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MOVEMENT PATTERNS AND HABITAT USE OF THE COPPERHEAD SNAKE IN SOUTHEASTERN VIRGINIA

by

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Abstract

MOVEMENT PATTERNS AND HABITAT USE OF THE COPPERHEAD SNAKE (*AGKISTRODON CONTORTRIX*) IN SOUTHEASTERN VIRGINIA

Christopher Edwin Petersen
Old Dominion University, 1995
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Radiotelemetry was used to study seasonal movement patterns, habitat use, and thermal relations of nine copperhead snakes, *Agkistrodon contortrix,* in southeastern Virginia from May 1993 to May 1995. Daily movements ranged from 0-450 m, with 0-5 m movements accounting for 65% of the observations. The seasonal movements of males were more extensive than those of females. Differences in seasonal movements between the sexes may be due to reproductive activity of the snakes. Both males and females significantly reduced their movements prior to shedding. More time was spent using upland deciduous forests than lowland river swamps or anthropogenic habitat. Copperheads selected open, less vegetated sites within the forest that differed significantly from random forested sites. The snakes hibernated in tree stumps within the upland forest. The results suggest that copperheads are able to survive body temperatures slightly below freezing during the hibernation period.

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Introduction

The copperhead snake, *Agkistrodon contortrix*, is a small species of pitviper that is distributed widely across the eastern United States (Gloyd and Conant, 1990). Throughout its range, the copperhead uses a variety of macrohabitats, including coastal marshes, mixed deciduous forest, and pine forests ranging in elevation from sea level to several hundred meters (Ernst and Barbour, 1989).

The copperhead has been studied in many locations across its geographic range, including the northeastern and midwestern United States. For example, Reinert (1984a,b) investigated the macrohabitat use of copperheads in Pennsylvania, and Fitch (1960) described general movement patterns of copperheads in Kansas. However, there have been no studies of habitat use or movement patterns of the species in the southeastern coastal plain. The absence of such information from that region limits our understanding of the role the species plays in community structure and function. To understand fully how the copperhead selects habitats, a variety of macrohabitats must be studied at different locations throughout the species' range. Studies of the same species in different habitats may not only reveal variation in habitat use, but may also suggest the factors that function as cues in habitat selection.

This study provides an evaluation of the movement patterns and habitat use of free-ranging copperheads in southeastern Virginia. The objectives of the study are: (1) to investigate daily and seasonal movement patterns and thus to determine activity ranges, (2) to examine habitat use by copperheads, and (3) to compare movement patterns and habitat use of copperheads in southeastern Virginia to other locations where the species has been studied.

Factors Influencing Habitat Use by Snakes

Studies of habitat use by snakes have lagged behind those of other taxa (Gregory et al., 1987). This may be due to the secretive nature of most snake species and to the difficulty of relocating cryptic snakes in natural habitats (Reinert, 1993). However, a review of the literature suggests that most snakes exhibit nonrandom use of the available landscape (Reinert, 1993). Factors such as sex and reproductive condition, availability of prey, thermoregulatory behavior, and learning apparently are important in habitat selection by snakes.

Sex and reproductive condition have been observed to affect habitat use in snakes (Reinert, 1984a,b; Duvall et al., 1985). For example, gravid females of many species use habitats that are warmer and that exhibit less temperature variation than those occupied by males and nonreproductive females. Because temperature affects the rate of development and thus the gestation period of viviparous snakes, habitat shifts by gravid females to warmer locations are believed to facilitate optimal embryonic development (Peterson et al., 1993). Only limited data are available to suggest habitat divergence between males and nongravid females. Fitch and Shirer (1971) reported that male racers (*Coluber constrictor*) used arboreal habitats more frequently than females.

The availability and distribution of prey in an environment also may affect habitat use by snakes (Gregory et al.,1987; Pough, 1966). Selection of sites in response to prey odors has been demonstrated for prairie rattlesnakes (*Crotalus viridis*) under laboratory conditions (Duvall et al., 1990), and observations of free-ranging timber rattlesnakes (*C. h. horridus*) suggest that foraging sites may be selected by detection of chemical cues left by small mammals on logs and tree bases (Reinert et al., 1984).

Thermoregulatory behavior may be linked to habitat use in snakes. Temperature has been shown to affect the rate of digestion and growth in snakes, as well as the speed of locomotion (Peterson et al., 1993). Therefore, selection of habitats with optimal thermal conditions may be vital to the survival of an individual. Competition for thermal resources may result in temporal or spatial habitat partitioning that may allow for the coexistence of several syntopic species of snakes. For example, More (1978) investigated thermoregulation and activity patterns of southwestern speckled rattlesnakes (*Crotalus mitchelli pyrrhus*) and Colorado Desert sidewinders (*C. cerastes laterorepens*) and determined that the sidewinders had a preferred body temperature of 25.8 C and were primarily nocturnal. In contrast, the preferred body temperature of the speckled rattlesnake, 31.3 C, was achieved by diurnal activity in spring and fall and nocturnal activity in the summer. Thus, by having different thermal preferences these two syntopic species of snakes were active at different times of the day for much of the year and could reduce competition for resources such as food.

Learning may play an important role in habitat selection by snakes. Studies have indicated that some snake species maintain stable home ranges during successive years and return to specific locations within a habitat during a single activity season (Brown and Parker, 1976). Returning to specific sites within an activity range, for example a foraging site or hibernaculum, may increase the efficiency of resource use by an individual.

Ciofo and Chelazzi (1994) investigated homing patterns of the green whipsnake (*Coluber viridiflavus*) in Italy. Eleven individuals showed a preference for shelters in stone walls and returned to those sites many times during an activity season. The snakes maintained stable home ranges between years and returned annually to the same hibernacula. Although the home range of many individuals overlapped, no territorial behavior was observed.

It is not clear what cues are used for homing behavior. Most likely, however, visual, celestial and chemical signals are used (Gregory et al., 1987). Pheromone cues are believed to play a major role in the trailing of female rattlesnakes by males during the mating season. It is also hypothesized that immature rattlesnakes may find hibernacula in the autumn by following pheromone trails laid down by adults (Brown and Maclean, 1983).

Factors Affecting Activity Patterns

Numerous studies have focused on the daily and seasonal movements of snakes in an attempt to identify activity patterns of individuals within a population or species (Fitch, 1960; Landreth, 1973; Gibbons and Semlitsch, 1982). The results of these studies have provided insight into the reasons why snakes move in their environment. For example, movement of an individual may reflect resource availability, reproductive condition, or sex. An evolutionary explanation may also be used to interpret activity patterns, with the hypothesis that natural selection has operated to produce the patterns of activity we observe today. Overall, the literature on species-specific annual activity can be organized into two patterns, daily and seasonal.

Studies that investigate the daily movements of snakes may try to determine when an individual is active (diurnally or nocturnally), or they may focus on other factors that induce an animal to move. Some investigators believe that daily movements may be closely linked to mate-searching and foraging activities (Duvall et al., 1985). Others however, believe that thermoregulation may be more important in determining daily activity patterns (Lillywhite, 1985).

Landreth (1973) reported that the daily activity patterns of diamondback rattlesnakes (*Crotalus atrox*) in Oklahoma were temperature-dependent. During the winter months, the snakes moved to basking sites at midday, when air temperatures were warmest. Daily activity in the late spring and early autumn was bimodal; the snakes were most active during the early morning and late evening. During the hot summer months, the snakes were most active at night. A shift from diurnal to nocturnal activity in the summer also was documented for copperheads (*Agkistrodon contortrix*) in Tennessee (Sanders and Jacobs, 1980). Although the snakes were active during the day in the spring and autumn, copperheads became nocturnal during the summer months. This shift in daily activity may have been an attempt to avoid hot daytime temperatures.

Several studies have provided detailed observations of seasonal activity patterns in snakes (Landreth, 1973; Brown and Parker, 1976; Gibbons and Semlitsch, 1982). Two major patterns of seasonal activity, bimodal and unimodal, have been identified.

A bimodal seasonal activity pattern, with increased activity in the spring and autumn and reduced activity in the summer, has been observed in the western diamondback rattlesnake (*Crotalus atrox*). For example, a two-year radiotelemetric study of the activity patterns of diamondbacks in Oklahoma determined that the movements of (*C. atrox)* fluctuated seasonally (Landreth, 1973). In the spring and early summer, the snakes performed long migrations to foraging areas located 1-2 km from the den. Short daily movements from hiding places to feeding sites were made during the summer months. In autumn, the snakes migrated long distances back to hibernacula.

Drift fence and pitfall trapping of several species of snakes from the Savannah River Ecology Laboratory has revealed that the smooth earth snake (*Virginia valeriae*) also has a bimodal seasonal activity pattern. This snake is most active during the months of May and August and least active during July (Gibbons and Semlitsch, 1982).

A unimodal seasonal activity pattern, with a single peak of activity between late spring and late summer, was observed for speckled rattlesnakes (*Crotalus mitchelli*) in California (Moore, 1978). After initially becoming active above ground in April, the hours of activity for speckled rattlesnakes increased during each successive month through September. Activity was reduced in October and November as air temperatures became cooler. Gibbons and Semlitsch (1982) found that the scarlet snake (*Cemophora coccinea*) and the southeastern crowned snake (*Tantilla coronata*) also display unimodal activity peaks. Both species exhibit a sharp peak of activity between early spring and autumn.

Influence of Sexual Differences and Reproductive Condition

Differential activity patterns between the sexes have been revealed in some snakes (Gibbons and Semlitsch, 1987). For example, female prairie rattlesnakes (*Crotalus viridus*) from Saskatchewan, Canada moved significantly further than males throughout the entire activity season (Gannon and Secoy, 1985). Male timber rattlesnakes from New Jersey had larger activity ranges (mean length = 1,436 m) than nongravid females (mean length = 995 m) (Reinert and Zappalorti, 1988). No significant differences were observed in the activity range areas, range lengths, or distances moved per day between radiotracked male and female western massasauga rattlesnakes (*Sistrurus catenatus*) in Pennsylvania (Reinert and Kodrich, 1982).

Reproductive condition also has been observed to affect the activity of snakes. Female snakes sometimes reduce their activity and occupy different habitats when gravid (Gibbons and Semlitsch, 1987). For example, a comparison of the movements of gravid and nongravid massasaugas *(Sistrurus catenatus)* in Pennsylvania revealed a significantly shorter mean range length for gravid females (Reinert and Kodrich, 1982). The shorter range length observed may have been the result of selection by gravid massasaugas of dry habitats with low, sparse vegetation.

Systematics of *Agkistrodon contortrix*

Although it originated in the Old World, the genus *Agkistrodon* also occupies a considerable geographic range from the United States to Costa Rica (Gloyd and Conant, 1990). In North America *Agkistrodon* includes three species: (1) the cantil (*A. bilineatus*), which inhabits dry forests of Mexico and Central America; (2) the cottonmouth (*A. piscivorus*), found in swamps and other wetlands from southeastern Virginia to Oklahoma and Texas; and (3) the copperhead *A. contortrix*, which largely occupies upland deciduous forests from New England to southern Florida to Kansas, Texas and Oklahoma.

Subspecies. Based on differences in color, pattern, and morphology, five subspecies of *Agkistrodon contortrix* have been described: (1) *A. c. contortrix*, the southern copperhead; (2) *A. c. mokasen*, the northern copperhead; (3) *A. c. laticinctus*, the broad-banded copperhead; (4) *A. c. pictigaster*, the Trans-Pecos copperhead; and (5) *A. c. phaeogaster*, the Osage copperhead (Gloyd and Conant, 1934, 1943; Fitch, 1959, 1960; Ernst, 1992).

Characteristics. Copperheads are grayish-brown to pink in ground color, with 10-21 reddish-brown or chestnut-colored dorsal crossbands (Ernst, 1992). In most subspecies the crossbands are hourglass-shaped, being wider (8-10 scales) on the sides and constricted (3-4 scales) at the dorsal midline (Gloyd and Conant, 1990). Although symmetrical bands are most common, some may be divided at the midline and displaced anteriorly or posteriorly. The venter of most copperheads is light-brown to pink, with irregular dark ventrolateral blotches that sometimes alternate with the crossbands (Gloyd and Conant, 1990). The head is brown to tan, with darker pigmentation above the eye. Small dark spots on the parietal scales are common (Fitch 1960).

Many investigators have noted unusual color patterns of copperheads (Fitch, 1959,1960; Gloyd and Conant, 1990), including such abnormalities as dark dorsal stripes, mixtures of striping and crossbanding, and patternless brown individuals.

Ecology of *Agkistrodon contortrix*

Habitat and Movement Patterns. Copperheads are common in a variety of habitats throughout their geographic range including coastal marshes, mixed deciduous forest, and anthropogenic habitats (Fitch and Shirer, 1971; Ernst and Barbour, 1989). Although it is common to think of copperheads as using dry forests, they may voluntarily enter coastal marshes and wetlands (Gloyd and Conant, 1990).

Reinert (1984a) investigated the habitat use of 21 timber rattlesnakes (*Crotalus h. horridus*) and 20 northern copperheads (*Agkistrodon contortrix mokasen*) in eastern Pennsylvania. Multivariate analysis of 14 structural habitat variables and five climatic variables revealed that the habitats used by the two species differed significantly. Copperheads used more open and less vegetated areas in a deciduous hardwood forest, with higher rock density and less surface vegetation, than did timber rattlesnakes.

Fitch (1960) identified three general types of movements by copperheads: (1) travel within the home range (which included most movements); (2) abandonment of an original home range and occupancy of a new one; and (3) seasonal migration between the hibernaculum and the summer range.

Home ranges of copperheads in Kansas (Fitch, 1960) varied from 3.4 ha for females to 9.8 ha for males. The home range diameter for females averaged 210 m and that for males averaged 345 m. Individual movements on the summer range varied from 1.5-378 m for individuals that remained in their home range. Male copperheads traveled longer distances from their hibernacula than did females ($\bar{x}$=656 m and 406 m, respectively).

A radiotelemetric study of copperheads in Kansas (Fitch and Shirer 1971) reported that the snakes used rocky ledges during the spring and fall, but preferred woodlands and grasslands in the summer. Mean displacement per movement, excluding days with no movement, was 18 m for males, 12 m for nongravid females, and 12 m for a single gravid female. However, Fitch and Shirer force-feed their radiotransmitters, which is believed to have affected the behavior of the snakes (Reinert, 1992). The average rate of travel of their telemetered snakes was slower than that previously recorded for marked and recaptured individuals on the same study site (Fitch and Shirer, 1971).

In autumn, copperheads return to a hibernaculum, or den. Gravid females may return much earlier than nonreproductive females or males and may give birth at these sites (Ernst, 1992). Fidelity to hibernacula has been reported for copperheads in Kansas (Fitch, 1960). Copperheads may hibernate communally with conspecifics or with other species such as timber rattlesnakes *(Crotalus horridus)* (Reinert, 1984a).

Hibernacula often consist of animal burrows, stumps, and rocky outcrops where soil temperatures remain above 10 C. (Ernst, 1992). In Tennessee, (*Agkistrodon contortrix*) overwinters at soil depths of 60-90 cm (Sanders and Jacob, 1981), and snakes hibernating at those depths had body temperatures equal to ambient soil temperatures.

Food and Feeding. Adult copperheads are primarily ambush predators, whereas young copperheads will stalk prey or use their brightly-colored yellow tails to lure frogs (Ernst, 1992). Both adults and young have highly hemolytic venom, which immobilizes prey and presumably aids in digestion (Ernst, 1992). The feeding behavior of copperheads differs according to prey type. Larger prey, which may injure the snake, are bitten and released, to be consumed after the venom takes effect. Smaller prey items, which can not injure the snake, are held in the jaws after the strike to presumably prevent the prey from escaping (Fitch, 1960).

Brown (1979) study of the food habits of (*Agkistrodon contortrix*) from North and South Carolina. Analysis of digestive tract contents from 35 specimens yielded 62 items, mostly small mammals and lepidoptera larvae. Small mammals remains ranked first in volume (59.2%) but second as percentage of total food items (37.1%). Small mammals identified from the digestive tract of the snakes included white-footed mice (*Peromyscus leucopus*), pine voles (*Microtus pinetorum*), prairie voles (*M. pennsylvanicus*), and shrews (*Blarina carolinensis*). Insects ranked first in percentage of food items (56.5%) and second in volume (24.9%). Lepidopteran larvae were the most abundant insect in the digestive tract of copperheads. Other insects included a dragonfly and a cicada nymph. Three of the copperhead specimens contained reptiles in their digestive tracts (*Diadophis punctatus*, *Carphophis amoenus*, and *Ophisaurus* sp.); however, reptiles did not contribute significantly to the biomass consumed. Other natural food items reported for North Carolina copperheads

(Palmer and Baswell, 1995) included salamanders (*Ambystoma opacum, Plethodon* sp.) ground skinks (*Scincella lateralis*), and a variety of insects such as luna moth larva (*Actias luna*), imperial moth larva (*Eacles imperialis*) and oakworms (*Anisota stigma*).

Reproduction. Both sexes of copperheads mature by three years of age (Fitch, 1960). Mating can occur any time during the active season, although it is most common in April-May and September-October (Ernst, 1992). Fitch (1960) estimated that approximately 60% of the adult females in a population in Kansas breed each season, a pattern suggestive of a biennial reproductive cycle. Mature males produce sperm throughout the active season and are continuously in breeding condition (Schuett and Gillingham, 1986). Gloyd (1935) examined 59 sexually mature females from April-May in eastern Kansas and reported that 21 individuals contained active spermatozoa in their cloacae.

Females are capable of sperm storage and delayed fertilization. Gloyd (1935) concluded that sperm may survive in the oviduct for approximately 11 days, but Schuett (1982) demonstrated that sperm from fall copulations retain their viability until spring. Using genetic markers, multiple paternity was shown to have resulted from autumn and spring copulations with two males of different subspecies (Schuett and Gillingham, 1986).

The gestation period ranges from 105-150 days, although factors such as temperature and food availability result in considerable variability in that period (Ernst, 1992). Broods of 1-21 young have been reported (White, 1979; Ernst, 1992), with a modal brood size of 4-8. In summary, female copperheads generally produce 4-8 young in alternate years, beginning at age three.

Methods

Study Site

This investigation was conducted at Northwest River Park in Chesapeake, Virginia. Located 5.6 km E of Rt. 168 on Indian Creek Road, Northwest River Park is a 309 ha municipal park ranging in elevation from 0-4 m above MSL. The park was surrounded by water on three sides, Indian Creek on the west, the Northwest River on the south, and Smith Creek on the east. Gravel roads and hiking trails provided access to many areas of the study site. The macrohabitats of the park were woodland and riverine swamp.

The major habitat of the park was mixed deciduous forest. Dominant species of forest trees included American beech (*Fagus grandifolia*), white oak (*Quercus alba*), and red maple (*Acer rubrum*). The major understory vegetation of the woodlands was American cane (*Arundinaria gigantea*), a native bamboo that grows in large stands. The woodland habitat was bisected by a narrow lake system 1.5 km long and approximately 15 m wide. The lake was artificially dredged to connect with a natural drainage system. Spoil berms, created during the construction of the lake, were located along the edge of the waterway and were considered anthropogenic habitat for the purpose of this study. The berm, which was about 5 m tall and 10 m wide, contained abundant treefalls, tree stumps, and holes in the soil.

Dominant plants of the spoil berm were Japanese honeysuckle (*Lonicera japonica*), loblolly pine (*Pinus taeda*) and greenbrier *(Smilax rotundifolia*).

Riverine swamp bordered three sides of the park. Wind tides periodically flooded the swamp, which contained such dominant plant species as baldcypress (*Taxodium distichum*), black tupelo (*Nyssa sylvatica*), and wax myrtle (*Myrica cerifera*).

Radiotelemetry

Temperature-sensitive radiotransmitters (Model SM1; AVM Instrument Co.) were used in this study. The transmitters ranged from 6-11 g and did not exceed 5% of the snake's body mass. Before implantation, the transmitters were calibrated by recording the pulse interval of each unit in eight water baths, ranging in temperature from 0-45 C. For each transmitter, a least squares regression was performed to derive a regression equation for pulse interval vs. temperature. A linear relationship was established for each transmitter, with a regression coefficient of 0.996-0.998.

Radiotransmitters were coated with beeswax and paraffin (1:1 by mass) and then implanted surgically into the pleuroperitoneal cavity according to the procedure developed by Reinert and Cundall (1982). Individuals were anesthetized with isoflourine anesthesia, after which an incision was made through the skin between the first and second scale rows of the right side. The abdominal muscles and peritoneal wall were perforated, and the transmitter was then inserted through the incision into the body cavity. Finally, the whip antenna was inserted subcutaneously anterior to the incision, and all incisions were closed with Prolene sutures. All transmitter implantations were performed at Old Dominion University by me and by Drs. Alan and Barbara Savitzky. Snakes were released at the site of capture one day after surgery. Two male copperheads, AN-1 and AN-4, died shortly after release as a result of the implantation of radiotransmitters. Later surgeries employed a smaller transmitter package to reduce trauma to the subjects.

Unmarked copperheads occasionally were observed with telemetered snakes or were located while crossing roads within the park. Those specimens were captured and transported to Old Dominion University, where their sex, weight and length were recorded. Those individuals were also palpated for food items and photographed for individual identification. All snakes were then released at the site of capture.

Movements

Nine snakes (six males, three females) were monitored for varying lengths of time from May 1993 to May 1995. Tracking usually was performed once every 24-48 h between 0900 and 1700 h. Maximum transmission distances were estimated to be about 300 m. The location of each implanted snake was detected with a radio receiver (TRX-1000S; Wildlife Materials) equipped with a hand-held three-element Yagi antenna (AVM Instrument Co.).

A surveyor's flag bearing an identification number was placed at the site of each location, within 0.05 m of the snake. To aid in locating a site in the future, the date, flag number and radio frequency of the snake were written on fluorescent plastic flagging and tied to a nearby tree.

Distances and directions between successive flagged locations were measured between November and April for both years of the study. Movements of less than 10 m were measured using a tape measure, whereas distances greater than 10 m were obtained using an electronic measuring device (Combo PRO; Sonin). A compass was used to determine the direction of movement from the snake's previous location. Positions were plotted by hand from the movement data on a map of the study site, using a ruler and protractor.

Total distance moved was calculated by summing the linear distances between location points, whereas the mean distance per day was calculated by dividing the total distance moved by the number of days tracked. The mean distance per movement was calculated by dividing the total distance moved by the number of movements an individual performed (observations of no movement were omitted from this calculation). The computer program McPAAL (Conservation and Research Center, National Zoological Park; Michael Stuwe) was used to determine the activity range of each snake from the map of movements, using both the harmonic mean and minimum convex polygon methods. The harmonic mean was considered to be the area enclosed by the 95% isopleth, whereas the minimum convex polygon was the area enclosed by outlying location sites. The range length was considered the linear distance between the two most distant locations on seasonal activity maps for each individual.

A two-sample Student's t-test was used to determine whether the mean distance per day, mean distance per movement, mean activity range, and mean range length differed significantly between male and female copperheads. In order to evaluate seasonal movement patterns, mean biweekly movement distance per day was calculated. Biweekly means were calculated for the activity season by dividing the total distance moved during a two week interval by 14 days. The mean movement distances per day, 14 days before and after an observation of shedding, were compared with a Mann-Whitney Rank Sum Test to evaluate the effect of shedding on the movements of copperheads.

In order not to violate the assumption of independence, calculations which included movement data for subject AN-3 for 1993 and 1994 were averaged before being used to determine male movement results. Subject AN-4 was not included in the analysis of activity range due to the small number of observations.

Thermal, Climatic, Habitat, and Behavioral Data

At the time each telemetered animal was located, a series of climatic variables was recorded. A digital thermometer (Model SH66A; Electro-Therm) was used to record the air, surface, and soil (at 9 cm depth) temperatures within 2 m of the location site. Precipitation for the last 24-48 h was recorded using a standard rain gauge. Regional weather data were obtained from National Weather Service reports for Norfolk International Airport, approximately 35 km by air from the study site.

Habitat variables recorded each time a snake was located included macrohabitat type (forest, swamp, or anthropogenic) and use of cover objects (ground holes, tree stumps or leaf litter). The transmitter pulse interval, a function of body temperature, was also recorded by either a stopwatch or using a pulse interval timer (AVM Instrument Co.). Finally, observations of a recent meal or shedding event were noted. Habitat measurements were made for 62 randomly selected sites where snakes had been observed. All measurements were made during May-July 1995, regardless of when the snakes had been recorded at a given location. The habitat variables sampled included a subset of the structural variables used in Reinert's (1984a) study. Nine structural habitat variables were recorded within a 1 m^2 quadrat centered on each location point (Table 1). Recorded variables included leaf litter cover (%), fallen log cover (%), woody stem density, and diameter at breast height of understory and overstory trees.

To determine whether copperhead positions differed from a random selection of available habitat, 70 random sites within the forest were sampled following the same procedure as for the 62 snake locations. The distance and direction from a randomly selected starting point was chosen from a six-digit random number table. The first three digits of the random numbers were used as a compass direction, and the last three digits were used as the number of paces to the next site where habitat variables were to be measured. If the randomly selected value for the number of paces exceeded 300, it was divided in half.

A test of correlation was performed on the sampled habitat variables collected from snake sites and random sites to avoid statistical problems associated with linear dependence and singular covariance matrices (Reinert, 1992). A multiple analysis of variance MANOVA was used to determine whether habitat centroids (multidimensional means) differed significantly between copperheads sites and random sites. The MANOVA was also used to determine which habitat variables were significantly different between snake sites and random sites. Finally, a canonical analysis was used to determine which habitat variables were most important in discriminating between snake sites and random sites.

Table 1. Structural habitat variables measured at 62 snake location sites and at 70 randomly selected sites within the study area.

Variable Name	Abbreviation	Sampling method
Leaf litter cover	LEAF	Coverage (%) of leaf litter within a $1m^2$ quadrat
Vegetation cover	VEG	Coverage (%) of herbaceous and shrubby vegetation within a $1m^2$ quadrat
Log cover	LOG	Coverage (%) of logs within a $1m^2$ quadrat
Woody stem density	WSD	Total number of woody stems within a $1m^2$ quadrat
Woody stem height	WSH	Height (cm) of tallest woody stem (exclusive of understory and overstory trees)
DBH of overstory tree	DBO	Diameter at breast height (cm) of nearest overstory tree
Distance to overstory tree	DOT	Distance (m) to nearest overstory tree (>7.5 cm dbh)
DBH of understory tree	DBU	Diameter at breast height (cm) of nearest understory tree
Distance to understory tree	DUT	Distance (m) to nearest tree (< 7.5 cm dbh)

Results

Movements

Nine adult *Agkistrodon contortrix* (6 males, 2 nongravid females, and 1 gravid female) were radiotracked for various periods of time between May 1993 and May 1995. The number of tracking days per animal ranged from 45-522 d ($\bar{x}$ = 296±59 d) and the mean number of observations per snake ranged from 33-375 ($\bar{x}$ = 225±46 d). Male subjects AN-1 and AN-5 were eliminated from the analysis because of limited observations, leaving only seven animals for analysis of patterns of movement and habitat use.

The mean total distances that males moved during the activity period ($\bar{x}$ = 2962±737 m) was significantly greater than that of the females ($\bar{x}$ = 1580±219 m) (t=2.71, P=.0534; Table 2). The mean distance moved per day was significantly greater for males ($\bar{x}$ = 22.3±3.1 m d^{-1}) than females ($\bar{x}$ = 10.4±1.3 m d^{-1}) (t=3.12, P=0.013; Fig. 1). The mean distance per movement for males ranged from 28.5-79.1 m ($\bar{x}$ = 43.5±6.9 m), whereas for females was 13.1-28.3 m ($\bar{x}$ = 21.4±4.4 m). The largest percentage of observations (52.2%) involved daily movement distances <1 m, whereas distances >100 m represented the smallest percentage of observations (3.5%; Fig. 2). The remaining classes of movement distances ranged between

Table 2. Male and female movements during the activity season (April-November).

Subject	Sex	No. of obs.	Total distance moved (m)	Distance moved per day (m d^{-1})	Mean distance per movement (m)
AN-3 (1993)	male	92	4747	29.5	79.1
AN-3 (1994)	male	163	3354	15.9	39.9
AN-4	male	33	1288	28.6	49.5
AN-6	male	155	4340	23.9	36.5
AN-7	male	127	2169	13.9	28.5
$\bar{x}$ ± SE	male	114±24	2962±737	22.3±3.1	43.5±6.9
AN-2	female	98	1724	11.6	28.3
AN-8	female	125	1868	11.9	22.7
AN-9	female	107	1149	7.8	13.1
$\bar{x}$ ± SE	female	110±8.0	1580±21	10.4±1.3	21.4±4.4

Figure 1. Mean movement per day for male and female *Agkistrodon contortrix*.

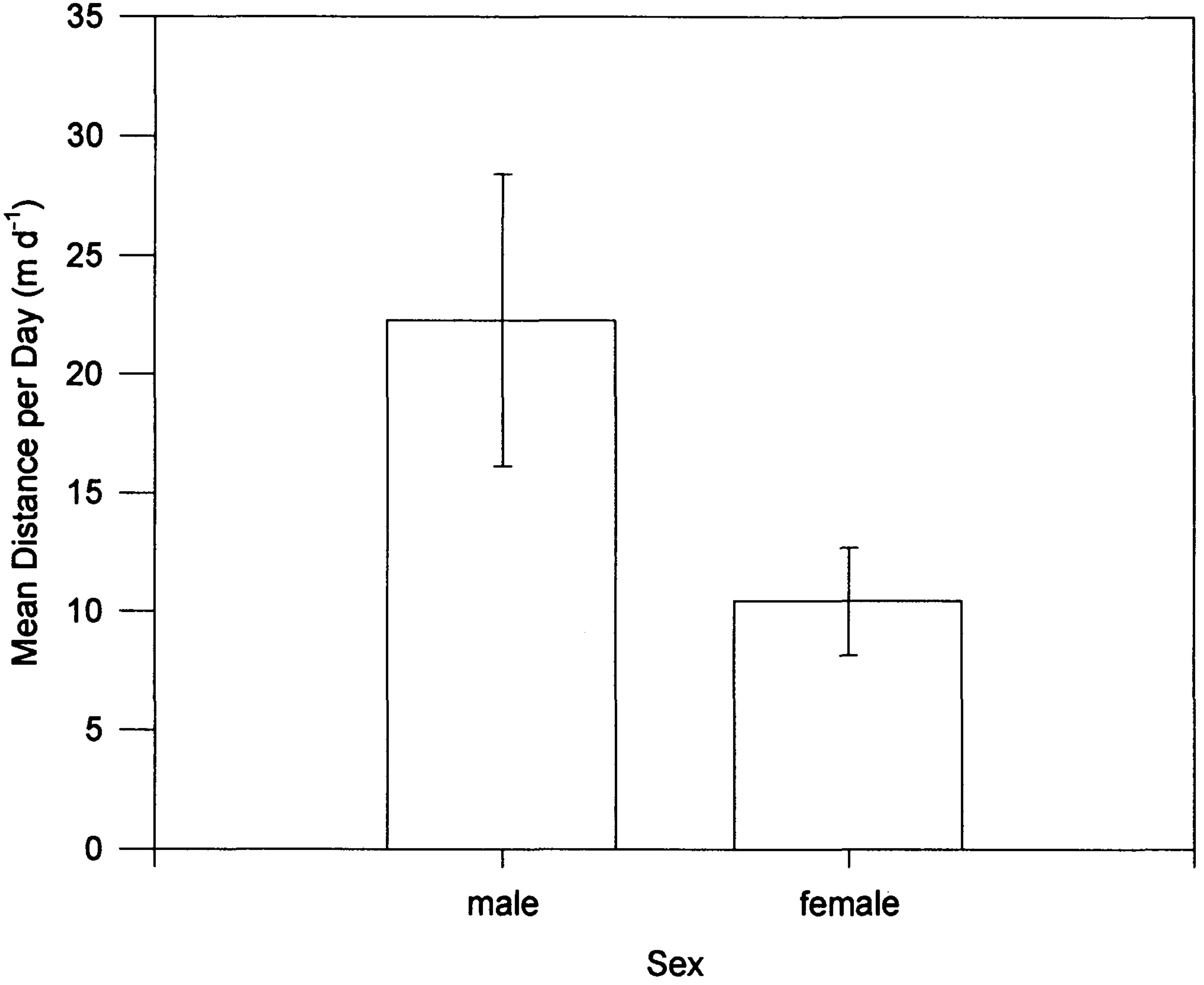
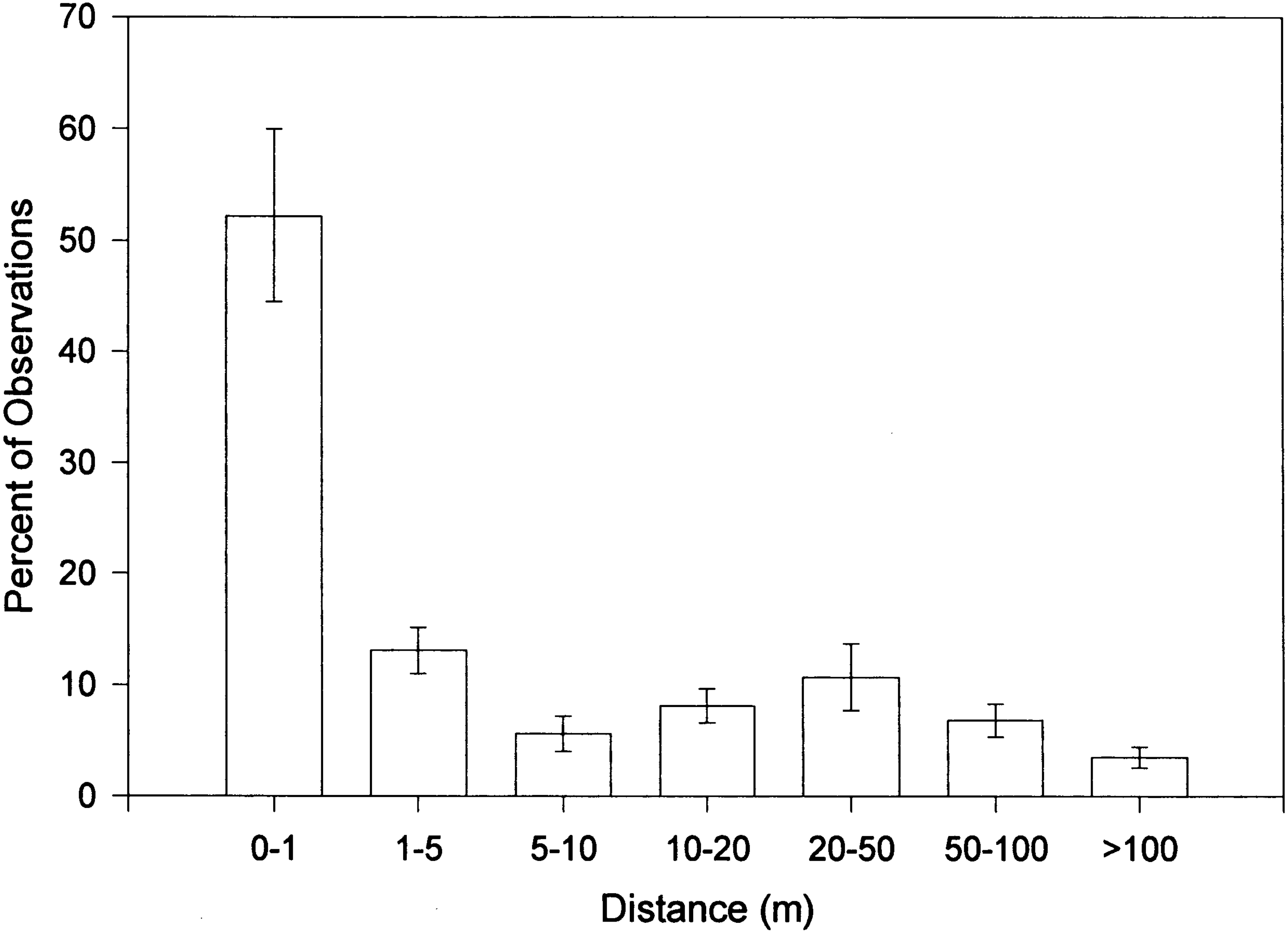

35
30
25
20
15
10
5
0
Mean Distance per Day ($m\ d^{-1}$)
male
female
Sex

Figure 2. Daily movement distances of *Agkistrodon contortrix*, based upon 26-164 movements per subject ($\overline{x}$ = 100.2±16.6).



Percent of Observations
70
60
50
40
30
20
10
0
0-1
1-5
5-10
10-20
20-50
50-100
>100
Distance (m)

5.6-13.1% of the observations. The longest daily movement was 450 m (male AN-6, 1 September 1994).

The activity ranges among the telemetered copperheads varied considerably (Figs. 3-7). As a result, activity ranges for male and female copperheads did not differ significantly (t=1.39, P=0.12). The mean activity ranges for males, calculated using the harmonic mean analysis (95% isopleth), was 8.07 ha, whereas the minimum convex polygon method, yielded a mean of 7.16 ha (Table 3). In contrast, the mean activity range for females, calculated using the harmonic mean analysis (95% isopleth), was 3.93 ha, compared to 3.77 ha using the minimum convex polygon method. The mean range lengths for males ($\bar{x}$ = 540±080 m) did not differ significantly from that of females ($\bar{x}$ = 357±85 m; t=1.09, P=0.34).

Both sexes returned to sites within their activity ranges which they had previously occupied months or even years earlier. For example, Subject AN-3 visited a specific (*Vitis rotundifolia*) tangle on three occasions in 1993 (27 July, 2 August, 17 September) and returned to the same site in 1994 (29 April, 9 August, 1 September; Figs. 4-5). Subject AN-7 returned to a pile of railroad ties on several occasions, even after traveling over 200 m away from the site (Fig. 3).

A bimodal seasonal activity pattern was observed for the three male subjects for which longterm data are available (Fig. 8). The first peak in activity for the males varied among the three individuals. Each of the males had peaks of activity between early June and late July

Figure 3. Seasonal activity map for Subject AN-7, 1994. Dotted lines are movements prior to translocation; solid lines are movements after translocation. (Activity range calculated by minimum convex polygon (MCP) and harmonic mean (HM) methods.)

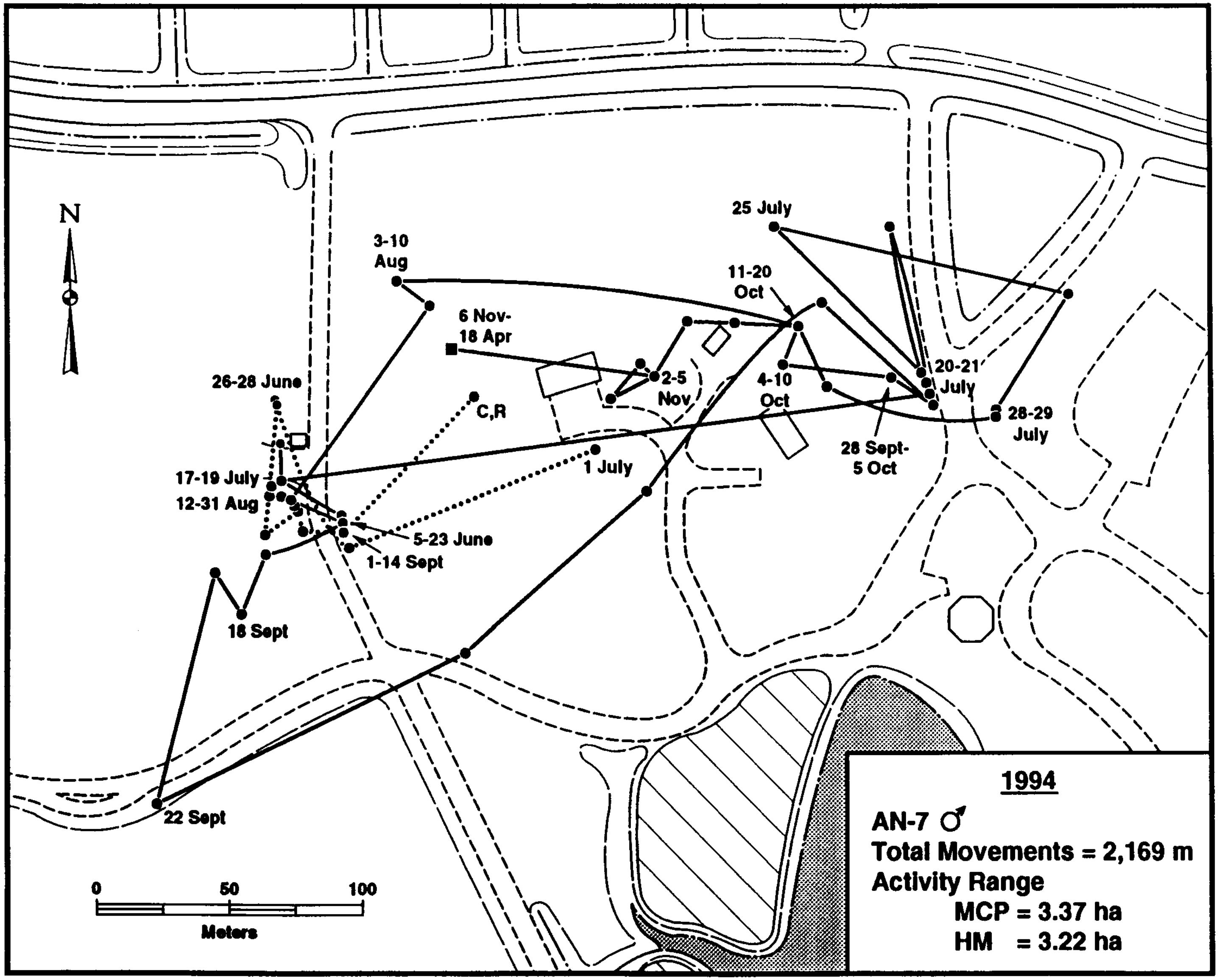
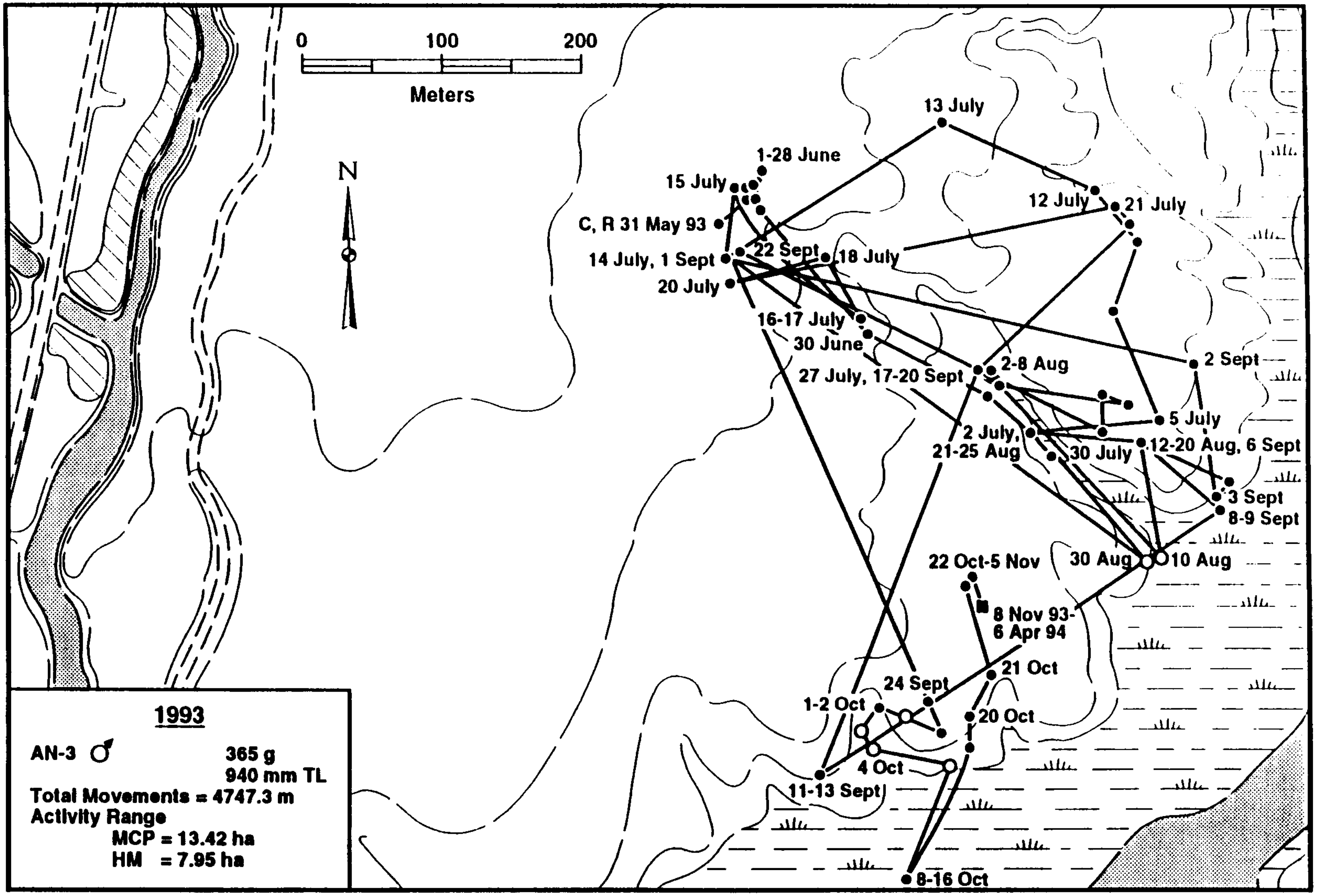

N
25 July
3-10
Aug
11-20
Oct
6 Nov-
18 Apr
2-5
Nov
4-10
Oct
20-21
July
28-29
July
26-28 June
C,R
28 Sept-
5 Oct
1 July
17-19 July
12-31 Aug
5-23 June
1-14 Sept
18 Sept
22 Sept
0
50
100
Meters
1994
AN-7 ♂
Total Movements = 2,169 m
Activity Range
MCP = 3.37 ha
HM = 3.22 ha

Figure 4. Seasonal activity map for Subject AN-3, 1993. (Activity range calculated by minimum convex polygon (MCP) and harmonic mean (HM) methods.)



0
100
200
Meters
N
13 July
1-28 June
15 July
12 July
21 July
C, R 31 May 93
22 Sept
14 July, 1 Sept
18 July
20 July
16-17 July
30 June
2-8 Aug
27 July, 17-20 Sept
2 Sept
5 July
2 July,
21-25 Aug
30 July
12-20 Aug, 6 Sept
3 Sept
8-9 Sept
22 Oct-5 Nov
30 Aug
10 Aug
8 Nov 93-
6 Apr 94
21 Oct
24 Sept
1-2 Oct
20 Oct
4 Oct
11-13 Sept
8-16 Oct
1993
AN-3 ♂
365 g
940 mm TL
Total Movements = 4747.3 m
Activity Range
MCP = 13.42 ha
HM = 7.95 ha

Figure 5. Seasonal activity map for Subject AN-3, 1994. (Activity range calculated by minimum convex polygon (MCP) and harmonic mean (HM) methods.)

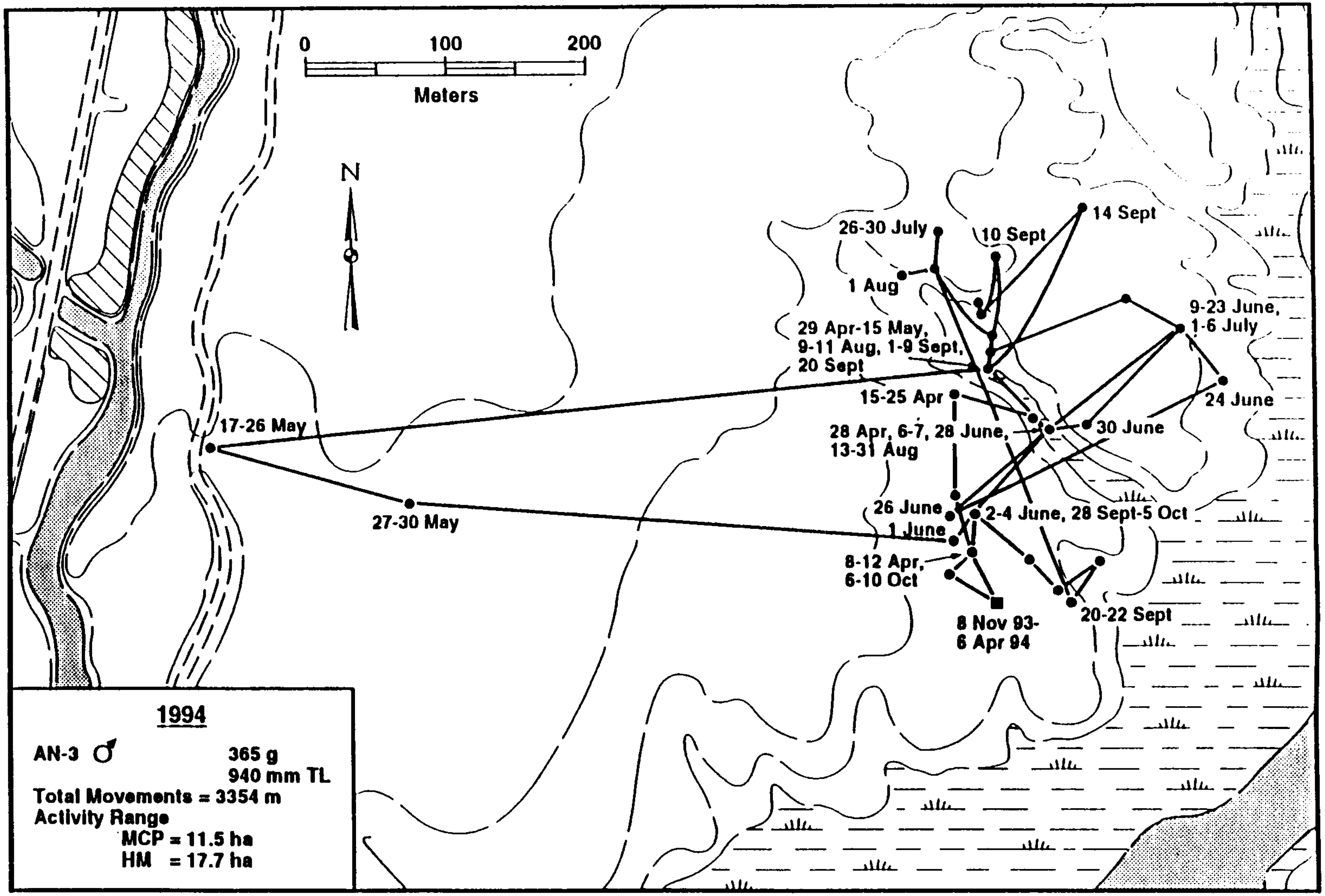
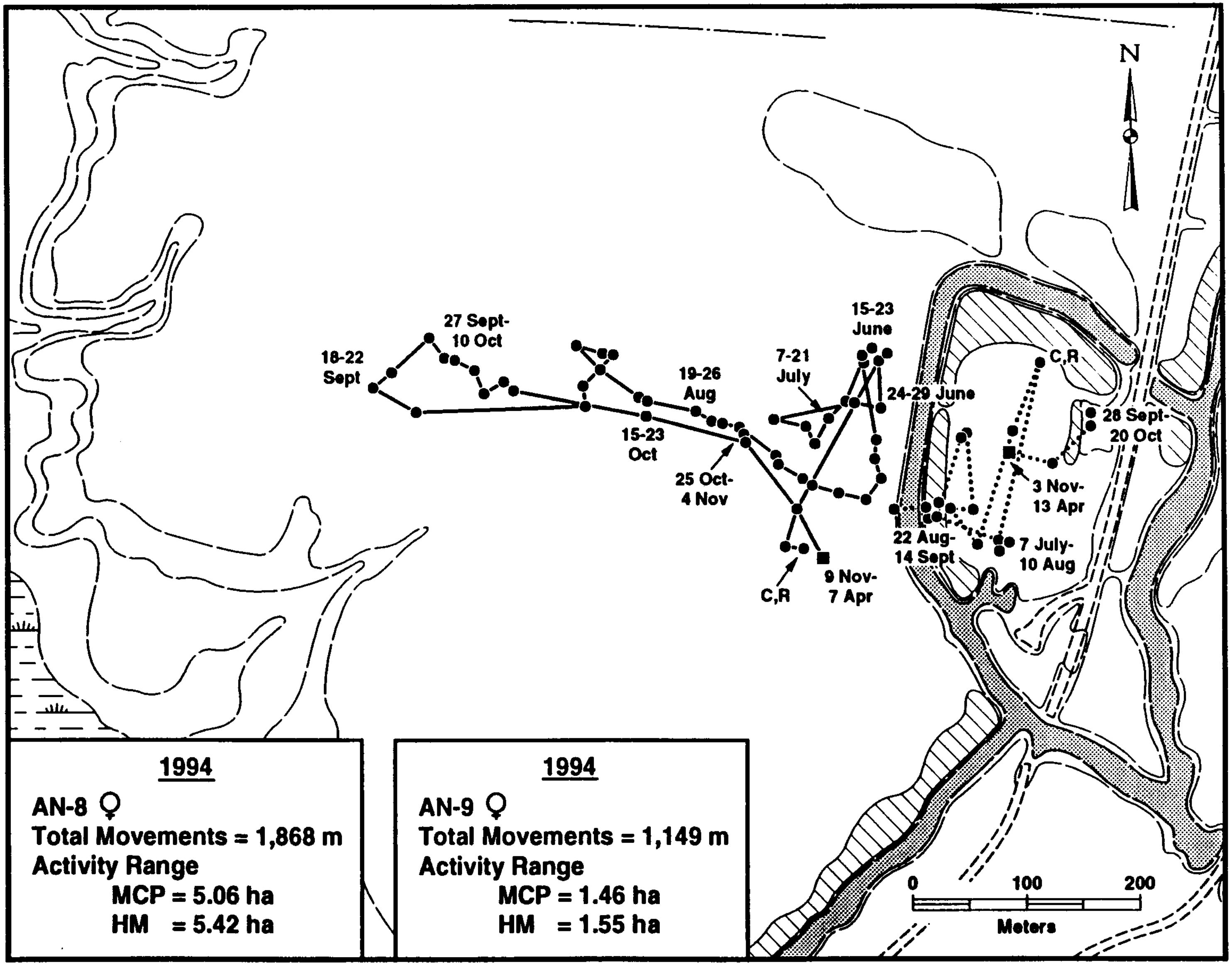

0
100
200
Meters
N
14 Sept
26-30 July
10 Sept
1 Aug
9-23 June,
1-6 July
29 Apr-15 May,
9-11 Aug, 1-9 Sept,
20 Sept
15-25 Apr
24 June
17-26 May
28 Apr, 6-7, 28 June,
13-31 Aug
30 June
26 June
2-4 June, 28 Sept-5 Oct
27-30 May
1 June
8-12 Apr,
6-10 Oct
20-22 Sept
8 Nov 93-
6 Apr 94
1994
AN-3 ♂
365 g
940 mm TL
Total Movements = 3354 m
Activity Range
MCP = 11.5 ha
HM = 17.7 ha

Figure 6. Seasonal activity map for Subjects AN-8 (solid lines) and AN-9 (dashed lines), 1994. (Activity ranges calculated by minimum convex polygon (MCP) and harmonic mean (HM) methods.)



1994

AN-8 ♀
Total Movements = 1,868 m
Activity Range
MCP = 5.06 ha
HM = 5.42 ha

1994

AN-9 ♀
Total Movements = 1,149 m
Activity Range
MCP = 1.46 ha
HM = 1.55 ha

Figure 7. Seasonal activity map for Subject AN-2, 1993. (Activity range calculated by minimum convex polygon (MCP) and harmonic mean (HM) methods.)

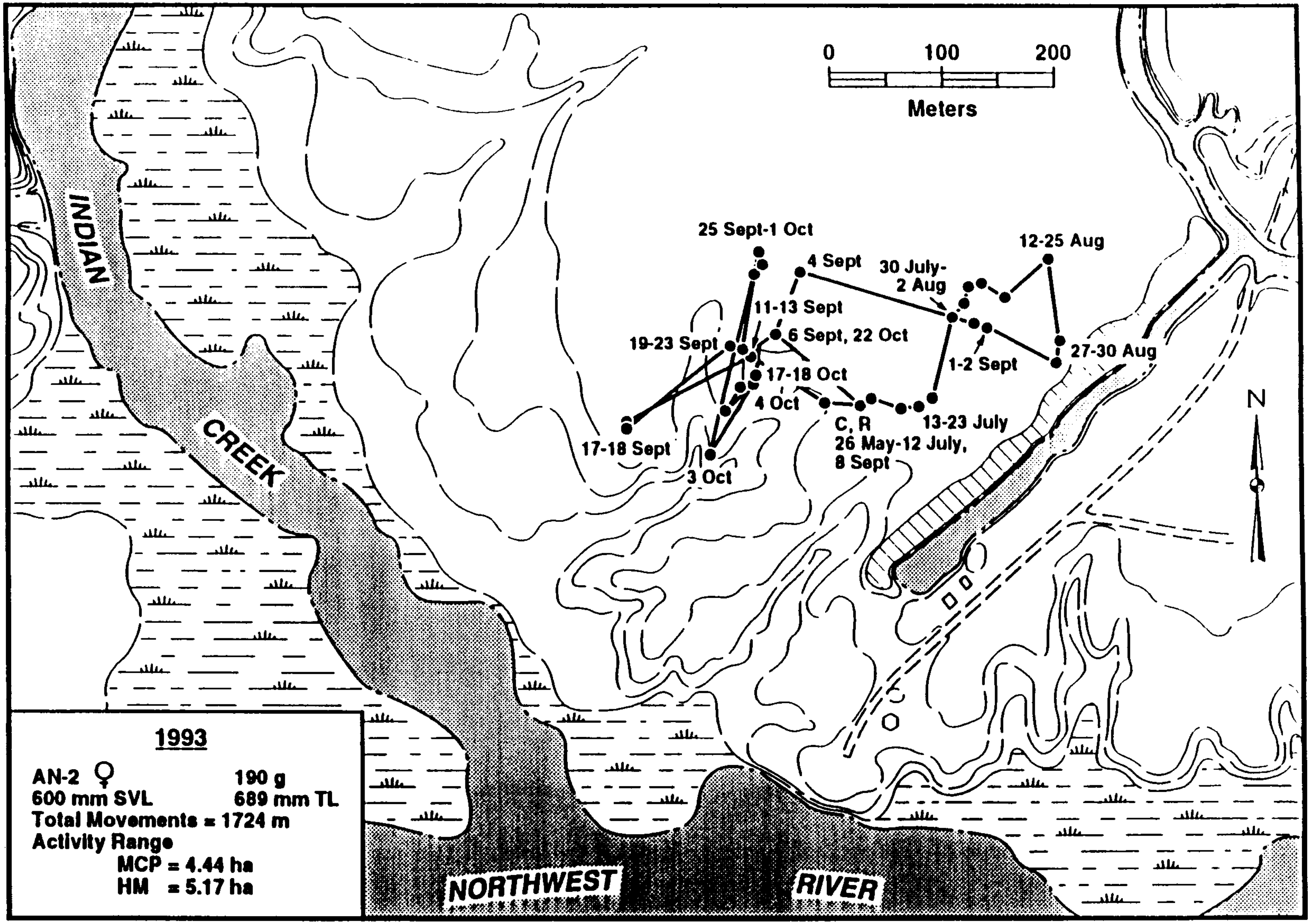
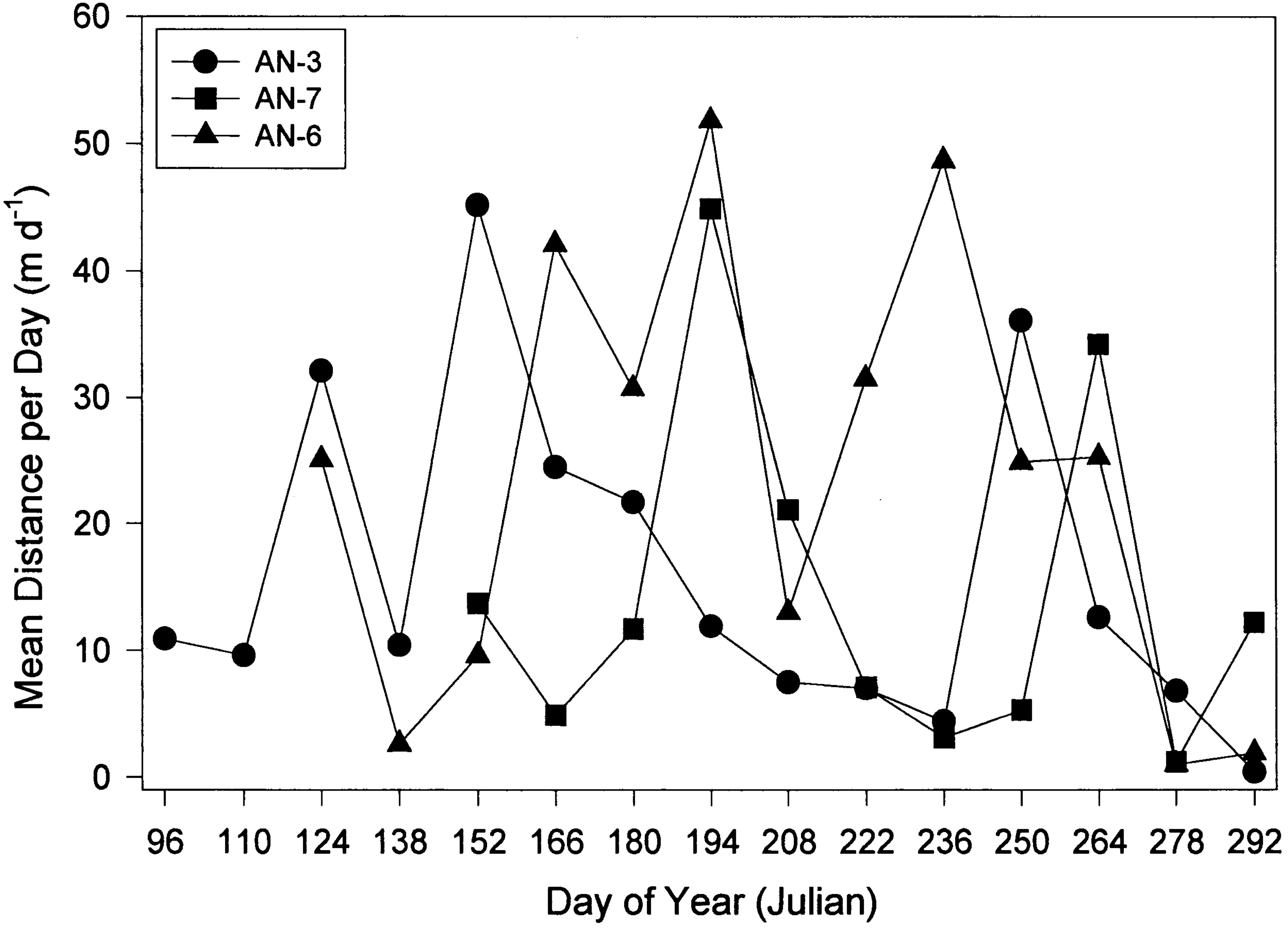

0
100
200
Meters
N
INDIAN
CREEK
NORTHWEST
RIVER
25 Sept-1 Oct
4 Sept
30 July-
2 Aug
12-25 Aug
11-13 Sept
6 Sept, 22 Oct
19-23 Sept
1-2 Sept
27-30 Aug
17-18 Oct
4 Oct
13-23 July
C, R
26 May-12 July,
8 Sept
17-18 Sept
3 Oct
1993
AN-2 ♀ 190 g
600 mm SVL 689 mm TL
Total Movements = 1724 m
Activity Range
MCP = 4.44 ha
HM = 5.17 ha

Table 3. Activity range areas and range lengths for male and female *Agkistrodon contortrix* in southeastern Virginia. Subject AN-4 omitted from this table due to small number of observations.

Subject	Sex	Harmonic mean (ha)	Minimum convex polygon (ha)	Range length (m)
AN-3 (1993)	male	7.95	13.42	526
AN-3 (1994)	male	17.66	11.52	722
AN-6	male	12.76	11.08	616
AN-7	male	3.22	3.37	379
$\bar{x}$ ± SE	male	9.60 ± 3.2	8.97 ± 2.8	540 ± 80
AN-2	female	5.17	4.44	405
AN-8	female	5.06	5.42	474
AN-9	female	1.55	1.46	192
$\bar{x}$ ± SE	female	3.93 ± 1.2	3.77 ± 1.2	357 ± 85

Figure 8. Mean distance moved per day by male *Agkistrodon contortrix* (biweekly means vs. day of year), 6 April-19 October.

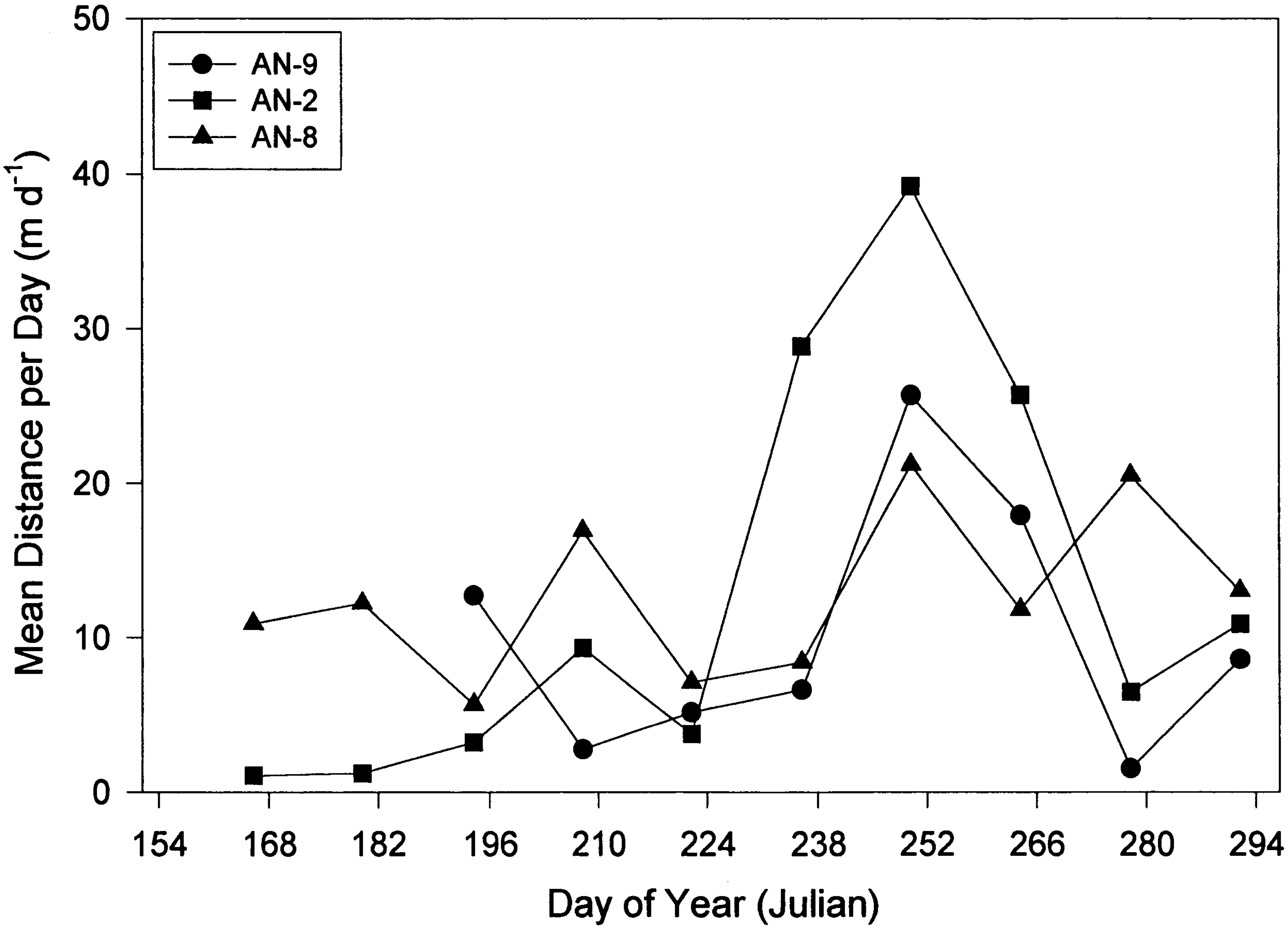

AN-3
AN-7
AN-6
Mean Distance per Day (m d^{-1})
0
10
20
30
40
50
60
96
110
124
138
152
166
180
194
208
222
236
250
264
278
292
Day of Year (Julian)

(Julian days 152-208). A reduction of activity for the three males was observed throughout most of the month of August, followed by a second, fairly constant, increased activity from late August to late September (Julian days 236-271). Male copperheads were frequently observed guarding and copulating with females during the second period of increased activity.

A unimodal activity pattern was observed for the three female subjects (Fig. 9). Females increased their activity between 1 September and 5 October (Julian days 244-278), especially between 7 and 21 September (Julian days 250-264). Females were most frequently observed with males during that period.

Shedding events significantly affected the movements of both male and female snakes. The mean distance per day fourteen days prior to shedding ($\bar{x} = 4.82 \pm 1.64$ m d^{-1}) was significantly less than the mean distance per day 14 days after shedding ($\bar{x} = 34.24 \pm 5.88$ m d^{-1}; $t=67.0$, $P=.0001$). Pre-shed snakes often remained coiled at the same site for many days with no movement; small daily movements were likely the result thermoregulatory behavior. Shedding often was followed by frequent movements by snakes, typically distances greater than 40 m d^{-1}.

Figure 9. Mean distance moved per day by female *Agkistrodon contortrix* (biweekly means vs. day of year), 1 June-19 October.


AN-9
AN-2
AN-8
Mean Distance per Day (m d^{-1})
0
10
20
30
40
50
154
168
182
196
210
224
238
252
266
280
294
Day of Year (Julian)

Habitat Use

Macrohabitats used by male and female *Agkistrodon contortrix* included forest, swamp and anthropogenic habitat (Table 4). The greatest percentage of observations (75.2%) were in forest, whereas the fewest observations (2.1%) were in swamp. Subjects AN-2 and AN-3 had activity ranges that encompassed swamp habitat; however, swamp use for these two individuals was less than 12% of their observations. Use of anthropogenic habitat accounted for a mean of 22.7% of the total observations. However, man-made habitat accounted for 46.6-55.2% of the observations of the three individuals whose activity ranges included anthropogenic habitat. Anthropogenic habitats used by copperheads included the spoil berm near the lake and artificial cover objects such as railroad ties and cement piles.

Cover objects used by snakes within the forest included treefalls, leaf litter and root tunnels. Snakes were under cover in over 50% of the observations. Specifically, snakes were located entirely under cover in 36% of observations, and partly undercover in 14.9% of observations (Fig. 10). Use of cover was most frequently observed approximately one month before and after hibernation. Generalized descriptions of the habitat at snake plots (those centered on location sites) and random plots can be derived using the means of the nine habitat variables (Table 5). The descriptions of the two groups can be used to compare and

Table 4. Habitat association of individual *Agkistrodon contortrix* (% of observations, by individual).

Subject	Sex	Anthropogenic	Swamp	Forest
AN-2	female	0	3.2	96.8
AN-3	male	0	11.2	88.8
AN-4	male	0	0	100
AN-6	male	46.5	0	53.5
AN-7	male	57.5	0	42.5
AN-8	female	0	0	100
AN-9	female	55.2	0	44.8
$\bar{x}$ ± SE		22.7 ± 10.8	2.1 ± 1.6	75.2 ± 10.1

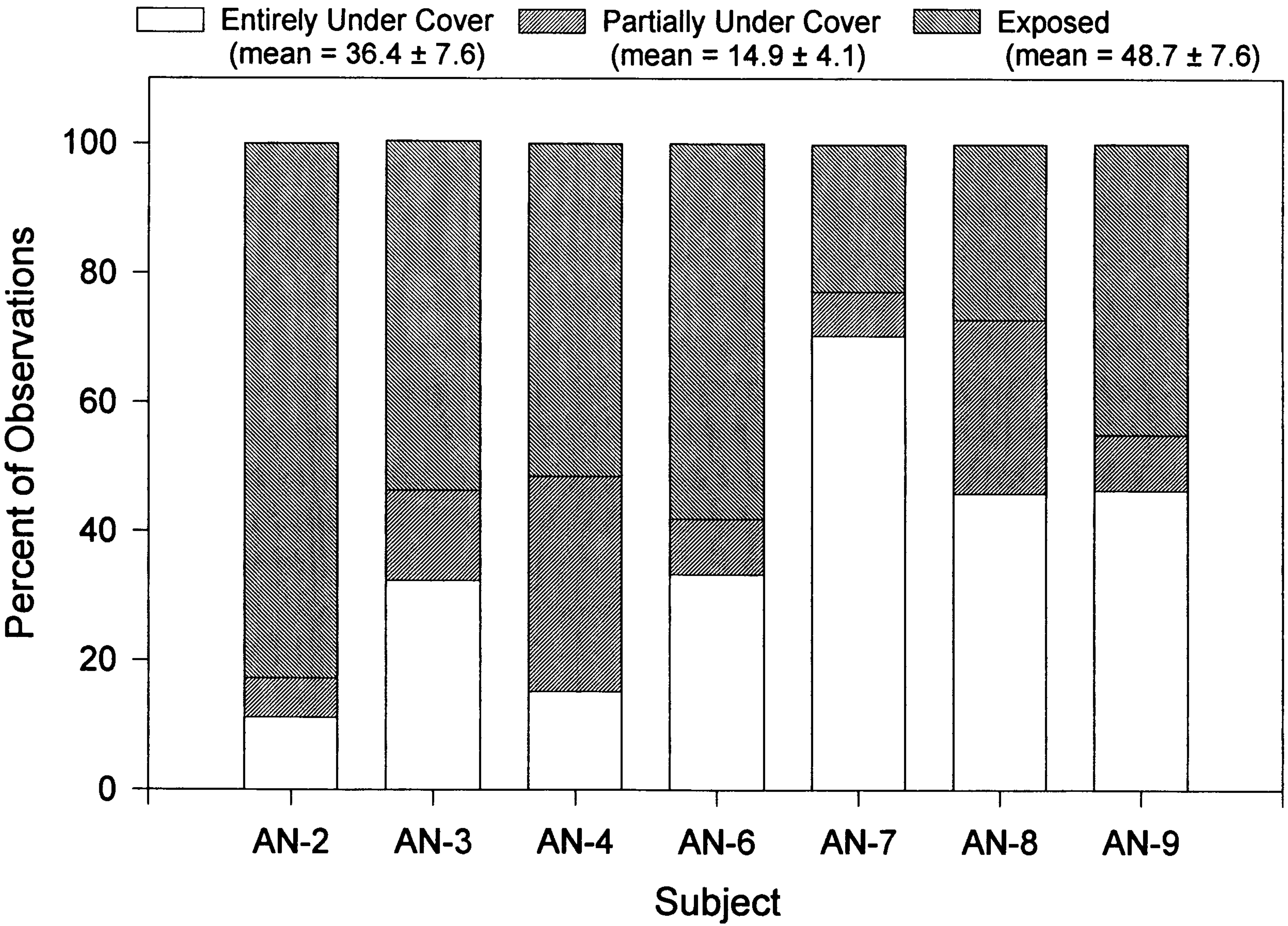

Entirely Under Cover (mean = 36.4 ± 7.6)
Partially Under Cover (mean = 14.9 ± 4.1)
Exposed (mean = 48.7 ± 7.6)
Percent of Observations
100
80
60
40
20
0
AN-2
AN-3
AN-4
AN-6
AN-7
AN-8
AN-9
Subject

Table 5. Means and standard errors of habitat variables at random sites and at sites used by *Agkistrodon contortrix*. An asterisk indicates variables that differ significantly between copperhead sites and random sites. (Habitat variables are defined in Table 1).

Variable	Random sites (*n* = 70) $\bar{x}$ ± SE	Sites occupied by *Agkistrodon contortrix* (*n* = 62) $\bar{x}$ ± SE
LEAF (%)*	98.20 ± 0.70	86.90 ± 2.94
VEG (%)*	31.60 ± 3.38	18.30 ± 2.64
LOG (%)*	2.50 ± 0.67	10.70 ± 2.44
WSD (#)	10.20 ± 1.11	8.90 ± 1.03
WSH (m)	1.13 ± 0.26	1.14 ± 0.32
DBHO (cm)*	22.30 ± 1.9	30.80 ± 2.4
DOT (m)*	1.83 ± 0.12	2.88 ± 0.28
DBHU (cm)*	3.40 ± 0.20	5.50 ± 0.34
DUT (m)	1.60 ± 0.15	1.26 ± 0.12

contrast general habitat parameters, and do not reflect statistical differences between the two groups.

The typical random forested plot was characterized by a thick canopy cover (CAN=89%), high percentage of leaf litter (LEAF=98.2%), and a low percent of fallen log cover (LOG=2.5%). Moderate vegetation cover (VEG=31%, WSD=10%) was observed on the random plots. Cane (*Arudinaria gigantea*) was the most abundant vegetation cover (WSH=1.13 m); however, other low vegetation included wild grape (*Vitis rotundifolia*), Virginia creeper (*Parthenocissus quinquefolia*) and wild ginger (*Hexastylis arifolia*). Dominant understory trees were American beech (*Fagus grandifolia*) and red maple (*Acer rubrum*) (DBHU=3.4 cm), whereas overstory trees included beech, red maple and white oak (*Quercus alba*) (DBHO=22.3 cm). The distance from a random plot to the nearest understory or overstory tree was < 2 m (DOT=1.83 m, DUT=1.60 m).

Agkistrodon contortrix used predominantly forested plots with high surface leaf litter (LEAF=86.9%), low vegetation cover (VEG=18%, WSD=8.9), and moderate fallen log cover (LOG=10.7%). As with random sites, vegetation cover was largely cane, but also included greenbrier (*Smilax rotundifolia*) and a variety of tree saplings approximately 1 m in height (WSH=1.14 m). Understory and overstory trees at snake plots were larger (DBHU=5.50 m, DBHO=30.80 m) than at random sites. As with random sites, dominant tree species included beech, maple and oak. The mean distance from a copperhead site to the nearest understory tree (DUT) was 1.26 m and to the nearest overstory tree (DOT) was 2.88 m.

A multivariate analysis of variance MANOVA on the ranked habitat data showed that group habitat centroids (multidimensional means) differed significantly between copperhead sites and random sites (Wilks' Lambda=0.602, F=9.04, P=.0001). The MANOVA was also used to determine which habitat variables differed significantly between the groups. Compared to random sites, copperheads sites had significantly lower leaf litter (LEAF; F=18.19, P=.0001) and vegetation cover (VEG; F=6.09, P=.0149) and significantly greater log cover (LOG; F=5.39, P=.0218). Overstory trees (DBO) at copperhead sites were significantly larger (F=5.80, P=.0174) and at a greater distance (DOT; F=8.60, P=.0040) than at random sites. Lastly, copperhead sites had significantly larger understory trees (DBU; F=29.41, P=.0001 than did random sites. A canonical analysis revealed that percent leaf litter density (LEAF) and diameter at breast height of the nearest understory tree (DBHU) were the most important discriminators of copperhead sites and random sites.

All *Agkistrodon contortrix* hibernated in the root tunnels of decaying tree stumps in the forest. No other snakes of any species were observed hibernating with any of the monitored subjects. Subject AN-3, the only snake followed into hibernation for two consecutive years, hibernated at the same tree stump both years.

Snakes entered hibernacula between 6 and 10 November (ingress) and emerged between 6 and 18 April (egress). The mean length in hibernation was 149±6 days. Female subject AN-9 was observed basking on six occasions during the winter months (28-29 November; 3-4, 6-7 December) during a warm period when air temperatures exceeded 20 C. All other telemetered snakes remained in their hibernacula throughout the winter without recorded emergence.

Temperature

Temperature-sensitive radiotransmitters were used to determine the body temperatures of subjects each time they were located. In order to evaluate snake body temperatures more critically, body temperatures for the hibernation period and the activity period were analyzed separately (Table 6). The mean hibernation period (8 November-13 April) was considered the interval between the mean ingress and egress dates for of the five subjects through hibernation. Conversely, the mean activity period (14 April-7 November) was the interval between the mean egress and ingress dates.

The mean minimum and maximum body temperatures during the activity period were $\bar{x}$ = 9.3±2.1 C; $\bar{x}$ = 32.9±.76 C respectively, and the mean body temperature was 22.4±1.9 C. The highest body temperature of any of the telemetered snakes (37.1 C) was recorded for

Table 6. Body temperatures (T_b) in dgrees Celsius of *Agkistrodon contortrix* during mean activity period (14 April-7 November) and mean hibernation period (8 November-13 April).

Subject	T_b during activity period (C) $\bar{x}$ ± SE (Range)	T_b during hibernation period (C) $\bar{x}$ ± SE (Range)
AN-2	23.9 ± 5.3 (0.5-31.9)	- -
AN-3	21.9 ± 5.7 (8.1-37.1)	12.1 ± 3.1 (6.8-17.9)
AN-4	25.3 ± 2.9 (18.2-31.5)	- -
AN-6	19.6 ± 6.8 (6.0-31.1)	5.7 ± 4.2 (-1.2-26.2)
AN-7	23.1 ± 4.6 (12.8-33.1)	14.2 ± 3.6 (7.1-20.6)
AN-8	21.7 ± 5.0 (10.1-33.2)	10.3 ± 2.5 (3.6-15.9)
AN-9	21.3 ± 6.2 (9.3-32.2)	11.9 ± 4.9 (5.1-31.2)
$\bar{x}$ ± SE	22.4 ± 1.9 (0.5-37.1)	10.8 ± 3.2 (-1.7-31.2)

subject AN-3 on 19 June 1994. On that day this reading was recorded, AN-3 was located partly exposed in full sunlight within the forest at an air temperature of 28.4 C. Snake body temperatures during the activity period were most strongly correlated with air temperatures (r=0.78). However, surface temperatures also were strongly correlated to snake body temperatures (r=0.74).

The mean minimum and maximum body temperatures during the hibernation period (8 November-13 April) were $\bar{x}$ = 4.3±1.5 C; $\bar{x}$ = 22.4±2.8 C respectively, and the mean body temperature was 10.83±3.2 C. The lowest body temperature (-1.7 C) was recorded for subject AN-6 on 9 February 1995, when the surface temperature was 0.4 C and the soil temperature was 2.2 C. During the hibernation period, snake body temperatures were most correlated with soil temperatures (r=0.76) and least strongly correlated with air temperatures (r=0.58).

Discussion

Daily movements of *Agkistrodon contortrix* ranged from 0-450 m, and movements <5 m represented 65% of the observations. Daily movements >100 m represented 3.5% of the observations and were commonly observed during the early summer and autumn, apparently in response to reproductive activity. Overall, the daily movements of copperheads in this investigation were similar to those reported in Kansas. Based on successive recapture of copperheads in Kansas, Fitch (1960) reported 1.5-378 m movements of individuals on their summer ranges and movements of 442-762 m for those believed to have shifted home ranges. Fitch and Shirer (1971) reported that copperheads equipped with force-fed transmitters were generally sedentary, and 0-3 m movements represented 69% of the observations. Thus, short-distance movements (<5 m) are most frequently observed for copperheads throughout the majority of the activity season, although long-distance movements may be observed during the reproductive seasons.

The seasonal movements of male copperheads were more extensive than females. Males exhibited a significantly greater mean distance moved per day and total distance moved than did females. On average the mean seasonal activity range was greater for males (9.6 ha) than females (3.9 ha). Fitch (1960) reported more extensive movements of male *Agkistrodon contortrix* than females in Kansas. Home ranges in Kansas varied from 9.8 ha for males to

3.4 ha for females, and the home range diameter averaged 345 m for males and 210 m for females. Fitch and Shirer (1971) reported that the mean distance moved per day for copperheads in Kansas was 11 m d^{-1} for males, 7 m d^{-1} for nongravid females, and 5 m d^{-1} for gravid females.

An explanation for the extensive movements of male copperheads in this investigation may be due to the mating system of these snakes. It has been suggested that increased activity and larger activity ranges of males during the courtship season may increase the probability of locating a receptive female (Gregory et al., 1987). The greater activity of male copperheads during early summer and autumn was attributed to activities such as mate searching and guarding. In contrast, females showed no increase in activity during the early summer, as did the males, and only a slight increase in activity during the autumn. High energy costs associated with reproduction may leave females with lower energy reserves than males, and therefore females may be less active in mate searching (Reinert and Zappalorti, 1988). A comparable increase in activity during the mating season has been observed for male *Crotalus h. horridus* and *C. viridis*, both pitvipers (Reinert and Zappalorti, 1988; Duvall et al., 1985) and *Coluber viridiflavus* (Ciofi and Chelazzi, 1994) a colubrid. The extensive seasonal movements of males were attributed to greater distances moved by males when searching for mates.

Reproductive condition affected the seasonal movement patterns of female *Agkistrodon contortrix*. Gravid subject AN-9 had the smallest total distance moved, mean distance moved per day, mean displacement per day, and activity range among the female subjects. That individual spent the entire activity season within a 1.5 ha site that consisted primarily of anthropogenic habitat. She was frequently observed basking on artificial spoil berms, even on days when all other copperheads were under cover. Similar observations of decreased movements in gravid pitvipers have been made for *Crotalus horridus* (Reinert and Kondrich, 1982) , *Crotalus viridus viridis* (Gannon and Secoy, 1984), and *Sistrurus catenatus catenatus* (Reinert and Zappalorti, 1988). The reduced movements of gravid females may reflect selection of fewer sites with warmer, less variable climatic conditions that enhance embryonic development (Reinert, 1993; Gibbons and Semlitsch, 1987; Reinert and Kodrich, 1982).

Shedding events had a significant effect on the movement patterns of both male and female snakes. Prior to shedding, daily movements of snakes decreased or ceased whereas after shedding long-distance movements were common. Reduced activity prior to shedding may reduce the chance of predation during the vulnerable period when the opaque skin impairs vision (Reinert, 1993). Fitch (1960) reported that pre-shed snakes in captivity were usually sluggish, whereas post-shed snakes showed renewed animation, moving more than usual.

The activity ranges of *Agkistrodon contortrix* were computed by both the minimum convex polygon and harmonic mean methods. Similar results were obtained by the two techniques. The similarity of the results from the two methods suggests that copperheads have multiple areas of intense occupation distributed throughout their activity ranges, typical of snakes that exhibit shifting activity centers (Reinert and Zappalorti, 1988). Slight differences in the areas obtained by the two methods may reflect the shape of an activity range.

Seasonal activity data indicated that *Agkistrodon contortrix* in southeastern Virginia are not nomadic wanderers that travel farther and farther from a given location (as reported in Kansas by Fitch and Shirer, 1971). On the contrary, all monitored copperheads frequently returned to exact locations within their activity ranges where they had been located previously (Maps 1-4). In fact, subject AN-3, which was monitored for two activity seasons, returned during the second year to sites where it was located the previous year, including a tree stump used as a hibernaculum. In addition to exhibiting site fidelity, one copperhead may have demonstrated homing behavior. On July 1, 1994 subject AN-7 was located moving toward an area of the study site where it was in danger of being injured by humans. The snake was translocated approximately 0.5 km to an area where it had not been located previously by radiotelemetry. Within two days the snake was relocated at an anthropogenic log pile at which it had been found in June. In comparison, a marked copperhead in Shenandoah National Park, Virginia exhibited homing ability when it returned to its place of capture after being translocated 0.8 km (Gloyd and Conant, 1990).

Learning presumably plays a role in the site fidelity of *Agkistrodon contortrix*. Individuals may learn the location of prime foraging, mating or hibernation sites within their activity ranges and return to those sites during a single activity season or over successive years. Site fidelity observed in copperheads may allow increased efficiency of resource utilization. *Crotalus h. horridus* has been observed to have stable activity ranges over many years and to return to areas within those ranges (Reinert, 1993; Reinert and Zappalorti, 1988; Gibbons and Semlitsch, 1987). *C. atrox* was observed to occupy the same summer range each year, and movements to summer areas were usually directly along particular routes

(Landreth, 1973). *Coluber viridiflavus* showed a preference for shelters in stone walls and returned to those sites many times during an activity season (Ciofi and Chelazzi, 1994). Those snakes also maintained stable home ranges between years and returned annually to the same hibernacula.

Agkistrodon contortrix have been reported to use many different habitats throughout the species' geographic range, including woodlands, swamps, rocky ledges, grasslands, and river valleys (Fitch and Shirer, 1971; Reinert, 1984a, b; Gloyd and Conant, 1990). Considerable variability in macrohabitat use by copperheads was observed in this investigation. Individuals inhabited forest, river swamp, and anthropogenic habitat.

Although *Agkistrodon contortrix* was observed in a number of macrohabitats in this study, the results indicate that these snakes are primarily forest-dwellers. Forest sites selected by copperheads differed significantly from random forest sites. *A. contortrix* used forested sites with significantly lower surface leaf litter and vegetation cover than random sites. Understory and overstory trees at snake sites were larger than at random sites, and the mean distance from a snake site to the nearest overstory tree was significantly greater than that of random sites. All of those habitat variables seem to reflect the selection by copperheads for open, less vegetated areas of the forest. Reinert (1984) reported that *A. c. mokesen* in Pennsylvania used relatively open areas with low vegetation cover and moderate rock cover. Rock cover in Pennsylvania resulted in lower vegetation cover. Although there is an absence of rock cover on the coastal plain of southeastern Virginia, less densely vegetated spaces occur within mature forested areas of the study site, perhaps resulting from treefalls or edaphic factors. Gloyd and Conant (1990) also report the preference of copperheads for relatively open deciduous forests.

Cover objects are important structural components of the habitat for *Agkistrodon contortrix*. Leaf litter, root tunnels, and treefalls were frequently used by copperheads. In fact, in over half of the observations snakes were using a cover object. Fitch and Shirer (1971) reported that copperheads were often observed partly under vegetation cover, whereas Gloyd and Conant (1990) reported that an abundance of cover objects is an essential part of the species' habitat.

The frequency of cover use may differ among habitats. For example, subjects AN-7 and AN-9, which used primarily anthropogenic habitat, were most frequently observed entirely under cover. In contrast, subjects AN-2, AN-3, AN-4, and AN-8, which used primarily undisturbed forest habitat, were most frequently observed exposed. The frequent use of cover by subjects that used primarily anthropogenic habitat may be due to thermoregulatory requirements. Commonly, anthropogenic habitats were located along the edge of a road or lake, where sunlight was abundant. Those snakes may have been able to reach preferred body temperatures under cover objects without exposing themselves to bask. In contrast, the snakes that used forest habitat may have needed to bask more extensively to thermoregulate effectively under the more continuous canopy.

The mean minimum and maximum body temperatures reported for *Agkistrodon contortrix* during the activity period (14 April-7 November) were 9.28 C and 32.87 C, respectively. The mean body temperature reported for adult copperheads in Tennessee (24.57 C; Sanders and Jacob, 1981) was greater than that reported in this investigation (22.4 ± 1.86

C). Fitch (1960) reported that body temperatures of 26-28 C were preferred for copperheads in Kansas.

The mean minimum body temperature for hibernating copperheads was 4.27 C. In fact, the lowest recorded body temperature was -1.7 C (AN-6, 9 February 1995). It is possible that hibernating copperheads may be able to survive even when body temperatures approach freezing, at least briefly. Lowe et al. (1971) reported that many reptiles are able to escape the lethal effects of freezing by supercooling their bodies below the freezing point of body tissues, without the formation of ice. For example, pitvipers such as *Crotalus cerastes* and *C. lepidus* can survive body temperatures as low as -5.22 C. Fitch (1960) reported that copperheads were able to survive after being cooled to -1.5 C, although the critical thermal minimum differed among individuals. Sanders and Jacob (1981) reported a significant negative correlation between snout-vent length and the critical thermal minimum of individual copperheads. Snakes with larger snout-vent lengths had lower critical thermal minima. Thus, it may be possible that copperheads are able to survive temperatures slightly below freezing during the hibernation period. This may explain how these snakes survive in shallow hibernacula where they may naturally be subjected to low temperatures, occasionally below freezing.

In conclusion, the major finding of my study conform in many respects to those of earlier wokers, notably Fitch in Kansas and Reinert in Pennsylvania. Short daily movements were most frequent for copperheads in both Virginia and Kansas, and in both locations the seasonal movements of males were more extensive than those of females. The extensive seasonal movements of males may be due to activities such as mate searching and mate guarding during the mating season. Copperheads in southeastern Virginia, like those of Pennsylvania, selected open, less vegetated microhabitats, despite differences in structural habitat. The selection of such sites by copperheads may be related to the thermoregulatory requirements of these snakes. Body temperatures of copperheads in Virginia were similar to those reported from other locations throughout its geographic range. Daytime body temperatures for copperheads generally ranged from 24-28 C, and body temperatures near freezing may be attained during hibernation. Future ecological research on *Agkistrodon contortrix* would benefit from investigation of the movement patterns and habitat use of juvenile individuals, the seasonal activity of translocated individuals, and the interactions between copperheads and sympatric ophidian species.

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