one, also may have been a case of an adult male interacting with a juvenile near dispersal age. Although studies in recent years have produced no evidence that male bobcats play a direct role in care of offspring, Young (1958) alleged that both parents may bring food to the young before and after the den is abandoned when kittens are about 2 months old.

As noted by McCord and Cardoza (1982), present evidence indicates considerable flexibility in bobcat social structure. This applies to felids in general (Eisenberg 1986). Although some of the reported variation in spatial relationships may be due to differences in methods of study or insufficient data, actual differences within the same population at different times and between populations in different regions or habitats probably reflect variation in food resources, mortality patterns, weather conditions, and other ecological factors. Although specific correlations between bobcat social organization and demographic characteristics or environmental conditions remain to be demonstrated, it is possible that the tendency for males and females to be associated in pairs is characteristic of stable populations with a good prey base.

Female-Young Behavior and Home Range Use.— Five family groups involving three females and five litters were monitored until the young had apparently dispersed. These young associated with their mothers for 8-11 ($X = 9$) months. For the first 1.5-2 months after birth, while the kittens were immobile, the movements of the mothers were more restricted, although they

continued to use their entire home range. The most detailed record of adult female movements shortly after parturition was obtained for F1 (Fig. 5C, 6), who was monitored intensively from 8 to 14 April 1981 after birth of a litter on or about 1 April. During this period, she covered the entire area she used prior to parturition and after the young were 3-4 months old (Fig. 6). On two afternoons she made short trips to the nearest range boundary, and on four nights between 1800 and 0100 hr she made long distance movements that involved travel over most of the other portions of her pre-parturition range. On one of these extended excursions, she rested for about 30 minutes at a site 1 km from the natal den area then returned directly to the den.

Maximum distances moved by adult females from natal and secondary den sites during the first two months postpartum usually occurred in late afternoon and at night. Because calculations of home ranges of females F1, F9, and F11 with newborn young during the period of 1 May-19 July 1980 were based largely on radio locations during morning and afternoon, their observed home ranges (Table 5) during this interval are probably underestimates of the areas actually used.

The mothers apparently carried the kittens short distances to new rest sites every 1-6 days, as no kitten tracks were observed where adults crossed sand roads between consecutive known sites. The best example of this pattern of rest-site shifting was obtained for F9 (Fig. 7) during the first 30 days after the birth of her 1980 litter. In this period she used eight sites an average of four (range = 1-6) days each. Mean and extreme distances moved between sites were 0.3 km and 0.1-0.4 km, respectively. The total area within the polygon defined by the perimeter rest sites was about 0.4 km². At least six other sites in the immediate vicinity were used during the second month after the birth of the litter. The semi-tame female (F1) also moved her litters about in a similar fashion. For example, at least six sites were used during the first 51 days after the birth of her May 1980 litter. All sites were within an area of about 0.3 km². She apparently made her first long distance movement (1.8 km) with the kittens on 22 June in response to disturbance by farm machinery in the immediate vicinity of the rest site used during the preceding few days. Winegarner (1985b) also observed similar shifts in rest sites of F1 with young about 1 month old in 1982.

Adults with kittens ranging from about 2 to 4 months of age also used rest sites for periods of 1-6 days. The rest sites during this period tended to be more generally dispersed throughout the adult's range than earlier. The kittens sometimes accompanied the mother on short excursions in the vicinity of the rest site. On several occasions females with kittens over 2 months of age were observed carrying food to the rest site area. The family usually travelled between rest sites with the mother in the lead and the kittens following single-file. During this period the mothers continued to make independent excursions along the boundaries of their range and occasionally used a rest site

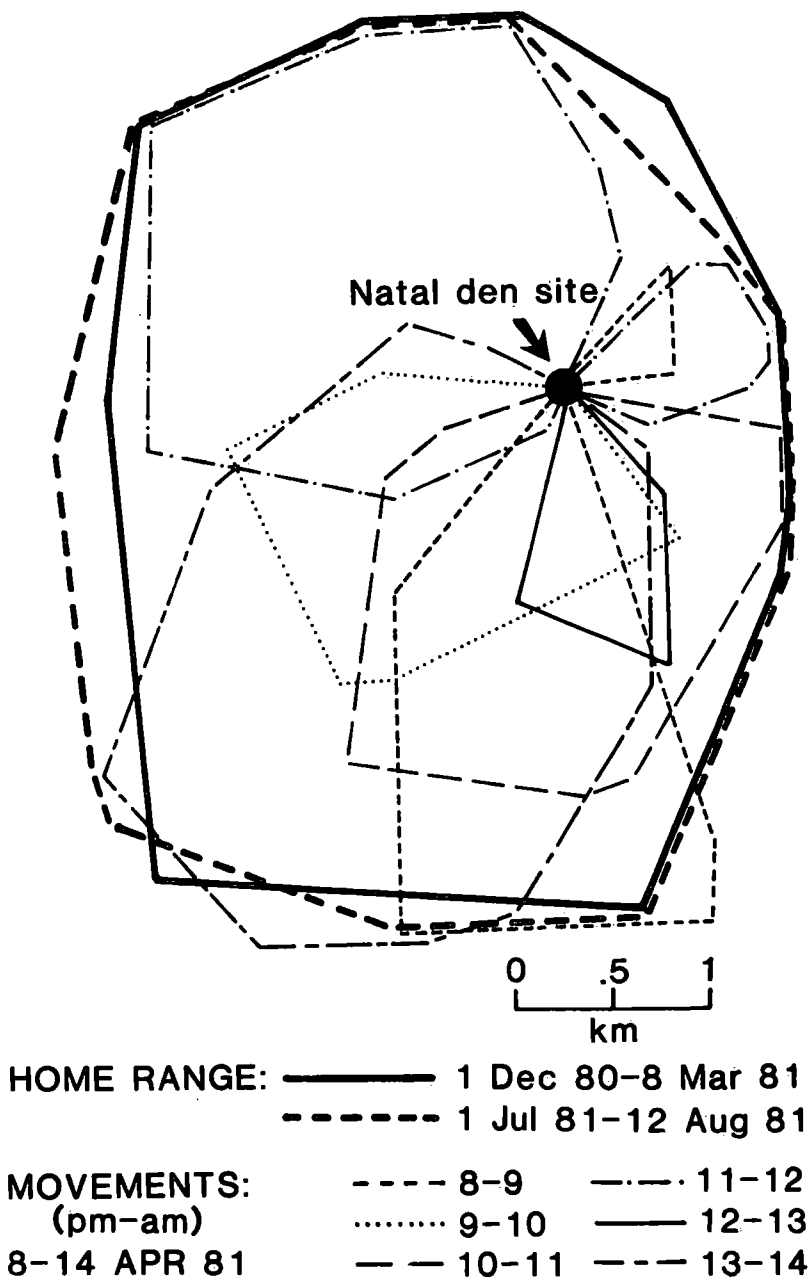


Figure 6. Movements of adult female F1 over a 6-day period following birth of a litter on or about 1 April 1981.

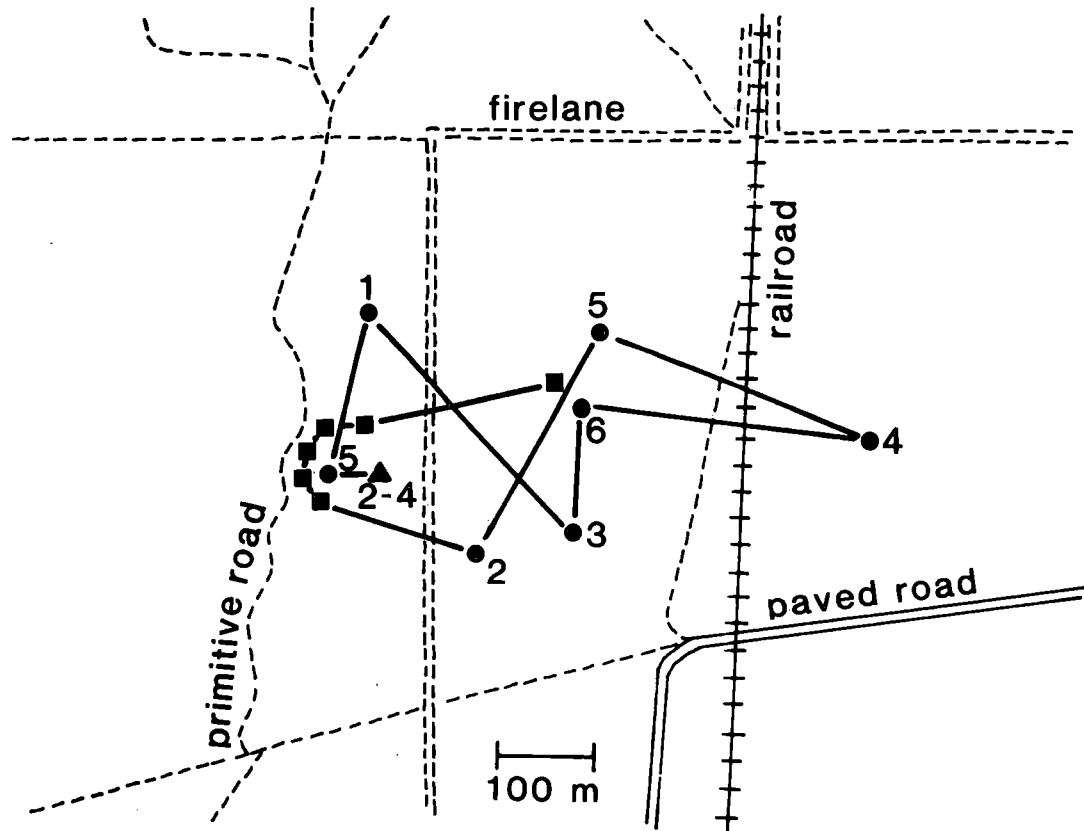


Figure 7. Pattern of den site use by an adult female (F9) following birth of a litter in April 1980. Key to symbols: triangle = natal den site; numbered solid circles = secondary den sites used the first month and number of days spent at each site based on daytime resting fixes of the adult; squares = presumed secondary den sites on six days during the second month.

separate from that of the kittens. In some instances the adult rest site was on the opposite side of the range from that of the young.

Females with kittens over 4 months old continued independent movements throughout their ranges but also were frequently accompanied by kittens when traveling. These family group movements often included trips along home range boundaries. The adults continued occasionally to rest separately from the kittens. When adults were not present, kittens made independent excursions around the general area of the rest site. On several occasions when she had kittens 5 months of age or older, F1 was recorded (visual observations, tracking) traveling without her full litter, indicating that young at this age may not remain together in the same area while the female is away. By 5-7 months of age, kittens traveling with the mother often walked abreast or preceded her along the route. Signs of apparent play were most noticeable during this period. Based on tracks, one young would frequently move ahead along a travel route and then "ambush" the others when they came past. Mothers also participated in such play, as recorded at night on 16 September 1979. F1 and her three young about 5.5 months old were observed for 20 minutes in the light of vehicle headlights as they engaged in mock attacks on each other. The juveniles were intent on ambushing one another, one jumping on the back of another from behind a bush as it walked past. The attacks were usually followed by a short chase, with either animal being the pursuer. A kitten also would occasionally jump on the mother who would then chase it. The family moved slowly along as they engaged in this play. Radio fixes, tracks, and sightings indicated that young made occasional contact with adult males beginning about their fifth month.

From about 7 months until they dispersed, juveniles were increasingly independent of the mother. The family did not use a given rest site for more than a day or two, and successive sites were often located on opposite sides of the home range. The family group frequently traveled throughout all parts of the range. Juveniles also wandered about more on their own, their individual rest sites being up to 0.5 km apart. On several occasions when her older young were resting at scattered sites, F1 was radiotracked as she moved through the area to round them up. On 6 July 1981, L. Saul (pers. comm.) observed F1 giving 23 sheep-like "m-a-a" vocalizations in a 2-minute interval after which three or four young appeared and followed her as she left the area. The vocalizations were distinctly audible from a distance of about 60 m. On occasion, when a mother was moving about the range with some of her young, others would be located in a distant part of the range. Such instances became increasingly frequent as the young neared the age of dispersal.

In one case, F1 and her two young born in 1980, the juveniles apparently restricted their movements to separate areas at the periphery of the adult's range from about 10 months of age (January 1981) until disappearing 3 or 4 months later. The only occasion during this period when they were recorded

elsewhere in the natal range was on 22 February when their tracks were found together in a region of the adult range 1 and 3 km from their respective areas. We last observed tracks of the juveniles within the mother's range in mid-April, and Winegarner (1985a) could not find their tracks in June and July. The adult gave birth to a new litter on or about 1 April, indicating that females may mate and bear young while juveniles of their previous litter are still within the natal range. Adult female F1 also was apparently still associated with one or more juveniles of her April 1981 litter in December 1981 after the birth of a new litter in mid-October, based on observations of her tracks accompanied by those of a young individual. Evidence for breeding while still associated with young of the last litter was not confined to the semi-tame female. F9 was observed on 30 November 1980 with one of her two kittens born in mid-April and gave birth to her next litter in early January 1981. Based on a 2-month gestation period (McCord and Cardoza 1982) mating probably occurred in early November.

Winegarner (1985a) also monitored female F1 and her older young in 1981 (see above) by means of tracks. She believed that the mother actually abandoned the portions of her range occupied by the juveniles, then reoccupied the areas following dispersal of the young. She concluded, therefore, that dispersal of juvenile bobcats is preceded by "a period of solitude" in the natal home range and this "temporary tenure" of the young in the mother's range "insures that the home range is occupied." Although she did not elaborate as to why establishment of exclusive home ranges by young at the edge of the adult female's range is necessary to insure its occupancy, she may have assumed that breeding females during late pregnancy and early postnatal care of the young reduce their home range and that the presence of their older young at the periphery helps to hold the area against other bobcats so that the female can reoccupy it when her new litter is old enough to travel with her. Our combined radiotracking and trailing data do not support this interpretation. Although the female tended to visit the periphery of her range less frequently and for shorter periods for about 2 months after the birth of her litter in April, radio fixes regularly placed her in the area where the activity of the juveniles was concentrated during this period. In addition, by searching for her tracks in areas where she had been radio located the previous night, it was confirmed that she continued to mark her former range boundary in these areas. Although the last contact between F1 and her old juveniles, based on close proximity of adult and juvenile tracks, recorded by Winegarner (1985a) was in late January, we observed evidence of the adult and one or both young in the same area on two nights in late February. On one of these occasions the female and both young were in an area remote from the areas in which the young were usually found (see above). Our data, therefore, indicate that the young did not establish exclusive home ranges prior to dispersing from the natal area and suggest that the young probably did not play a significant role in

maintaining the boundaries of the adult female's home range. Even if young on the periphery of the adult range were effective in preventing encroachment on the adult's range by other bobcats, only a relatively small fraction of the total range perimeter would be "protected." The tendency of the young to concentrate their activity at the periphery of the natal range during the late pregnancy and postnatal period of the mother may have been due to the combination of their age and the increased aggressiveness of the mother during the breeding season. In this connection, Winegarner (1985a) once observed the semi-tame female attacking one of her older young when it returned to "her domain."

There are few comparative data on movements of bobcat family groups in other parts of the geographic range. The best description is that of Bailey (1979) for Idaho bobcats. General patterns in the movements of Florida kittens were similar to those observed in Idaho in that movements were generally restricted to den areas until the kittens were past 3 months of age. After this age, more of the range was used by the offspring. In South Carolina, Marshall (1969), found that an older juvenile used the entire range of its mother, and Kitchings and Story (1979) reported the same behavior for a juvenile in eastern Tennessee.

Few data were obtained on dispersal and establishment of home ranges by juveniles, but we believe that most moved out of the study area. However, one apparent case of a male (M6) and a female (F8) of the same litter becoming established as a breeding pair in the natal range was recorded. These presumed young of F3 remained in the mother's range after the deaths of the overlapping adult males (M1, M3) and abandonment of the range by the mother. With time, both individuals extended their movements beyond the natal range, and the female had litters in spring 1980 and 1981. The northward expansion of the male's range apparently coincided with the disappearance of an unmarked male in that area and probably resulted in overlapping part or all of the range of his mother (F3), who had shifted her range into the area earlier (Figs. 4D-5D).

Little information is available on dispersal and subsequent home range establishment of young bobcats in other geographic regions. Bailey (1974) in Idaho noted that young bobcats appeared to avoid settling in areas occupied by residents and recovered five tagged kittens 1-2 years later as adults from sites outside the study area, although he had no data on their movements during the intervening period. Two subadults radiotracked in South Carolina by Griffith et al. (1980) abandoned their initial activity areas (in the natal range?) in early spring and began a pattern of movements involving temporary localization of activity for varying periods of time. They concluded that their data supported a model of subadult bobcat dispersal characterized by "nomadic search for unoccupied, resource-adequate home range sites," as implied by Bailey (1974). The tendency of the subadults monitored by Griffith et al. (1980) to use

temporary activity areas in the course of their long-term movements is reminiscent of the localization of movements within the natal range of older juveniles prior to their disappearance observed in this study. This behavior may be a normal precursor to dispersal of young bobcats from their mother's home range. The data for male M7 (see above), although sparse, suggest that his movements might also have followed the pattern of temporarily localized activity in the course of long-distance wandering exhibited by the subadults studied by Griffith et al. (1980).

Daily Travel

Adult males tended to move greater distances from one day to the next than did adult females, and juvenile movements were more restricted than those of adult females (Fig. 8). The average day-to-day distance moved by all bobcats was 1.6 km. Means and ranges of day-to-day movements of adult males, adult females, and juveniles were 2.1 km (0-7.6), 1.4 km (0-6.6), and 1.0 km (0-4.2), respectively. Mean distances moved by individual males were significantly greater than those of adult females ($U_{6,7} = 4.5, p < 0.05$, 2-tailed), and juvenile means were significantly lower than those of adult females ($U_{5,7} = 2.5, p < 0.05$, 2-tailed). The ratio of mean adult male to mean adult female day-to-day movements (1.5:1) was roughly proportional to the ratio of their respective mean overall home range sizes (1.8:1).

Longer day-to-day movements of males compared to females also were reported in other southeastern studies. Distances were 8.7 km for males versus 6.3 km for females (ratio 1.4:1) in South Carolina (Buie et al. 1979), 4.5 versus 1.2 km (ratio 3.8:1) in Tennessee (Kitchings and Story 1979), and 4.4 versus 2.9 km (ratio 1.5:1) in Louisiana (Hall and Newsom 1976). Ratios of male to female home range sizes in these studies were 2.0:1, 3.7:1, and 4.9:1, respectively. Straight-line day-to-day movements of males (2.2 km) and females (1.4 km) in Louisiana (Hall 1973) were about half the summed successive distances between captures (Hall and Newsom 1976), but the ratios were similar (1.6:1 vs. 1.5:1).

The same general correspondence between ratios of day-to-day movements and home range size of males and females also has been found in most studies in other parts of the range. In Minnesota, the ratio (1.6:1) of mean week-to-week distances moved by adult males (4.3 km) and adult females (2.6 km) was the same as the home range size ratio. Mean day-to-day distances moved by male and female adults in Idaho were 1.8 km and 1.2 km, respectively, a ratio of 1.5:1 compared with 2.2:1 for mean home range sizes (Bailey 1972). Lawhead (1978) reported mean day-to-day movements of 1.2 km for adult males and 0.9 km for adult females (1.3:1), while the male to

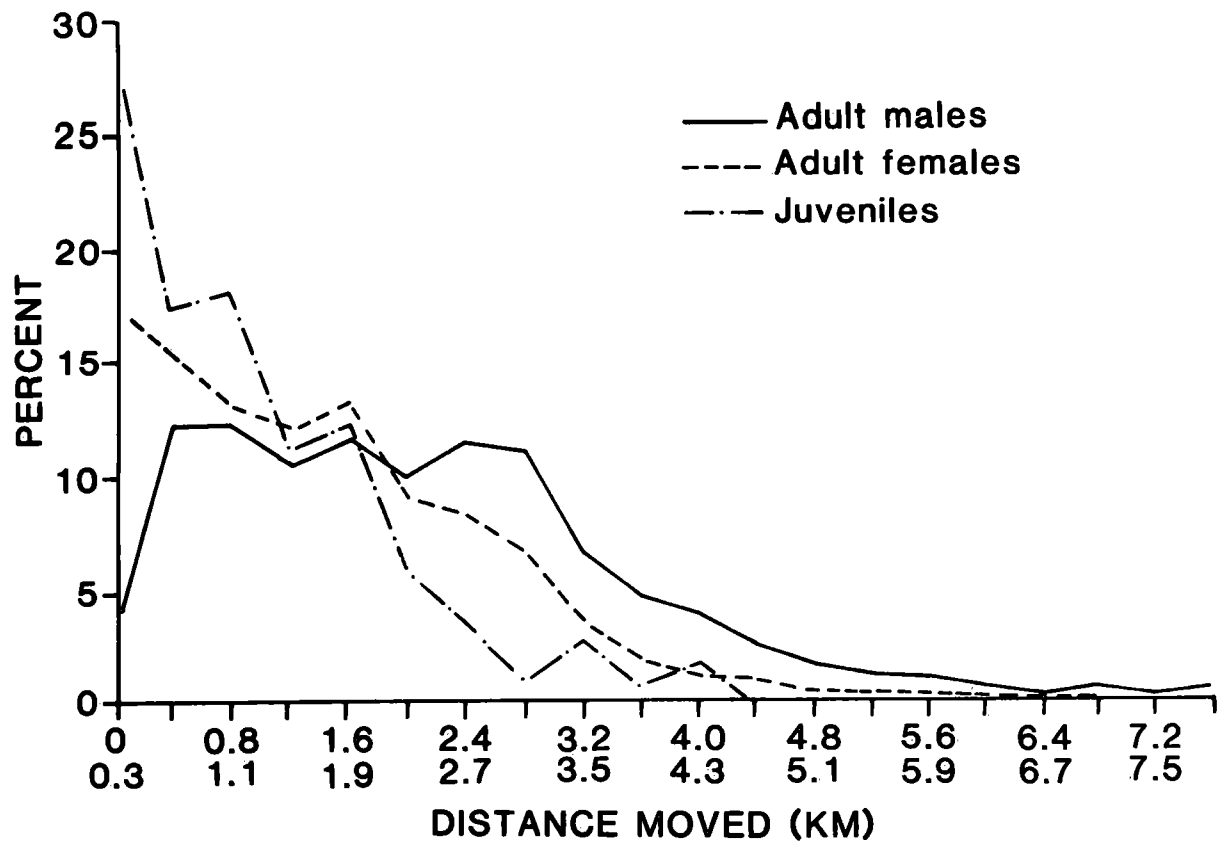


Figure 8. Percentage distribution of day-to-day distances moved by adult and juvenile bobcats.

female mean range size ratio was 2.1:1. The general trend of a lower male to female movement ratio than home range ratio shown by these data indicates, as suggested by the authors, that although males tend to have larger ranges than females, females tend to move around within their ranges proportionately more than males.

The means of day-to-day movements of adult males from December to February, March to May, June to August, and September to November were 2.5, 1.9, 2.1, and 2.1 km, respectively. Corresponding values for adult females were 1.6, 1.4, 1.2, and 1.4 km. Mean daily juvenile movements in fall, winter, and spring were 0.9, 1.1, and 1.3 km, respectively. Mean day-to-day movements of adult males during December-February were significantly greater ($U_{45} = 2.5, p < 0.05$, 1-tailed) than those during March-May but did not differ from other seasons. The only significant seasonal difference in adult female movements was between December-February and June-August ($U_{56} = 5.5, p < 0.05$, 1-tailed). Small sample sizes prevented statistical comparisons of juvenile seasonal movements. Daily distances moved by juveniles 8-10 months old averaged 22% greater than those of juveniles 5-7 months old ($U_{35} = 6, p < 0.05$, 1-tailed), reflecting the greater amount of travelling of older young with the mother.

In this study, day-to-day distances moved by adult females were least during the summer months (June-August) when the females had young kittens. Late spring to early summer reduction in female movements and/or home range size also has been reported by other workers (Bailey 1972, 1979, Berg 1979, Griffith and Fendley 1986, Kitchings and Story 1979, Lembeck 1978). As noted above, reduction in daily movements of females with young litters does not necessarily reflect a decrease in home range size as some workers have concluded. Intensive monitoring of females with small young in this study showed that they continued to use their entire home range but in such a way as to reduce the chances of their being detected in peripheral areas.

More extensive daily movements of both males and females from December to February were correlated with the main period of juvenile dispersal. Both breeding season activities and the mobility of older offspring probably influenced the movements of the females. Kitchings and Story (1979) reported that adult male bobcats moved longer distances in winter, with no apparent changes in home range sizes. In contrast, Bailey (1972) found that adult bobcats of both sexes moved least in fall and winter in Idaho. Among the possible causes of the apparently different trends in extent of movement in winter in southeastern and northwestern bobcat populations may be the more severe winter weather in the latter region, which may cause bobcats to restrict their movements to certain areas.

Activity

Diel activity patterns of adult and juvenile bobcats based on 4966 locations classified as active or inactive are shown in Figure 9. Sample sizes for adult males, adult females, and juveniles were 1716, 2859, and 391, respectively. Records of juvenile activity were not obtained during summer months or for the time period 0300-0600 hours in other seasons. However, for the combined data, each sex and age group had about the same proportion of observations for each time interval.

Bobcats were primarily crepuscular and nocturnal in their activity but also were occasionally active during the daylight hours. Greatest activity occurred between 1800 and 2400 hours and least activity between 1200 and 1500 hours, with 91% of the locations during the first interval representing moving individuals compared with 17% during the second. There was some suggestion of reduction in activity between midnight and 0300 hours (68% of fixes active) followed by a slight increase from 0300 to 0900 hours (78% of fixes active). There were no marked differences in the activity patterns of adult males, adult females, and juveniles based on the combined data for all seasons.

In summer, males tended to rest more during the daylight hours than in other seasons (Fig. 10). The higher frequency of inactive locations between 0900 and 1500 hours during summer (June-August) compared with other seasons was significant ($X^2 = 30.44$, 3 df, $p < 0.01$). Females (Fig. 11) were less active from 0300 to 0900 during the period March-May and from 0900 to 1500 hours in the interval from June to August than during the corresponding times in other seasons (0300-0900: $X^2 = 4.26$, $p < 0.05$; 0900-1500: $X^2 = 25.68$, 3 df, $p < 0.01$). However, the reduction of midday activity of females in summer was less pronounced than that of males.

The overall activity pattern of bobcats in south-central Florida agrees closely with that observed in northeast Florida by Progulske (1982). Data from other regions of southeastern United States also indicate that activity is mainly crepuscular and nocturnal but may also occur during the day. Hall (1973) reported peaks of movements in summer from 1500 to 2300 hours and from 0300 to 0700. Buie et al. (1979) found peaks in activity in fall, winter, and spring to occur from 0400 to 1000 and from 1800 to 2400. Miller (1980) reported least activity from 0700 to 1500 with a second, less pronounced, rest period from 2200 to 0200.

The reduced daytime activity of adult males during June through August in this study probably reflects a response to high day-time summer temperatures. Day-time rest sites were usually in dense closed-canopy habitats, which were about 3-5°C cooler in summer than open canopy areas. In South Carolina, Buie et al. (1979) also noted that activity was less bimodal during winter than in early spring and in fall, suggesting greater activity during winter

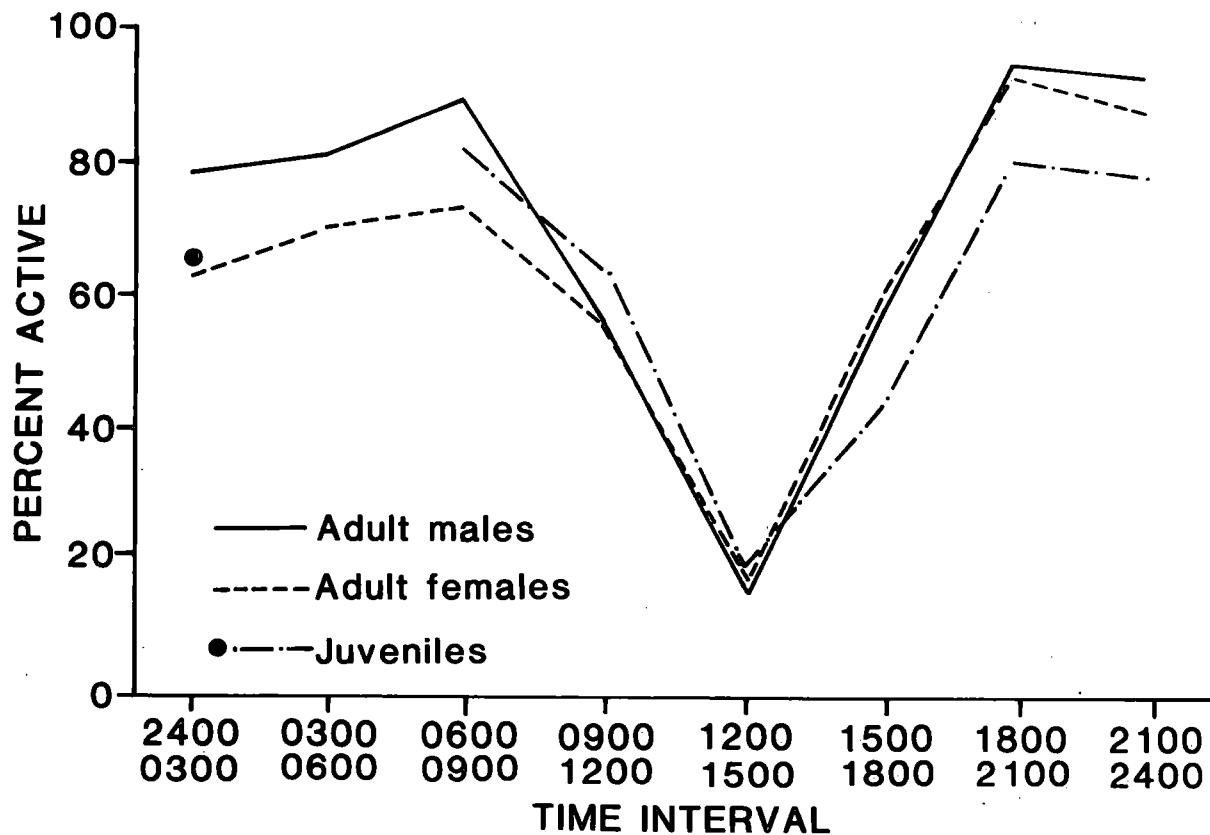


Figure 9. Activity patterns of adult and juvenile bobcats based on combined data for all seasons from April 1979 to December 1981.

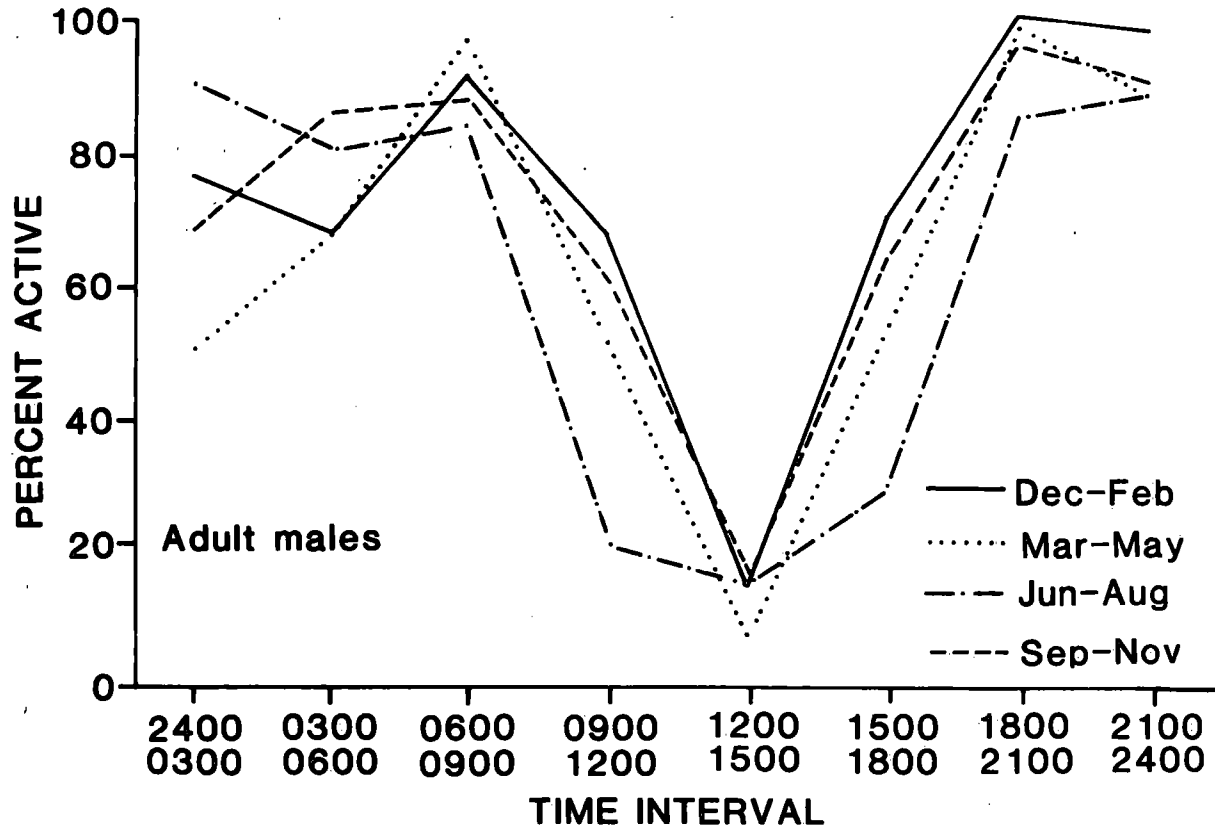


Figure 10. Activity patterns of six adult male bobcats during different seasons from April 1979 to December 1981.

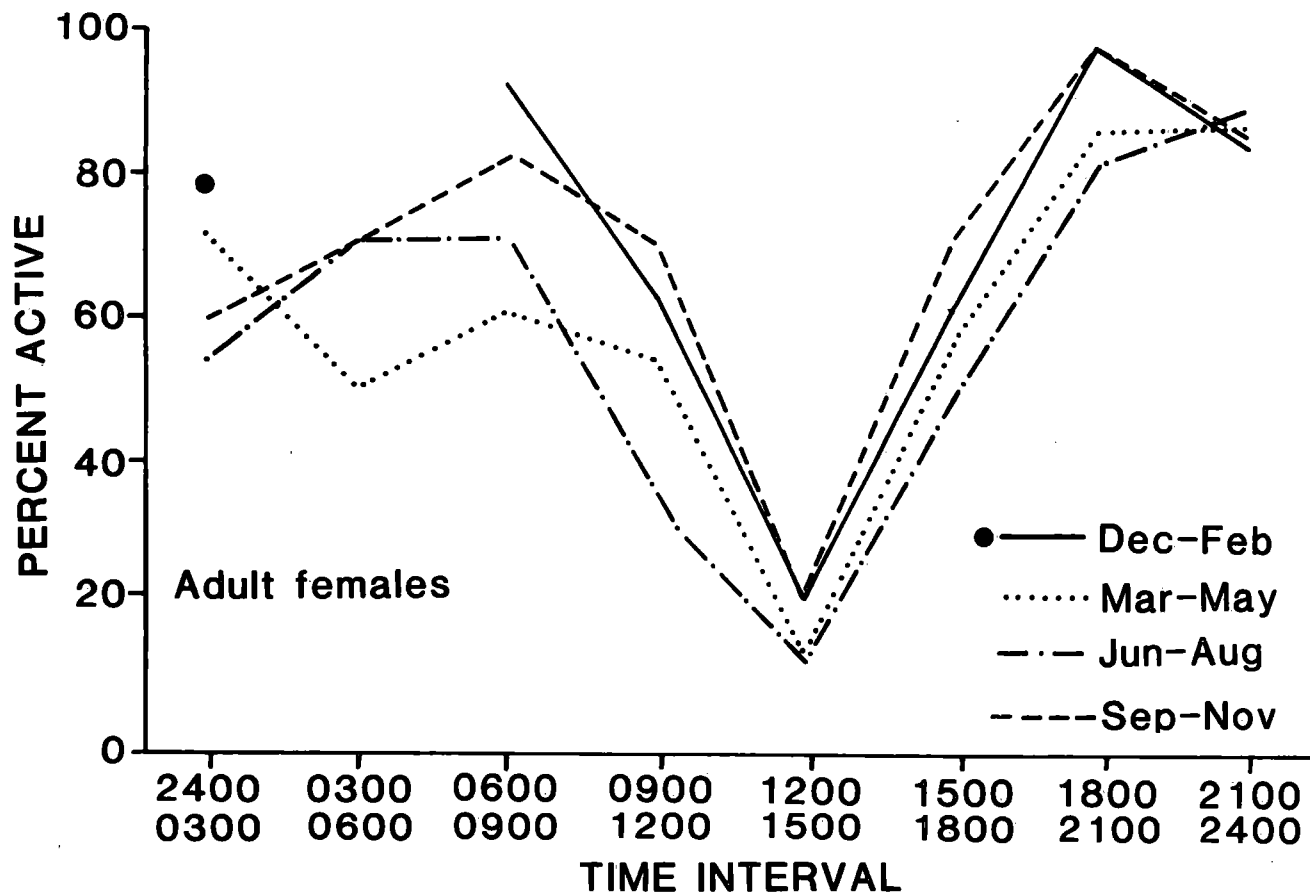


Figure 11. Activity patterns of seven adult female bobcats during different seasons from April 1979 to December 1981.

daylight hours when it was warmer. Bailey (1972) stated that bobcats in Idaho were inactive under conditions of extreme winter weather and that the use of caves was important in water conservation during hot-dry summer months.

Seasonal differences in activity patterns of adult females in south-central Florida appeared to be linked more to the needs of their offspring than to weather conditions. Females with recently born young spent much time with the young, resulting in a decrease in activity in late-night and early-morning hours during the first month following birth of litters in spring. In summer, when young were past the nursing age, females tended to be more active during daylight hours than were males. This difference in activity levels may reflect more intense hunting effort required by the increased nutritional needs of the family unit. The changes in adult female activity pattern correlated with age of the young were clearly illustrated by the data for F1, whose activity was closely monitored from the birth of one of her litters in spring, until summer when the young were 5 months old (Fig. 12). Even though she was occasionally fed, this female usually became very thin when her kittens were 3-7 months of age, supporting the suggestion that energy demands of older young may force females to hunt more during the day. Hall (1973) also reported higher levels of activity for females than for males during daylight hours of summer months.

Habitat Use

Home ranges of all bobcats except two adult females (F10, F11) included each of the eight habitat types recognized (Table 6). Closed canopy xeric pine-oak habitat was not present in the ranges of F10 and F11, and one of them (F11) also had no man-occupied areas within her range. Xeric pine-oak association was the best represented natural habitat in bobcat home ranges. The average proportion of the closed canopy phase contained within individual ranges was double its relative abundance on the study area as a whole. Although most habitats were found in all home ranges, their proportions in different ranges were highly variable. In general, the relative amounts of a given habitat contained in home ranges varied less among adult males than among adult females. Adult male ranges also tended to contain more man-modified habitats than did the ranges of adult females, although the difference was not significant ($U_{57} = 8, p > 0.05$, 2-tailed).

Most bobcats did not use habitats in their ranges in direct proportion to their availability (Table 7). There were no consistent trends in intensity of use of particular habitats. However, there was an overall tendency for relatively more use of natural than man-modified habitats. Although adult males had relatively less natural habitat area within their home ranges than did females,

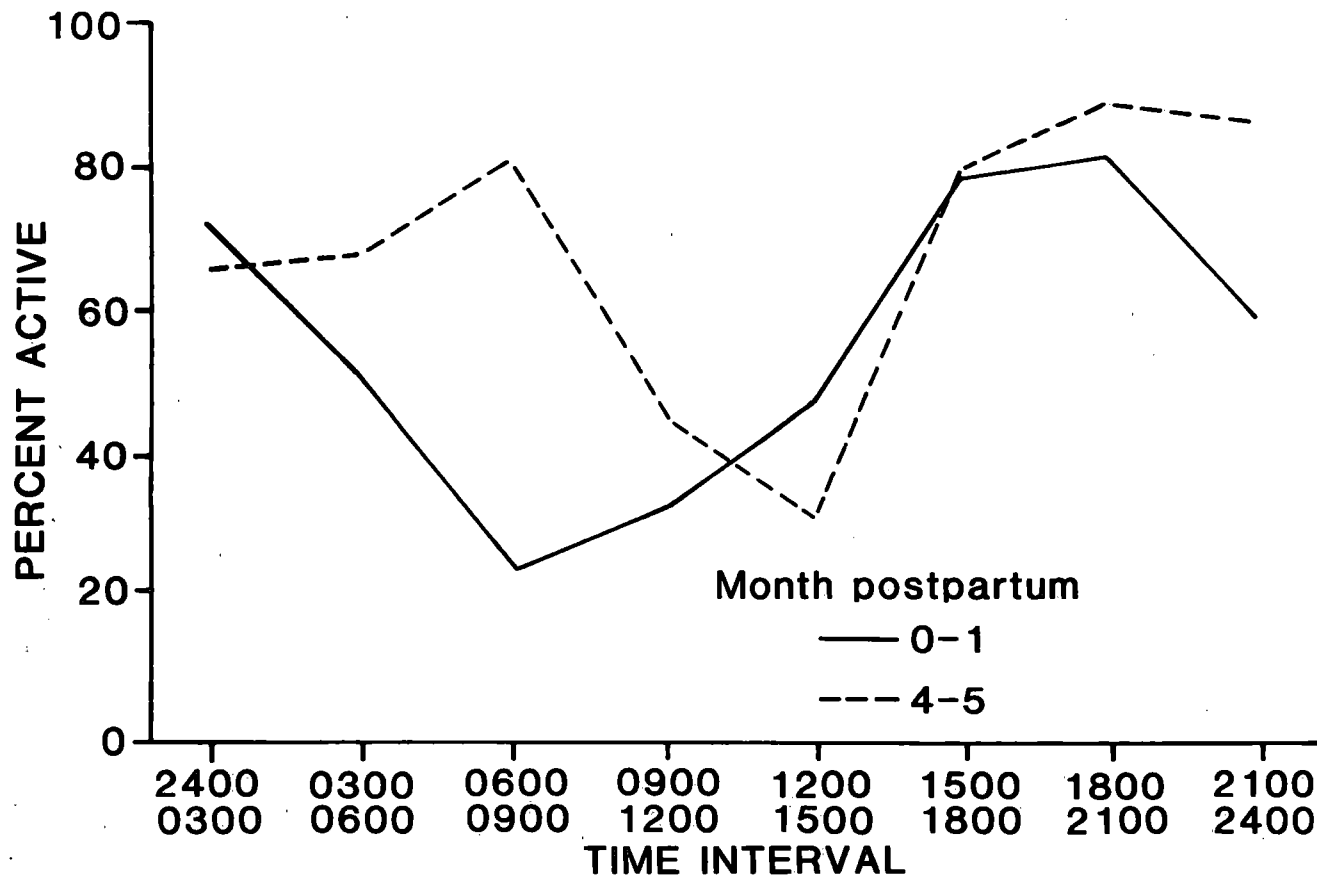


Figure 12. Activity patterns of an adult female bobcat (F1) during the 1st, 4th, and 5th months after birth of a litter.

Table 6. Percentage distribution of habitat types within overall home ranges of adults and juveniles (observed area of movements within mother's range). Habitat abbreviations as follows: XO = xeric pine-oak, open canopy; XC = xeric pine-oak, closed canopy; FW = flatwoods; BH = bayhead; CN = citrus grove or tree nursery; IP = improved pasture; OF = old field; MO = man-occupied. Percentages of each habitat type in the area of all ranges combined are given below habitat headings in parentheses.

Individual	Number of Locations	Natural					Man-modified				
		XO (28)	XC (4)	FW (21)	BH (7)	Total (60)	CN (16)	IP (12)	OF (10)	MO (2)	Total (40)
ADULT MALES											
M1	358	29	13	23	4	69	8	12	8	2	30
M2	150	30	5	18	14	67	19	6	6	3	34
M3	116	25	14	6	6	51	40	1	7	2	50
M6	422	27	13	7	3	50	38	3	7	3	51
M8	367	23	2	29	7	61	1	28	11	0.2	40
Mean	283	27	9	17	7	60	21	10	8	2	41
ADULT FEMALES											
F1	581	34	4	27	3	68	2	16	14	0.3	32
F3	167	14	44	10	1	69	22	1	2	7	32
F4	518	32	2	23	12	69	17	6	6	2	31
F8	430	22	28	10	5	65	25	1	6	3	35
F9	403	45	1	23	1	70	11	11	6	3	31
F10	34	34	0	27	12	73	2	12	11	2	27
F11	154	13	0	35	17	65	6	4	25	0	35
Mean	327	28	11	22	7	68	12	7	10	2	32
JUVENILES											
M4	163	38	5	34	4	81	3	13	4	1	21
M5	19	12	63	7	1	83	10	0.2	5	3	18
F5	51	38	4	36	5	83	1	12	4	1	18
F6	100	37	3	36	4	80	1	14	5	1	21
Mean	83	31	19	28	41	81	2	9	5	2	19

they averaged more intensive use of it. Both sexes tended to use open canopy xeric pine-oak habitats less frequently than other natural habitats. Among man-modified habitats, adult males used improved pastures more heavily than did females, but the difference was not significant ($U_{5,7} = 7, p > 0.05$, 2-tailed). Most of such utilization involved crossing pastures at night when traveling between areas of natural vegetation.

With the exception of semi-tame female F1 who was frequently located in the vicinity of the dwelling where she was fed, females were associated with man-occupied habitats less than males. Juveniles showed more intensive use of certain habitat types than did adults. For example, only one adult (M6) had a ratio over three for use of any habitat, whereas four out of the five juveniles had one or more ratios of habitat use ranging from 3.04 to 12.65. Two (M4, F5) of the four juveniles showed unusually intense association with man-occupied habitats. These were kittens of the semi-tame female, and their high use of the man-occupied category reflects visitations of the family group to the dwelling until the kittens were about 8 months of age. Although F6 was also a member of this litter, her relatively lower association with man-modified habitats is explained by the fact that she was the last of the three siblings captured and thus a greater proportion of the data on her movements was obtained when the young were older and less frequently accompanied the mother to the dwelling.

Progulske (1982) presented data on habitat utilization by several bobcats in northeastern Florida. In his study area, habitats with medium to dense understories were utilized more than habitats with open understories, and bottomland hardwoods were the most preferred vegetation association. Bobcats tended to avoid meadows and other open man-modified habitats but not pine plantations, which comprised a small fraction (8%) of the study area.

All known den sites of females with young in this study were in natural vegetation associations, usually thick patches of saw palmetto and dense shrub thickets. Winegarner (1985b) also recorded 1-month-old young going in and out of a gopher tortoise (*Gopherus polyphemus*) burrow. Adults without young also preferred dense palmettos or shrubs for rest sites. In Louisiana, Hall (1973) also found a preference for heavy cover as rest sites. In the present study, offspring of females other than F1 apparently were not exposed to man-modified habitats until about 2 months of age, when they began following the mother to different rest areas within her range.

Although radiotracking alone was seldom accurate enough to delineate the exact travel routes of individuals being monitored, a combination of radiotracking, tracking on foot, the placement of scats and scrapes, and occasional visual observations indicated that bobcats generally moved about their home ranges along firelanes, roads, footpaths, animal trails, or railroad tracks or followed natural openings through the vegetation rather than bushwacking through dense cover. For example, within the home range of

Table 7. Ratios of proportions of locations in various habitat types to the proportions of the respective habitats in overall home ranges of individual bobcats. Abbreviations of habitat types as in Table 5.

Individual	Natural					Man-modified				
	XO	XC	FW	BH	Total	CN	IP	OF	MO	Total
ADULT MALES										
M1**	1.18	0.85	1.34	1.28	1.18	0.12	0.84	0.60	1.16	0.60
M2**	1.07	0.59	1.17	1.06	1.06	0.55	1.21	1.17	1.72	0.88
M3**	0.73	1.80	1.51	1.99	1.28	0.53	5.46	0.87	2.52	0.73
M6**	0.58	2.90	1.62	1.42	1.39	0.49	1.56	0.69	1.25	0.62
M8**	1.38	2.80	1.16	1.03	1.27	0.19	0.47	0.80	5.58	0.59
Mean	0.99	1.79	1.36	1.36	1.23	0.38	1.98	0.83	2.45	0.68
ADULT FEMALES										
F1**	0.99	2.76	1.20	1.63	1.22	0.33	0.30	0.50	13.23	0.52
F3**	0.50	1.66	0.33	0.31	1.22	0.52	0.09	0.67	0.54	0.54
F4**	0.90	0.76	0.90	1.88	1.06	0.78	0.60	0.85	2.27	0.86
F8**	0.68	1.81	1.10	1.36	1.29	0.28	2.31	0.39	1.27	0.47
F9**	1.26	0.98	1.22	1.24	1.24	0.31	0.57	0.67	0.18	0.46
F10	0.80	-	1.08	0.61	0.88	1.08	0.62	2.23	0.02	1.34
F11**	0.42	-	0.95	0.71	0.78	0.76	0.55	1.73	-	1.42
Mean	0.79	1.59	0.97	1.11	1.10	0.58	0.71	1.01	2.92	0.80
JUVENILES										
M4*	0.85	3.61	1.05	0.52	1.07	0.12	0.33	0.45	12.65	0.69
M5	1.24	0.95	0.80	0.01	0.95	0.93	0.01	2.07	1.01	1.25
F5*	0.98	2.47	0.94	0.75	1.02	0.01	0.61	9.44	10.89	0.91
F6**	0.65	2.86	0.99	3.04	1.01	0.02	0.66	0.85	2.86	0.92
Mean	0.93	2.71	0.95	1.08	1.01	0.27	0.40	3.20	6.85	0.94

* Differences in observed and expected frequencies of locations significant at $P < 0.05$ level on basis of G-statistic

** Differences in observed and expected frequencies of locations significant at $P < 0.01$ level on basis of G-statistic

adult female F9 quadrats containing segments of roads, trails, railroad tracks, or paths ($n = 345$) comprised 64% of the total of 540 quadrats but contained 83% of active fixes ($X^2 = 39.58$, 1 df, $p < 0.01$). The cats also hunted along open travel ways, but usually carried prey into dense cover to consume it. Other studies in the southeastern United States indicated a similar predilection of bobcats for use of roads, paths, and other routes when traveling (Hall 1973; Miller 1980).

Marking Behavior

Frequency of Types of Marking Behavior.—Scrapes were the most frequent type of marking observed. Of 863 fresh scrapes recorded, 42% (363) contained feces, 57% (488) contained urine, and 1% (12) were empty. Scrapes were made by both adults and older juveniles. Young (a male and female) of the semi-tame female began making fecal scrapes when about 5 months old, at which age they began to accompany the mother to the periphery of her range. Prior to that age the young and mother tended to bury their feces in common sites in the vicinity of rest areas. Deposits of buried feces were also found in the vicinity of a rest site of another female (F9) with small kittens. Urine marking was done by both adults and juveniles. Among adults, both sexes were observed spray-urinating, but only females were observed squat-urinating without first scraping. A juvenile of unknown sex about 5-6 months old also was recorded squat-urinating without scraping. Fecal marking by adults and juveniles was frequent. Deposition sites were usually on paths, bare patches of ground, or mounds where the feces were conspicuous. Sometimes large numbers of feces accumulated at a particular site.

Scratching posts, trees or other places used by bobcats for sharpening their claws, also may have communicatory as well as maintenance functions. Only two scratching posts were encountered in the study area. Both were dead stubs. One of these was regularly used by the semi-tame female near the cottage at which she was fed.

Seasonal and Yearly Variation in Marking.—Counts of exposed scats in February, March, July, and August 1979 showed pronounced seasonal variation, ranging from 1.1 to 2.5 scats/km in February to 0.1-0.5/km in July and August. Similar seasonal trends occurred in the incidence of the three types of marking (Fig. 13). The peak of marking activity in this study coincided with the peak in breeding and period of high mobility of older juveniles, while reduced incidence of marking occurred during the period of late gestation and presence of young litters.

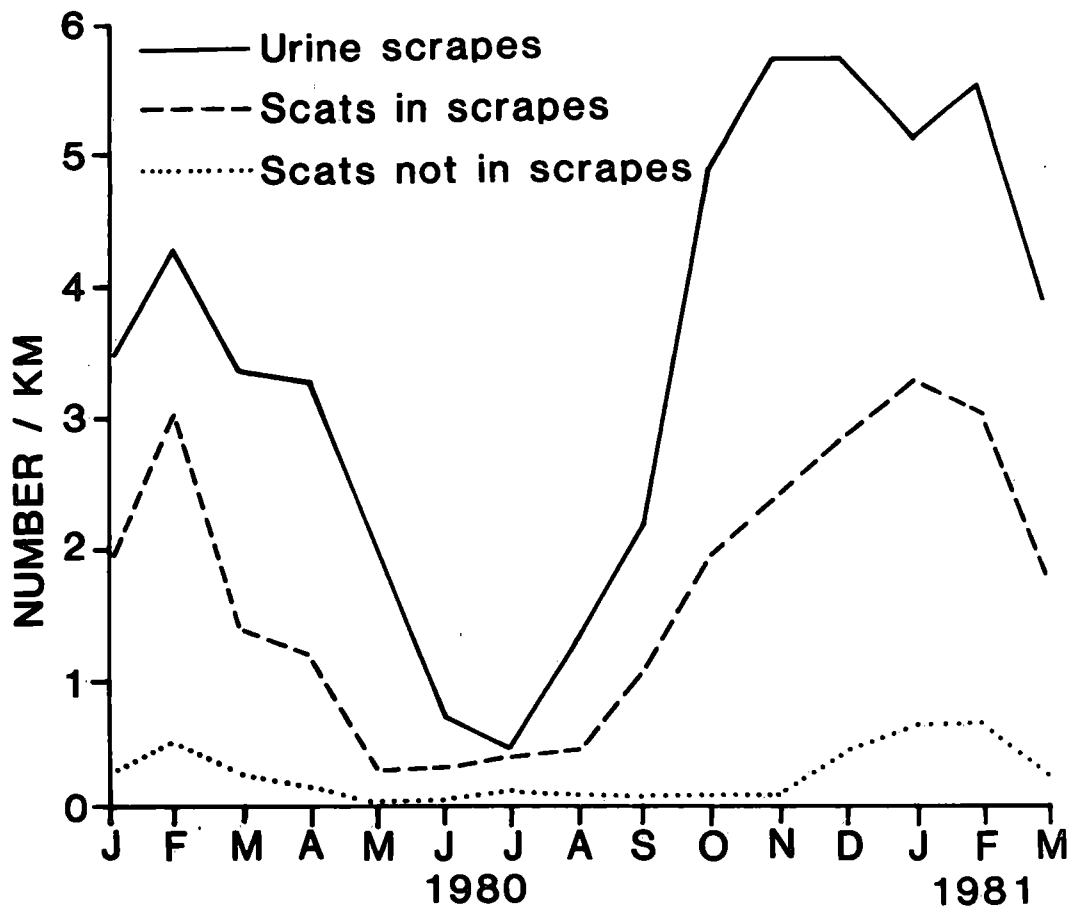


Figure 13. Monthly frequencies of three types of bobcat marking from January 1980 to March 1981.

The data suggest the following trends in marking behavior related to the reproductive cycle of the adult female: (1) Resident adult females with nursing kittens tend to bury their feces in the vicinity of the den site or elsewhere in their range but continue spray- and squat-urinating within the interior of their ranges and along range boundaries. Young kittens probably also bury feces near the dens. (2) Females and mobile juveniles 4-7 months old bury feces at common, frequently-used sites near rest areas within the female's home range and squat- and spray-urinate along travel routes. (3) At about 5-6 months of age, juveniles begin leaving feces exposed in scrapes and probably begin to urine-scrape as well as squat- and spray-urinate. (4) As juveniles continue to move about the mother's range and along its boundaries, they increasingly leave more feces exposed and make more urine and fecal scrapes. (5) About the time juveniles are ready to disperse (which often coincides with the breeding season of the mother), they are marking at their highest rate, as are adults. (6) After breeding and the dispersal of their young, resident adult females gradually decrease their rate of leaving feces exposed and increase their rate of burying scats so that by the time new litters are born fecal marking is minimal. (7) Intensity of adult male marking behavior parallels that of adult females and may be at least partly a response to the marking activities of the female and young.

The patterns of marking behavior of Florida females and young generally parallel those observed by Bailey (1972, 1979) in Idaho. Ontogenetic changes in marking behavior of the lynx are apparently generally similar to those in bobcats. Lindemann (1955) reported that European lynxes began to return to depositories to bury urine or feces at 100-120 days of age and initiated marking of ranges with exposed excrement at ages of 210-220 days. Saunders (1961) also noted that juveniles in North America switched from burying feces to leaving them exposed as they grew older and thus began marking like adults.

Few comparative data are available on seasonality of marking behavior in other bobcat populations, and quantitative information is limited to frequency of scat deposits. In northeastern Florida, Conner (1982) recorded greatest frequency of scats along roads, trails, and firelanes during winter and spring and the lowest incidence in summer and fall. In Virginia, 57% of scats observed along trails over a 1-year period occurred from mid-September through mid-March and 43% during the balance of the year (Progulski 1952). Frequencies of scats on Louisiana study sites were higher in winter and spring and lower in summer and fall (Hall 1973). Miller (1980) stated that scat deposition by bobcats in Alabama was more frequent in winter and early spring and less obvious in other parts of the year. In contrast to this and other southeastern studies, no seasonal pattern was evident in monthly scat collections made by Kight (1962) in South Carolina. Scat deposition in southwestern populations also showed seasonal variation. Percentages of scats recorded by Jones (1977) in Arizona in different months from October through

March were 38% in October and November, 7% in December and January, and 55% in February and March. He suggested that the differences were due to weather (which might account for the overall lower trend in early winter), changing activity patterns of bobcats, and possible seasonal differences in bobcat behavior. As in the present study, the peak frequency of scat deposition in late-winter was correlated with the period of mating. In another Arizona study, Small (1971) reported monthly frequencies of scats/km of 0.04 in March and April, 0.58 in May, 0.18 in June, and 0.12 in July.

The data, particularly counts of urine scrapes, suggested a higher incidence of marking activity in fall-winter 1980-1981 than the previous year. Frequency of exposed scats with and without scrapes on the 10 km census line in February was higher in 1979 (5.5/km) than in 1980 (2.8) or 1981 (2.7). The higher level of marking, particularly urine scrapes, in late fall and winter of 1980-81 compared with 1979-80 might have reflected the slightly higher adult male density in the second year, although estimated numbers of adult females and juveniles were higher in 1979-80. The lower level of marking in 1979-80 also might have resulted from the greater instability of home ranges that year than in 1980-81 caused by the deaths from feline panleucopenia.

Spatial Patterns of Marking Behavior.— The distribution of marking sites in a part of the study area that contained portions of the home ranges of two adult males and three adult females with mobile young during October-December 1979 (Fig. 14) provided detailed evidence on the relationship of marking behavior to social organization of the population. Marking clearly was concentrated along home range boundaries. Of 273 4-ha quadrats that contained segments of scat and scrape census routes, 60 also contained segments of home range boundaries while the remaining 213 were in the interior portions of home ranges. Quadrats with home range boundaries had a significantly higher frequency of marking than those within home ranges (85% vs. 31%, $X^2 = 54.38$, 1 df, $p < 0.001$). There was a greater tendency for urine scrapes than for fecal scrapes to be located at home range boundaries. Quadrats including home range boundaries contained 88% of 248 urine or presumed urine scrapes compared with 65% of the 265 fecal scrapes or exposed scats. Similar relationships between home range boundaries and marking sites were found in other seasons. For example, the same area was thoroughly searched for scats and scrapes in July 1980, and 22 exposed scats and 55 known or presumed urine scrapes estimated to be not over 2 months old were recorded; 14 (64%) of the scats and 50 (91%) of the urine scrapes were in quadrats containing home range boundaries. Four of the five remaining urine scrapes were located near two rest sites used by two females with non-mobile kittens. In fall and winter 1980-81, there was a shift in the focus of marking activity in this part of the study area which correlated with a shift in home range boundaries.

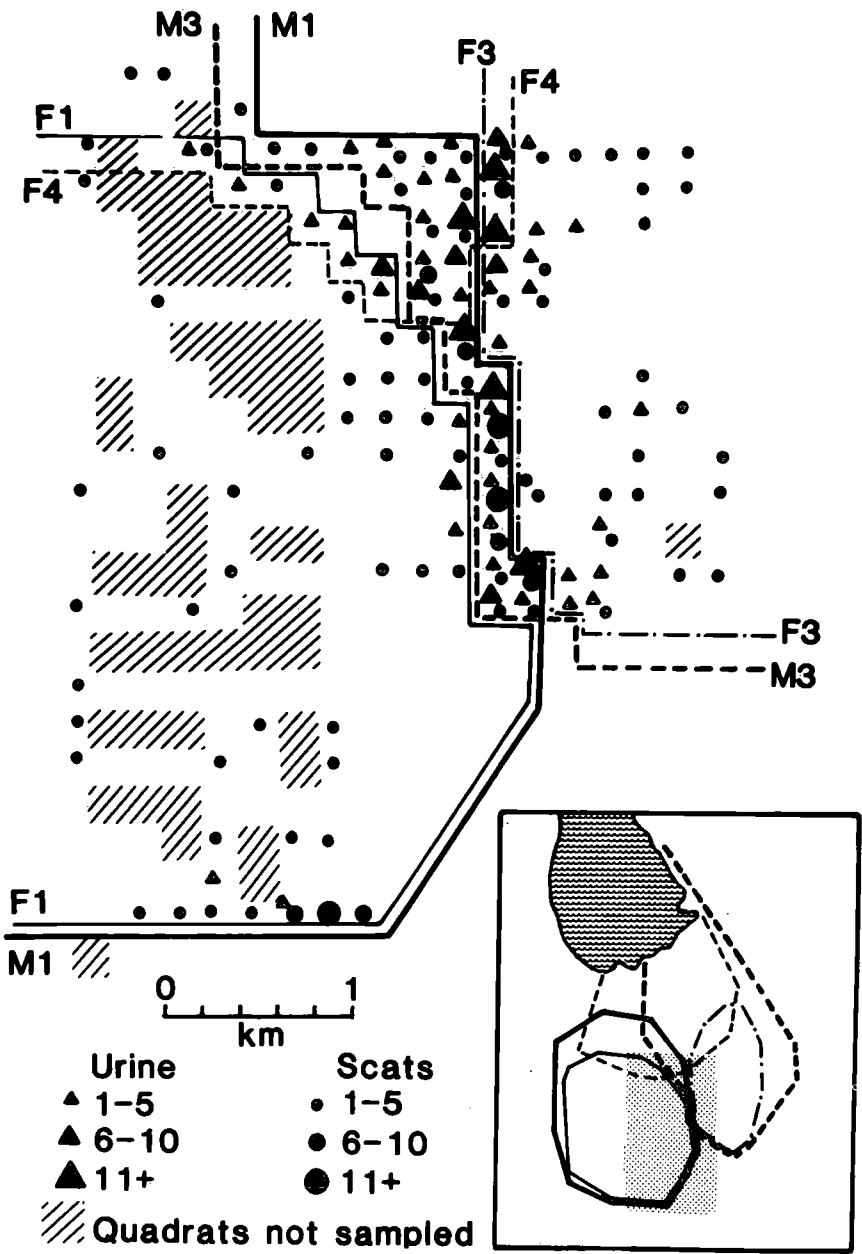


Figure 14. Distribution of scats and urine scrapes in 4-ha quadrats in relation to home range boundaries of two adult males (M1, M3) and three adult females (F1, F3, F4) during the period 23 October-19 December 1979 in a part of the study area represented by the stippled area on the inset map.

The distribution of various types of marks within bobcat home ranges supports the usual conclusion from home range configuration and other evidence that bobcats are territorial. Krebs and Davies (1978) recognized any occupied area as a "territory" whenever individuals or groups are spaced out more than would be expected from a random occupation of suitable habitats and when this spacing is due to interactions between these individuals or groups. By this definition, bobcat home ranges can be considered intra-sexual territories. Gorman (1980) noted that among mammalian carnivores non-territorial species mark throughout their home range, whereas territorial species mark more intensively at the borders of their ranges. He suggests that animals mark their range in order to orient themselves and that boundary marking is a specialized form of range marking, serving either to inform the animal doing the marking that it is at the edge of its territory or to warn and repel conspecifics. Marking also may have other functions, including providing information on an individual's identity, age, sex, reproductive state, or social status (see Leyhausen 1979, MacDonald 1980, Wemmer and Scow 1977 for further discussion).

Evidence of bobcats using marking to advertise the home range boundary was first presented by Marshall (1969). Bailey (1972) and McCord (*in* McCord and Cardoza 1982) provided further substantiation of this function of marking. Our observations on Florida bobcats add additional support to the hypothesis that one of the functions of marking is to inhibit bobcats from trespassing on another individual's home range. Bobcats deposited exposed feces and made fecal and urine scrapes more frequently at the periphery of the home range than in the interior, which suggests that this type of marking behavior was related to the maintenance of range boundaries. In addition, as home range boundaries shifted, there was a corresponding shift in the locus of marking, and bobcats regularly visited sites on their range boundaries and "refreshed" older marks with new ones. Type of deposit at a site was not necessarily consistent, as bobcats would often alternate between fecal-scraping and urine-scraping at the same location. Adjacent pairs regularly visited these sites and added their own deposits to them. Generally, feces tended to begin deteriorating after about a week, especially during the rainy season and when scarab beetles were active. Urine odor was strongest the first few days after the deposit. These observations suggest a need for bobcats to regularly renew levels of whatever substances might be used in advertising their status, and that neighboring individuals periodically inspected sites for information concerning other depositors. In this regard, it may be significant that bobcats were not known to invade the vacated ranges of same-sexed bobcats immediately after their death. Rather, 5-14 days elapsed before invaders were detected within the vacated ranges. The observed time-lag before invasion was about the same as the time taken for feces to deteriorate and for urine odors to diminish. In the case of adult female F3 who abandoned her home range to her daughter

(F8), the daughter had been marking at the mother's home range boundary prior to the adult's disappearance, and there were no apparent attempts by neighboring adult females to invade the range. This suggests that continued marking along the boundary, even by a different individual, served to maintain the integrity of the range.

CONSERVATION AND MANAGEMENT IMPLICATIONS

Several findings of this study appear relevant to conservation and management of bobcat populations. Our data indicate that even when not subject to significant direct exploitation by trapping or hunting, Florida bobcat populations may experience high mortality from natural and man-related causes. If, as found for the Canada lynx (Brand and Keith 1979), hunting and trapping mortality in bobcat populations is additive rather than compensatory, the mortality rate may be very high even in relatively lightly harvested populations. The importance of adult mortality in the population dynamics of bobcats was demonstrated by simulations based on data from Mississippi, indicating that a given percentage change in annual adult mortality has about twice the effect on population size as a similar change in litter size or kitten survival (Gluesing et al. 1987).

Most of the known litters were produced in the core area and females with young litters concentrated their activity there. General observations indicated that food resources also were better in the core than in the remainder of the study area, and all cases of man-related mortality occurred in the surrounding semi-developed area. This illustrates the important role of large tracts of protected habitat in developed areas in maintaining regional populations of bobcats and other large, mobile vertebrates. In landscapes characterized by interspersed natural and developed areas, the former probably serve as the primary source of new individuals and the latter as population sinks.

Death of resident individuals had a marked effect on the spatial relationships of surviving bobcats of the same sex. This is a factor that deserves consideration in assessing the potential impact of harvesting on a population. The disruption of the social organization of the population resulting from increased removal of individuals may lead to reduced productivity and an increase in mortality from other causes. Hornocker and Bailey (1986) also stressed the potential effect of man-caused mortality in felid populations in "creating behavioral instability and keeping the social organization in a perpetual state of flux."

In this study disease was a major cause of mortality and may play a more important role in bobcat population dynamics than previously suspected. Without relatively intensive and long-term monitoring of an adequate number

of radio-equipped animals, the occurrence of disease-related mortality in bobcats is unlikely to be detected. The role of domestic cats and other wildlife species, such as raccoons, as reservoirs and vectors of parasites and diseases of bobcats is an additional factor that needs to be considered in bobcat management. As more development encroaches upon Florida bobcat habitats, feral cats may become increasingly important as a source of FPLV outbreaks. The occurrence of feline panleucopenia in Florida bobcat populations may also pose a threat to the endangered Florida panther (*Felis concolor coryi*). Bobcats are common in areas of the confirmed remaining panther populations and could be a reservoir for feline panleucopenia, increasing the probability of the disease spreading to panthers. Roelke et al. (1984) reported FPLV antibodies in 8 of 13 bobcats and 9 of 10 panthers examined from areas of south Florida where the two species coexist.

Home range estimates for females based on daytime or infrequent radio fixes and density estimates derived from such data should take into account the seasonal variation in the pattern and timing of movements related to the reproductive status of the female. This study indicated that females with non-mobile young not only exhibit a temporal shift in activity but reduce the time spent at the periphery of their home range. Failure to monitor their movements intensively enough to compensate for the decreased probability of detecting them at the true limits of their home range could result in underestimation of home range size and overestimation of density.

The marked seasonal trends in marking behavior and tendency to mark more frequently at range boundaries have important implications with regard to census techniques that use counts of scats as an index of abundance. Censuses should be conducted at the same time of year, probably during late fall-early winter when marking is at its peak. Concentration of scent-marking along range boundaries could lead to erroneous interpretations of abundance if some census routes happen to be located along range boundaries, which often coincide with roads or trails, whereas others are not. These considerations may also apply to scent-post census techniques, because the responsiveness of a bobcat to a scent post is probably related to marking behavior and thus may vary both seasonally and in relation to the location of the scent post station within its home range.

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