To the Graduate Council:

I am submitting herewith a thesis written by Bridget Donaldson entitled "Aquatic Habitat Utilization Relative to Home Range and Seasonal Movement of Eastern Box Turtles (*Terrapene c. carolina*: Emydidae) in Eastern Tennessee." I have examined the final copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Ecology and Evolutionary Biology.

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Aquatic Habitat Utilization Relative to Home Range and Seasonal Movement of Eastern Box Turtles (*Terrapene c. carolina*: Emydidae) in Eastern Tennessee

A Thesis
Presented for the Master of Science Degree
The University of Tennessee, Knoxville

Bridget M. Donaldson
May 2001

ACKNOWLEDGMENTS

I am deeply grateful to my major professor, Sandy Echternacht, for offering the perfect combination of skillful guidance and freedom to self-direct. This provided me with the best possible learning scenario, and helped confirm my passion for this field.

I am also grateful to my field assistants, Chad Richmond and Jeff Greene, who not only substantially eased my load of fieldwork, but also helped make it the enjoyable and rewarding experience that it was. I thank Gordon Burghardt and Susan Riechert for their helpful criticism in reviewing my thesis, to various graduate students for their patient assistance in searching for turtles, and Todd Campbell, Phil Heise, Sandy Echternacht, and Ryan MacDonald for helping with grid construction. I also greatly appreciate the financial assistance I received from the Ecology and Evolutionary Biology Department.

I thank Wayne Turner and the Piney Hunt Club for granting me permission to work on their land, as well as Josh Green for providing me with this thesis topic and introducing me to the wonderful world of eastern box turtles.

Finally, the greatest dept is owed to Ryan MacDonald, and to my parents Mike Donaldson, Bonnie Clarke Kingsbury, and Steve Kingsbury, whose unconditional faith in me has given me the confidence to tackle anything.

ABSTRACT

Eastern box turtles are largely characterized in the literature by their terrestrial tendencies, with little attention paid to the ecologically important role of water in their lives. Their rapidly declining populations due to habitat loss and overcollection call for an urgent need to assess all aspects, terrestrial and aquatic, of their habitat requirements. Trailing devices and radio transmitters were used to evaluate seasonal movement and to determine the extent to which turtles utilized aquatic habitats within their home ranges. Home ranges were determined by minimum convex polygon (MCP) and fixed kernel methods. Home range sizes averaged 1.88 ± 0.49 ha via MCP analysis, and 2.26 ± 0.76 ha via 95% kernel analysis. Kernel estimators were more effective at representing uneven home range use, often demonstrating the heavy use of water relative to other areas. Turtles used creeks and temporary ponds in three separate areas from June through August. Extension of their home ranges frequently occurred when they took abrupt linear movements towards the water in response to high temperatures and low precipitation. One hundred thirty one turtles were found in two small temporary ponds, individuals remaining in the ponds for up to 21 consecutive days (range = 1-21, $\overline{x} = 6.1$). This study demonstrates that wet areas have a significant effect on eastern box turtle lifestyle. They should be considered in wetland area conservation decisions where appropriate.

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Introduction

Turtles (order Testudinata) occupy a broad range of habitats, and the most conspicuous adaptations they possess are often those that reflect their aquatic or terrestrial lifestyles. With the exception of tortoises (Testudinidae), the majority of turtles are semi to highly-aquatic, as evidenced by their streamlined shells and partially to fully webbed digits (Cogger and Zweifel 1998). Despite the general tendency of turtles in most families to spend much of their life cycles in bodies of water, many families include species that are highly terrestrial. The terrestrial forms are typified by domed carapaces and discrete clawed digits. Among these are box turtles of eastern and southern U.S. and Mexico (*Terrapene*, Emydidae). Although Coahuilan box turtles (*Terrapene coahuila*) are strictly aquatic (Cogger and Zweifel 1998), the other species of *Terrapene* vary in degree of semi-aquatic to terrestrial tendencies.

In order to understand the relative importance of water within the Emydidae, it is helpful to approach it from an evolutionary perspective. Proposed phylogenic relationships among emydids are debated and basically unresolved. Milstead (1969) suggested that the genera *Terrapene* and *Emys* derived from the monophyletic ancestor *Clemmys*. Burke et al. (1996), however, suggested that the genera *Emys, Emydoidea*, and *Terrapene* formed a monophyletic clade while the genus *Clemmys* is paraphyletic.

Milstead (1969) and Minx (1996) considered *Terrapene ornata and T. carolina* to be basal clades within the genus *Terrapene*; *T. coahuila* is believed to have appeared as an early derivative of the *carolina* group. There are six subspecies of ***Terrapene,*** all of which are considered terrestrial. *T. c. triunguis* formed a clade with *T. c. mexicana* and *T.*

c. yucatana. *T. c. carolina* has a terminal location and shares a sister relationship with *T. c. bauri* (Minx 1996).

There is no consensus on whether turtles ancestral to members of the genus *Terrapene* were aquatic or terrestrial. It is generally agreed that terrestriality has evolved independently several times within the Emydidae (Burke et al., 1996). Zug (1971) argued that based on gait analysis, the terrestrial *Terrapene* and *Emydoidea* shared a recent ancestor that was terrestrial, and that plastron closure (which is a trait exclusive to *Terrapene*) was an adaptation to terrestrial life. Burke et al.'s (1996) phylogenetic analysis, however, suggests that the common ancestor of the *Emys-Emydoidea-Terrapene* clade was aquatic, supporting Bramble's (1974) hypothesis that evolution of the plastron closure involved a series of modifications that probably could only have evolved in species supported by water.

Eastern Box Turtles

Eastern box turtles (*Terrapene carolina carolina*), one of four terrestrial subspecies of *T. carolina* in the United States, range across most of eastern, central, and southern U.S. (Conant and Collins 1998). They are found in a variety of wooded habitats (Stickel 1950) from New England, south to Georgia, west to Michigan, Illinois, Tennessee, and northern Alabama (Ernst et al. 1994).

Eastern box turtles mate almost continuously during their activity periods from March or April through October or November, with peaks from May to June and from September to October (Gould 1998). Females generally lay a clutch of eggs between May and July (Gould 1998). In Tennessee, hatchlings from clutches laid late in the year may over-winter underground before emerging in the spring (A.C. Echternacht, pers.com.). Eastern box turtles exhibit temperature dependent sex determination (Ernst et al. 1994). Nevertheless, percentages of males and females are basically equal in wild populations (Dolbeer 1969, Stickel 1950, Madden 1975). Carapace lengths reach 19.8 cm, with males being larger than females (Conant and Collins 1998). Natural longevity in both sexes is 45 to 50 years, though some are known to live longer than 60 years (Williams and Parker 1987).

Home Range

Eastern box turtles have a strong tendency to retain the same home range from year to year (Nichols 1939, Stickel 1950, Yahner 1974, Strang 1983). Home range size depends on habitat quality as well as population density among this and many other turtle species (Diemer 1992, Nieuwolt 1996, Stickel 1989). Because home range estimates are greatly affected by the number of locations on which each estimate is based (Seaman et al. 1999), however, comparisons of home range size between individuals and studies may be of limited use if these sample sizes are not considered (home range sizes reported in *T. c. carolina* studies, Fig. 1).

Eastern box turtles show non-aggressive social relationships (Stickel 1950), although fighting over food among captives has been reported (Allard 1935, Boice 1970). They are not territorial, evident partly by the significant degrees of home range overlap (Stickel 1989). Considerable home range overlap is common among many turtle genera (Calzohai and Chelazzi 1991, Chase et al. 1990, Geffen and Mendelssohn 1988, Stickel 1989). Because reproduction among Eastern box turtles relies on chance encounters among adults (Belzer 1999a), home range overlap is important in maintaining their populations.

Seasonal variations in home ranges are common among Eastern box turtles, though there is a great deal of individual variation in the extent to which home ranges vary over seasons. Changes in temperature and humidity were found to influence such habitat shifts (Regan 1974, Doroff and Keith 1990), though Cook (1996) did not find that these variables affected such shifts.

Other turtle species that show substantial terrestrial movement also exhibit seasonal home range use. Wood turtles (*Clemmys insculpta*, Emydidae), considered the most terrestrial of the North American emydids next to *Terrapene* (Kaufmann 1992), exhibited individual variation in the extent to which individuals used different areas on a seasonal basis. (Kaufmann 1995, Quinn and Tate 1991). Geffen and Mendelssohn (1988) found that the Egyptian tortoise (*Testudo kleinmanni*, Testudinidae) use of areas within home ranges varied significantly between the seasons.

In addition to the influence of environmental variables on home range use, searching for suitable nesting sites also incites home range shifts by gravid females. These home range shifts are common among female Eastern box turtles (Williams and Parker 1987, Stickel 1989) and ornate box turtles (*T. ornata*, Legler 1960), though many females nest within areas they use during the rest of their activity season. Female yellow-blotched map turtles (*Graptemys flavimaculata*, Emydidae) are also known to move seasonally within their home ranges while nesting and searching for receptive males (Jones 1996).

Movements

Because box turtles are ectothermic, their movements are largely a response to the surrounding climatic factors (Reagan 1974, Stuart and Miller 1987, Claussen et al. 1997).

Eastern box turtles have generally been found to be most active on warm and sunny days, especially following showers (Stickel 1950, Dolbeer 1971, Reagan 1974, Strang 1983, Stickel 1989) and they are least active in cold or dry weather (Dolbeer 1969, Strang 1983). In addition to warm temperatures, high humidity and rainfall is also correlated with peak activity among Florida box turtles (*Terrapene c. bauri*, Dodd et al. 1994).

In support of these findings, Adams et al. (1989) found that the body temperature of Eastern box turtles, which were clustered about the simultaneous ambient temperatures, was a good predictor of locomotor behavior. Though movement was very individualistic at higher temperatures, box turtles rarely moved at body temperatures averaging 10°C or less. Body temperatures between 24 and 32°C seemed to maximize turtle movement.

Dolbeer (1969) and Stuart and Miller (1987) found Eastern box turtles to be less active during the summer than in the spring or fall. This is likely a response to high heat coupled with lack of rainfall, possibly influenced by the fact that invertebrates are scarcer on dry days (Strang 1983). Desert tortoises (*Gopherus agassizii*, Testudinidae) in the Mojave Desert similarly experience significant decreases in activity, including amount of travel, during drought years.

During periods of inactivity, Eastern box turtles commonly retreat in cavities (given the term "forms" by Stickel [1950]) that they construct in leaves, debris, or soil. Shade and visual proximity to objects is thought to be important as indicators of suitable resting sites such as these (Davis 1981). Forms may provide some protection against temperature extremes while concealing turtles from predators.

Hibernation

Eastern box turtles begin establishing hibernation sites in mid-October in Maryland (Stickel 1989) and between mid-October and mid-November in Tennessee and Ohio (Dolbeer 1969, Claussen et al. 1991), although Dolbeer (1969) found that many turtles remained active until mid-December in the presence of showers. In Wisconsin, *Terrapene ornata* enter hibernation in September (Doroff and Keith 1990). Hibernacula were within the normal home ranges of *T. ornata* (Legler 1960) and *T. c. carolina* (Stickel 1950).

Eastern box turtles prefer woody habitats for hibernacula (Cook 1996, Dolbeer 1969), where they typically burrow under leaf litter, rotting wood, or stump holes (Dolbeer 1971). The depths of hibernacula increase as ambient temperatures decrease (Dolbeer 1971, Claussen et al. 1991), ranging from 0 cm (where the top of the carapace is even with the soil surface) to 15 cm beneath the soil surface (Dolbeer 1971, Congdon et al. 1989, Claussen et al. 1991). In Tennessee (Dolbeer 1969) and Ohio (Claussen et al. 1991) the turtles generally begin emerging from their hibernacula in March.

Water Use

Studies of some semi-terrestrial species have revealed the importance of water to their movement and home range use. Despite their heavy use of terrestrial areas, wood turtles (*C. insculpta*) in central Pennsylvania entered creeks in cool periods, and only 5% of observed movements were outside of the creek area (Kaufmann 1992). Quinn and Tate (1991) found that although 14% of observed wood turtles were in water, 73% of observations of turtles on land were within 30 m of water. Blanding's turtles (*Emydoidea blandingi,* Emydidae) in Wisconsin, commonly considered "semi-box turtles" (Conant and Collins 1998), used ponds more often than predicted based on the available habitat (Ross and Anderson 1990).

Drought-related responses have been studied in several aquatic and semi-aquatic turtle species. Many species respond to dropping water levels by emmigrating to other wet areas. Painted turtles (*Chrysemys picta belli*, Emydidae, McAuliffe 1978) and stinkpots (*Sternotherus odoratus,* Kinosternidae, Ernst 1986) have been reported to leave a drying pond for another body of water. Spotted turtles (*Clemmys guttata*, Emydidae) in Massachusetts exhibit cyclical movements in response to seasonal environmental changes. They migrate to vernal pools in late March until August, when they aestivate in terrestrial forms until migrating to permanent swamps for the fall (Graham 1995). The terrestrial movements of chicken turtles (*Deirochelys reticularia*, Emydidae) correlate with ponds in Virginia drying progressively from west to east (Buhlmann 1995). Japanese pond turtles (*Mauremys japonica*, Emydidae) move to brooks and ponds when the paddies they normally inhabitat are irrigated (Takashi 1992).

Behavior in response to drying wetlands varies among turtle species that share the same aquatic environment. In a study of five aquatic species in a South Carolina bay, yellow-bellied sliders (*Pseudemys scripta*, Emydidae) and Florida cooters (*P. floridana*) showed substantially higher emigration rates in drought years compared to previous years, while *Sternotherus odoratus,* Eastern mud turtles (*Kinosternon subrubum* Kinosternidae), and *Deirochelys reticularia* exhibited no change in emigration patterns (Gibbons 1986). Similarly, *K. subrubum* remained in an experimentally drained pond while the more aquatic species in these areas emigrated as soon as water levels began to drop (Gibbons et al. 1983).

Conversely, some of the more terrestrial species move to aestivation sites for the duration of the dry season. Decreasing pond water depths in the spring correlate with the dispersal of striped mud turtles (*Kinosternon baurii*) to aestivation sites in forests in west-central Florida (Wygoda 1979). In Mexico, *K. leucostomum* also dispersed to the surrounding forest to aestivate in response to the dropping lake level (Morales-Verdeja and Vogt 1997).

Accounts of *Terrapene carolina* in the water are rare, and generally do not address the significant role water can play in their lives. Overton (1916), Cahn (1933), and Stuart and Miller (1987) reported instances of several *Terrapene carolina* (the latter reference specifying T. *c. carolina*) soaking in shallow water during hot, dry periods. Madden (1975) found one *T. c. carolina* in an eight inch deep pool, and there have been reports of *T. c. carolina, T. c. triunguis* (Overton 1916, Stickel 1950, Tyler 1979) and *T. c. bauri* (Dodd et al. 1994). swimming around or across small ponds and streams. Despite these intermittent reports, studies of box turtles have not addressed the extent of nor the ecological importance of water use, possibly due to the common conception that these terrestrial turtles are poor swimmers and rarely enter water more than a few cm deep (Pritchard 1979).

Rationale for Study of Wet Habitat Use by Eastern Box Turtles

Eastern box turtle populations have dramatically declined in the past several decades. Williams and Parker (1987) recorded a 50% reduction in estimated population size of Eastern box turtles over 13 years due to habitat destruction and over-collecting. Stickel (1978) reported a similar reduction after 30 years, and Hall et al. (1999) found a decline of > 75% over 40 years. All North American box turtles are currently listed on

CITES Appendix II, which includes species that may become threatened with extinction unless trade is properly managed and regulated (Lieberman 1994). Despite this protection, their populations are continuing to decline and are becoming threatened in many areas.

Eastern box turtles rely on high densities in small areas to sustain their populations (Stickel 1950, Doroff and Keith 1990). Even small declines in density create instability, making populations more vulnerable to extirpation (Doroff and Keith 1990). Effective management for the conservation of the species will require detailed knowledge of all aspects of their habitat requirements and seasonal habitat use.

Perceiving eastern box turtles as highly terrestrial and therefore not reliant on bodies of water for their feeding and reproductive needs may undermine the important role water can have on their seasonal activity and use of space. In addition to assessing home range and seasonal activity, the goals of this study were to determine the extent to which these turtles utilize aquatic habitats, to consider the environmental variables that elicit water-seeking behavior, and to investigate the influence wet areas may have on their movement patterns and home range use.

Materials and Methods

Study Area

The majority of research was conducted within in a wooded area owned by Bowater Paper Company in Loudon County, Tennessee, approximately 51 kilometers south of Knoxville (35° 55' 03" N, 83° 57' 02" W). This area consists of an open logging road situated between an extensive tract of pine woodland (dominant = loblolly pines [*Pinus taeda L.*]), to the east and a large area of deciduous forest to the west. In several areas along either side of the logging road, blackberry bushes (*Rubus sp.*) are predominant (Fig. 1). The deciduous trees consist of tulip trees (*Liriodendron tulipifera*), white oak (*Quercus alba*), scarlet oak (*Quercus coccinea*), black walnut (*Juglans nigra*), black gum (*Nyssa sylvatica*), hickory species (*Carya sp*), several maple species (*Acer sp.*), osage-orange (*Maclura pomifera*), and sassafras (*Sassafras albidum*). The herbaceous cover in all areas of the site is dominated by poison ivy (*Rhus toxicodendron*), Christmas ferns (*Polystichum acrostichoides*), and Virginia creeper (*Parthenocissus quinquefolia*). The substrate in the pine-dominated areas consists of a thick layer of pine leaf litter, creating a soft consistency and greater depth than that of the substrate in areas dominated by broad-leafed trees.

Two small temporary ponds (referred to hereafter as northern and southern ponds) of standing water are located on the logging road, both of which collect rain as it runs off the adjoining hills. The highest hill, just south of the southern pond, is approximately 310 m in elevation, and both ponds are approximately 260 m in elevation (Fig. 2). The southern pond consists of two 3.0 m x 11.0 m pools, separated by a grassy strip 1.0 m in width. After heavy rains, these pools hold water to a maximum depth of 33 cm. The northern pond, 430 m north of the southern pond, is 3 m x 7 m at its maximum depth of 26 cm. A stream approximately 2.5 km east of this study sight was also occasionally searched for turtles.

Data on use of wet areas was also obtained at a creek 2.5 km east of the main study area, and at the University of Tennessee Cherokee Woodlot in Knoxville, Tennessee. Dolbeer (1969) and Yahner (1971) conducted research in this woodlot and presented extensive data of Eastern box turtle movement patterns, though turtle activity in relation to water was not investigated. The specific area of interest within the woodlot consists of a small stream and a small pond adjacent to a wooded flood plain which remains wet a large part of the year.

Study Grid. – The study area in Loudon was gridded with quadrats in 20 m intervals on either side of the logging road. The initial plot was laid out in a 220 x 120 m grid and divided into 66 quadrats of 20 x 20 m each. The corner of each quadrat was marked by rebar stakes labeled with a unique letter-number combination. The numbers progressed from east to west and the letters from south to north, with the main wet area slightly off the center of the grid towards the south-east corner. The grid was later increased to 660 x 460m once it became apparent that many turtles' home ranges extended beyond the original grid. Labeled markers were added to the original grid along the logging road, some extending on either side of the road into the woods (Fig. 3). Despite the increase in grid size, the far majority of tracked turtles were found within or near the initial grid.

Environmental Data and Turtle Measurements

Daily air temperature was recorded by a StowAway TidbiT® temperature data logger (Onset Computer Corporation; Range: -30C to 50C) placed in the main study area, and was also obtained from a nearby NOAA meteorological station (35° 50' 03" N, 3° 57' 02" W). Daily precipitation records were also obtained from the NOAA station. Water depth of the two temporary ponds was recorded biweekly and three temperature data loggers were placed in the ponds; two loggers were placed in the center, and one was placed in a crevice (dug out and occupied by turtles part of the year) along the border of a pond.

Captured turtles were found as a result of non-random searches throughout the study area. The most heavily searched areas were those within the original rectangular grid, particularly within and immediately surrounding the southern pond centered in that grid. The northern pond (outside of the original grid) was also regularly searched once turtles were found there.

Each turtle captured within the study area was marked by notching different combinations of marginal scutes (Cagle 1939) with a triangular file. In addition, the number of the turtle was marked with nail polish on the carapace for easier field identification. Date, time of day, habitat, carapace length, sex, weight, morphological abnormalities, and approximate age were noted for each new turtle encountered. Carapace length was measured with a plastic ruler to the nearest tenth of a centimeter. Juveniles were arbitrarily defined as individuals with a carapace length less than 9.5 cm; the weights of these turtles correspond with Dolbeer's (1969) method of assigning 170 g as the cutoff point for juveniles. Weight was measured with a Pesola® 600 g scale to the nearest five grams. Collecting locations were recorded according to the distance and compass direction of the turtle from the two nearest labeled markers.

Trailing Devices

To accurately document routes and distance traveled within an individual's home range, trailing devices were attached to 20 individual turtles. The locations of the turtles were charted daily from May 9 through August 22, 2000. The trailing device consisted of a 35mm film canister, containing a spool constructed out of a screw with a plastic washer fastened on either end. For juvenile turtles, the film canisters and spools were shortened. The small (19 g) and large spools (24 g) hold up to 180 m and 250 m, respectively, of extra-strong cotton thread, wound with the aid of a flex shaft. After placing the loaded spool inside the canister, the end of the thread was passed out through a pin-sized hole and the device was bonded to the anterior end of the carapace with PC-11 epoxy and duct tape. The thread was attached to a nearby object at the capture site, allowing the thread to be deposited behind the turtle as it moved. This method was modified from that of Breder (1924) and Reagan (1974) in order to ensure stability of the device on the carapace and to fit a maximal amount of string in the canister. Stickel (1950) reported that the behaviors of *T.c.carolina* were completely unaffected by attached trailing devices, including distance traveled.

Distance Traveled. – The 20 turtles fitted with trailing devices were tracked from five to 106 days. In cases where a trailed turtle was lost due to string breakage or detachment of the trailing device, the next turtle found was affixed with a device. The lines were measured and retied every day, and spools were replaced when less than half of the thread remained. Distances traveled were paced out (two paces = 1.0 m) (Hailey

1989) as the string was followed. Routes were drawn on graph paper in reference to the location markers and with the aid of a compass to measure angles when the turtle's direction changed. Date, time of day, habitat, general weather conditions, and activity were recorded each time the turtle was located at the end of his/her string path.

Mean distance traveled per day was calculated for each of the 17 turtles that were trailed for at least two weeks. Due to occasional difficulties, such as string breakage, any incomplete movements recorded in a day were excluded from the analysis. In order to determine possible relationships between distance traveled, temperature, and precipitation, these variables were assessed by Pearson correlation and linear regression analyses. Gender differences in average daily distance traveled were analyzed via an independent samples t-test.

Water Use

Every one to two days during the entire duration of pond use (June 19 to August 20), the two temporary ponds in the Loudon study site were thoroughly searched for new and previously marked turtles. Searching these ponds became unnecessary once the ponds dried August 22 for the remainder of the season. New turtles were marked and recaptured turtles were recorded and repainted, if necessary, for clearer number recognition.

Although both northern and southern temporary ponds were searched every two days, the far majority of tracked turtles were closer to the vicinity of (and utilized) the southern pond; therefore the analyses related to pond use were generally applied to the southern pond. Relationships between precipitation or temperature (air and water) and southern pond use were evaluated by Pearson correlation and linear regression analyses.

Turtle densities in the southern pond were analyzed with temperature and precipitation values from the previous day to illustrate a more accurate reflection of turtles' responses to these variables. The number of turtles captured, if any, was also recorded for the wet areas in the Cherokee Woodlot and for the stream 2.5 km east of the Loudon study site (searched 11 and 9 times, respectively).

Radio Transmitters

On September 8, 2000, radio transmitters were attached to the rear carapaces of six turtles (subsequent to trailing device removal) in order to continue home range data collection and to locate the test subjects before and upon entrance of hibernacula. Each transmitter, weighing 22.6 grams, was bonded to the rear of the carapace with PC-11 epoxy and duct tape. Locations of these turtles were recorded in reference to the labeled markers biweekly.

Hibernation. – The date of entrance into hibernacula of each of the six turtles was recorded, as well as the corresponding weather conditions, hibernacula depth, and vegetation that comprised and immediately surrounded each hibernacula. Turtles were located until they remained in hibernacula for four weeks. Date and duration of temporary emergence from hibernacula were recorded and compared to corresponding weather conditions.

Home Range Analysis

Locational and movement data collected from turtles equipped with trailing devices for at least four (not always consecutive) weeks were transferred to a grid of the study area created on ArcviewGIS® (Environmental Systems Research Institute, Redlands, California, USA). For clearer visibility of locations plotted on the maps, locations were plotted in two-day intervals, though paths were recorded daily for each turtle. Data collected from the six turtles fitted with radio transmitters were plotted along with their previous positional data obtained from string trailing. Movements and locational data obtained from string trailing and radio transmitter data were evaluated in reference to the standard U.S. calendar dates (spring: March 21-June 20, summer: June 21-September 20, fall: September 21-December20) in order to assess seasonal variation in home range use.

Home range for this study is defined as "...that area traversed by the individual in its normal activities of food gathering, mating, and caring for young" (Burt 1943). The animal movement extension (Hooge et al. 1999) in ArcViewGIS® was used to determine home ranges via minimum convex polygon (MCP) and fixed kernel methods. The minimum convex polygon, formed by connecting the outermost locations of an animal to create the smallest possible polygon, is the most widely used home range estimator (Madden 1975, Harris et al. 1990). MCP is also the most conservative of the commonly used techniques, providing the smallest estimate of home range (Madden 1975). The kernel method is one of the least biased and most precise home range estimators (Worton 1995, Seaman et al. 1998), using animal locations to create probability density estimates. Fifty percent and 95% contours were created via the fixed kernel method; 50% contours reflected turtle core home ranges (where there was high intensity of use), and 95% contours indicated total home range size.

Home ranges were based on points in which turtles were located; routes of travel obtained from string trailing were not used in home range construction. Because the paths of each turtle depict its total as well as core home range, they serve as effective indicators in comparing accuracy between MCP versus kernel home ranges. Since kernel estimation is especially sensitive to sample size (Seaman et al. 1999), only home ranges of turtles with > 30 locations ($n = 6$) were averaged for comparison with MCP estimators. Relationships between carapace length and home range size calculated by both MCP and kernel methods were also considered, and were assessed by Pearson correlation and linear regression analyses.

Results

Turtle Measurement Data

A total of 166 turtles were found in the main study area in Loudon County, Tennessee from March through December, 2000: 90 males (54.2%), 50 females (30.1%), and 26 juveniles of undetermined sex (15.7%). Females (N=8) fitted with trailing devices or radio transmitters had carapace lengths between 9.7 and 11.9 cm, and males (N=12) between 12.0 and 13.6 cm (Fig. 4). The mean carapace length of all males (± SE) was 12.1 ± 0.11 cm and was significantly greater (t-test, $p = 0.002$) than that of females (11.52 ± 0.15 cm). Despite their greater lengths, the mean mass of males (336.1 ± 8.56 g) was not significantly greater than that of females (324.4 ± 13.23 g) (Table 2).

Distance Traveled

Twenty turtles fitted with trailing devices were tracked between five to 106 days ($\bar{x} = 45$ days). In order to obtain an accurate representation of distance traveled for each individual, daily averages were calculated only for healthy turtles tracked for at least two weeks. One individual's travel records were disregarded due to the fact that he became ill and died after remaining in the pond the entire 42-day duration for which the trailing device was attached. The mean distance traveled per day for the remaining 17 turtles was 26.0 ± 3.1 m; in four instances, previously trailed turtles were recaptured days to weeks after inadvertent trailing device detachment (Fig. 5). Average distances traveled were not significantly different between males and females.

Distances traveled were also averaged over five-day intervals for these 17 turtles, as were the corresponding precipitation and temperature averages (Table 3). A great deal of variation was found among individuals in terms of extent of movement under various environmental conditions; some individuals remained in forms or the temporary ponds for days to weeks at a time throughout the summer, while a few exhibited considerable daily movement despite extreme high temperatures.

A significant negative relationship existed between daily distance traveled and high temperature ($r=0.364$, $p<0.001$, Fig. 6). There was a significant positive relationship between daily distance traveled and precipitation ($r=0.408$, $p<0.001$, Fig. 7). When temperatures remained high with no precipitation for days, the majority of trailed turtles either traveled relatively little to none on land or remained submerged in the temporary pond.

Water Use

Ambient daily high temperatures during the range of temporary pond use by turtles ranged from 22.7°C to 30.6°C. Precipitation levels during this time varied from periods of no rain for up to 6 days, to 43.7 mm of rain in one day (Fig. 8). Turtles began entering both temporary ponds in the study area in mid-June, and had left by the end of August (Fig. 9). A total of 131 turtles was found in northern and southern temporary ponds during this time frame, 96 of which were found in the southern pond. The peak density of 32 individuals in the southern pond occurred during the first week in July. No newly discovered turtles entered the pond after the last week in July (Fig. 10). One turtle was repeatedly seen drinking from the pond; this was the only tracked individual that also visited the pond when it was dry.

Periods of low rainfall coupled with high temperatures were associated with migration to the temporary ponds. As temperatures decreased and pond depths increased, turtle density in the ponds decreased (Fig. 11). Turtle density in the southern temporary pond increased with increasing temperatures (r=0.588, p=0.001, Fig. 12). Average turtle density was negatively correlated with precipitation (r=-0.428, p=0.023, Fig. 13); turtles density in the temporary pond dropped after each period of substantial rainfall. Open water high temperatures in the southern pond averaged 26.1° C (Range: 22.2° C - 30.8° C). Average turtle density was negatively correlated with average pond temperature (r=-0.656, p=0.039, Fig. 14).

Turtles were seen in one of three areas while in the temporary ponds. In four instances, a turtle that had not been previously captured was found paddling on the surface of the water. These individuals would wander seemingly aimlessly until they discovered the observer, whereupon they would quickly swim under water and conceal themselves under leaf litter or mud. Once they were marked, they were not seen engaged in this behavior again. The majority of turtles spent their time partly to completely buried under leaf litter and/or the bottom substrate of soft mud. The temporary ponds, never exceeding a depth of 33 cm, were generally shallow enough to allow for little effort to break the surface for a breath. Crevices excavated by turtles on the walls of the ponds always contained at least one turtle the entire duration of pond use. Along the only three vertical edges of the two ponds, turtles packed themselves into these side depressions; from late June to early August, the 0.25 to 0.75 m long crevices generally contained 3 to 8 individuals whether they were dry or filled with water.

Crevice temperature (when filled with water) averaged 3.0° C cooler than open pond water temperatures. For several days after showers, the water level remained slightly higher than the crevices. Once the water level dropped, turtles would bury themselves in the soft mud that remained.

During the two-month period of temporary pond use, there was considerable individual variation as to the number of times turtles fitted with trailing devices visited and the length of time they remained in the temporary ponds. These turtles visited the southern temporary pond from one to five times (n=10), remaining within the perimeter of the pond from one to 23 consecutive days. One juvenile that eventually died in the pond had stayed within a three meter radius in the water for 42 consecutive days. Because it was unknown when this turtle became ill, its records were not considered; it appeared healthy, however, until one week before it died. For individuals that visited the southern pond at least one time ($n=10$), the furthest distance traveled from the pond averaged 219 m (Table 5). Abrupt linear movements to the temporary pond were common during June and July. After circling a core area, seven individuals on nine different occasions moved in a straight path directly towards the temporary pond (only distances longer than 40 m were considered). These movements began as far as 105 m from the pond (Figs. 15, 16).

Water Use in other Study Areas. – Two other sites that contained wet areas were searched intermittently from May to August, 2000 for *Terrapene c. carolina.* Seven individuals were found at least once over 9 searches in the stream 2.5 km east of the main study area. Despite the moving water and seemingly much cooler temperatures than those of the temporary ponds, all turtles were found in crevices along the sides of the stream similar to those along the pond edges. Turtles were not found in the open rocky area of the stream, though they would have had to swim in the stream at some point in order to enter the crevices.

The areas searched in the Cherokee Woodlot consisted of a narrower, shallower soft-bottomed stream and a small pond, which was smaller yet deeper than the temporary ponds at the main study site. No turtles were found in this pond, possibly due to its greater depth and much steeper edges than those of the temporary ponds. Turtles did, however, utilize the small stream in this area. The stream was generally shallow enough that the water remained below mid-carapace. Over 11 searches, six individuals were seen resting in the center of the stream, and three were found in crevices along the edges. There were several elliptical pockets in the muddy bottom along the stream, likely left by turtles that had partly buried themselves. Twelve other turtles were found along the adjacent flood plain and hillside.

Home ranges

Locations were regularly plotted for 13 turtles fitted with trailing devices for at least four weeks; six of these turtles were fitted with radio transmitters subsequent to the removal of the trailing device. Home ranges varied drastically in size and shape (Fig. 17). The core home ranges of nine turtles (indicated herein by 50% kernel contours) included the southern temporary pond (Fig. 17). Home ranges of the ten turtles that visited the southern pond overlapped a great deal. This pond was at the edge of the home ranges of a majority of these turtles (Fig. 18). Home range sizes averaged 1.88 ± 0.49 ha via MCP analysis, and 2.26 ± 0.76 ha via 95% kernel analysis. For those fitted with radio transmitters for an additional three months after removal of the trailing device, the average MCP home range size increased by only 0.09 ha (Table 5).

A significant negative relationship existed between the home range size determined by the kernel method and turtle carapace length ($r=-0.590$, $p=0.034$), though not between home range size determined by the MCP method (Fig 19). Although the analyses suggest that home range size decreased as carapace length increased, it is important to consider that a few small individuals who had relatively large home ranges skewed these relationships. It is inappropriate, therefore, to conclude from these data that home range size is related to carapace length.

Some turtles exhibited pronounced seasonal variation in habitat use (Figs. 15, 16), while others did not (Fig. 20). Home ranges with distinct seasonal differences belonged to turtles that extended their spring ranges to incorporate the temporary pond during the summer.

Fall and Winter Movement

The six turtles fitted with radio transmitters were followed biweekly from September until they had remained in hibernacula for at least four weeks. Home ranges after the addition of fall and winter locations to those of spring and summer were, on average, not significantly larger than spring and summer ranges alone (paired samples t-test: n=6, p=0.076). The largest increase in fall MCP home range from that of spring and summer was that of the only turtle tracked that was known to not use any wet areas (turtle # 23, 55% increase). This turtle's fall home range increase was significantly larger than the other five turtles' fall home range increase (one-sample t-test: n=6, p=0.007). Hibernacula were located within the spring and summer home ranges for all but one turtle (# 14), whose hibernaculum was 35 m outside of its spring and summer home range (Fig. 21).

Turtles changed locations less as temperatures dropped (Fig. 22). One of the six turtles fitted with transmitters had ceased movement by November 13. Four turtles had stopped moving by November 28, and the remaining individual changed locations during the second week of December after remaining under a thin layer of leaves in the dry pond for over three weeks. Hibernacula were located in the woods for all but one turtle, which hibernated along the edge of the forest near the dirt road. For three of the six turtles, hibernacula consisted of forms underneath leaf litter, with carapaces even with the soil surface. Two of the turtles retreated underground in holes formed by roots, where they also dug until their carapaces were even with the soil; trailed turtles did not enter this type of underground retreat prior to hibernation. While these turtles were among deciduous trees, one turtle's hibernaculum was in the deep bed of dried pine needles among the Loblolly pine area. The thickness and pliability of the bed of needles allowed this turtle to be buried deeper (25 cm) relative to the top layer of the leaves than did the leaf litter from deciduous trees.

Illness

In early August, 2000, seven turtles in the southern temporary pond became ill and died. These turtles had remained at the pond longer than the majority of healthy turtles. Symptoms were similar among the turtles, consisting of a constantly extended neck with the head hanging slightly to the side, eyelids that were swollen shut, and nasal discharge. In addition to these symptoms, one of the sick turtles also had a blister-like abscess on the side of the head. The likely cause of this is a middle ear infection, which may also be induced by a respiratory infection (Gould 1998). This same turtle also had small punctures on the front limbs, possibly a result of Myiasis (Botfly) (Gould 1998).

Four dead specimens and one live, but ill (and subsequently euthanized), individual were taken into the University of Tennessee Veterinary Teaching Hospital within 24 hours of death. *Pasteurella testudinis* was isolated in all five turtles. This has been said to cause upper and lower respiratory disease (D.A. Bemis, D.V.M., pers.comm). Histopathological tests were conducted on two turtles (these could not be performed on the others due to severe post-mortem autolysis), both of which had marked pulmonary hemorrhages in the lungs. No significant lesions were found in the liver or kidneys. Although the cause of illness was inconclusive, severe bacterial overgrowth and necrosis of nasal and oral mucosal surfaces were found in the euthanized individual. The final diagnosis for this individual was ulcerative rhinitis and stomatitis (J.E. Wilkinson, D.V.M., pers.comm.). No ill turtles were found in the northern temporary pond.

Discussion

Movements and Home Range

Movements and Environmental Variables. – The results of this study generally concur with those of several studies of Eastern box turtles that found that turtle movement increased with precipitation during spring and summer (Stickel 1950, Dolbeer 1969, Reagan 1974, Stuart and Miller 1987, Dodd et al. 1994). Although this was the general trend, there was a substantial amount of individual variation. Even with episodes of heavy rainfall, one turtle (# 23) remained in forms most of the summer, with the longest period of inactivity (24 days) in July. During the same period, another turtle (# 21) traveled an average of 190 m per day (despite high temperatures and no rainfall) in a three-day period before finally stopping at the temporary pond. This turtle also traveled the greatest distance in one day of the trailed turtles: 216 m before the trailing device ran out of string. Because turtles that utilized the temporary ponds during the summer remained in or nearby them for days to weeks at a time, there was a considerable decrease in average movement by trailed turtles as turtle density in the ponds increased.

Distances moved decreased with decreasing temperatures in the fall (Fig. 22). Hibernation (which began in late November for the majority of individuals) began later than for the Eastern box turtles studied by Claussen et al. (1991) in Ohio and Stickel (1989) in Maryland, and began slightly earlier than those studied by Dolbeer (1969) in Tennessee. Contrary to Dolbeer's (1969) findings, turtles fitted with transmitters remained in their hibernacula through December. This may be attributed to differences in December temperature and precipitation between the studies.

Routes and Types of Movements. – There was high variability in types of movement among individuals. Concentrated areas of use were patchily distributed within some home ranges. Madden (1975) defined patches as areas within which encountering an animal is high compared to other areas in which it is low. Some turtles circled or looped within the same vicinity for days to weeks at a time, presumably due to food availability, access to water, or preference for a particularly canopy and/or ground cover. Vegetation cover also affects the sinuosity of turtle trails (Claussen et al. 1997). Looped paths for many turtles were common along the forest edges, where the vegetation predominately consisted of blackberry bushes; blackberries were seen in turtles' mouths in several instances. Two individuals circled a small open grassy area near the temporary pond for weeks in spring and summer, where one of them was seen eating a caterpillar. In addition to proximity to the water, an abundance of invertebrates may explain their preference for this area.

While some individuals seemed to move only linearly to reach the next patch, linear paths were the primary types of movement for others (Fig. 17). Just as Reagan (1974) found that three-toed box turtle movement to the forest edge was generally linear, linear movement in this study often led directly to either blackberry bushes along the forest edge or to the temporary pond. Rather than circling through blackberry bushes, some would travel straight through them until they changed direction to re-enter the forest. For many turtles, some routes were traveled more frequently than others. Linear movements were often repeated over the same area, commonly in traveling from one area of intense occupation to another. Quinn and Tate (1991) found that among wood turtles (*Clemmys insculpta*), which are essentially terrestrial, abrupt linear movements to late summer ranges in mid June was a common event. Among the trailed Eastern box turtles in this study, the most obvious and extensive linear movements were towards the temporary pond in June and July.

Directional movement towards a location is likely a result of orienting ability. *Terrapene carolina* possess a Type II, or sun-compass orienting ability, which allows them to maintain a compass course in unfamiliar territory (DeRosa and Taylor 1980, Gould, 1959). Maze experiments have also revealed pronounced spatial memory in turtles (Burghardt 1977). Orienting ability and spatial memory may explain the site fidelity exhibited by terrestrial turtles over several years (Stickel 1950, Lue and Chen 1999, Legler 1960, Yahner 1974). In addition to allowing the animals to return to preferred basking and/or feeding sites, orienting mechanisms provide the advantage of an increased efficiency of movements towards resources (DeRosa and Taylor 1982). Orienting ability and/or spatial memory is illustrated in this study by the return of individual turtles to previously visited blackberry patches and by direct linear movement towards the temporary pond. Linear movement towards the pond occurred during the period of pond use by turtles in mid summer, and from as far as 105 m away. In nine out of the ten records of linear movement toward the pond, the sky was sunny to mostly sunny.

One possible explanation for 131 turtles finding these small ponds when they contain water is an ability to sense and locate a body of water in unfamiliar territory. Yeomans (1995) found that under clear conditions, adult yellow-bellied pond slider turtles (*Trachemys scripta*, Emydidae) oriented non-randomly in the direction of the nearest water when placed in an unfamiliar habitat; orientation was random under overcast conditions. Although *Terrapene c. carolina* are not aquatic (whereas *Trachemys scripta* are), it seems unlikely that when the small pools were *first* formed by the wheels of construction vehicles, that many turtles happened to come across them in their daily travels. Furthermore, the most heavily used pond was at the edge of nine out of ten of the turtles' home ranges (Fig. 18), indicating that they do not use the areas in and around the ponds until high temperatures and lack of rain attract them to the water (Fig.11).

Turtles often climbed up considerably steep hillsides and over fallen trees with circumferences up to approximately four times the length of the turtle. The study area consisted of many hills (Fig. 2), and individuals did not avoid traveling up and down even the steepest slopes. While Davis (1981) found that *Terrapene c. carolina* tended to move uphill more than downhill, no obvious preference of this kind was found in this study.

Home Range Size. – Home range sizes, which averaged 1.88 and 2.26 ha using MCP and 95% fixed kernel methods, respectively, were similar to those reported by Williams and Parker (1987), Stickel (1989), and Strang (1983). Home ranges were considerably larger than those reported by Dolbeer (1969) and Davis (1981, Table 1), likely due to a combination of habitat quality (Diemer 1992) and the more limited area of suitable habitat where their studies were conducted. The validity of making home range size comparisons between studies with different home range estimators and sample sizes (number of individual animal locations) is questionable, however. One individual's home range (based on 52 consecutive observations on alternate days) was 1.13 ha using the MCP estimator and 1.95 ha using the kernel estimator (Table 5), a substantial difference of 0.82 ha (42.1%). Home range estimates are greatly affected by the number of locations on which each estimate is based (Seaman et al. 1999), which are often unreported in the literature. Reporting these sample sizes and conforming to one to two standard methods of calculating home range, now that more sophisticated techniques are widely available, is essential for legitimate comparisons among studies.

Home range size variation found in this study was likely dependant upon the degree of mating and nesting activity (Cook 1996, Diaz-Panigua et al. 1995) in addition to resource distribution. While female sample size was too small for valid home range size comparison with males, the largest home range (MCP: 6.50 ha, Table 5) of the trailed turtles was that of a female. This may have been a gravid female, as they are known to greatly extend their home ranges in search of adequate nesting sites (Cook 1996, Stickel 1989, Madden 1975).

Home Range Method Comparison. – Minimum convex polygons are the most widely used home range estimators because of their ease in calculation and value for comparison to other studies (Harris et al. 1990). By using the outer most points of the area traveled, they depict the total home range a turtle utilizes in finding a suitable habitat. The kernel method illustrates the total home range as well (represented by 95% probability contours), but also gives weight to heavily used (core) areas (represented herein by 50% contours). Another popular estimator in earlier literature (Stickel 1950, Madden 1975, Stickel 1989) is the bivariate normal method, proposed by Jennrich and Turner (1969). This method assumes that an animal's locations follow a bivariate normal probability distribution, where more points are closer to the center of the distribution, and increasingly fewer points further from the center. This estimator is biased for any data that is not normally distributed (Seaman et al. 1999) and was not used in this study.

Kernel estimates are nonparametric: they are not based on an assumption that the data conform to specified distributional parameters (Seaman et al. 1999), and are therefore less biased than most methods (Worton 1995). They also give shape to a home range, which reflects the total utilized area more accurately than the polygon produced by MCPs. Because home range methods are created based on animal locations, and because turtles' locations in this study were obtained daily for relatively long periods of time, it was possible to analyze the effectiveness of kernel verse MCP methods by examining the relationship of the route of travel with the respective home range illustration (Fig. 17). The 50% probability contours are generally effective at illustrating patchy use within an individual's home range. The looped paths in these patches are contained within the 50% contours. In cases where looped paths do not exist within the 50% patches, the contours surround either the temporary pond or an aestivation site where the individuals remained for days to weeks at a time.

Minimum convex polygons, while unable to illustrate core areas within a home range, rather accurately depict the turtles' total home ranges based on known locations. Unlike kernel estimators, MCPs do not widen the boundaries surrounding locations (referred to here as "buffers"), thereby providing a more conservative estimate of home range. These buffer zones are important, however, if an individual travels just outside of the peripheral locations recorded by the observer. For example, the right-hand boundary of the minimum convex polygon for turtle number 14 (Fig. 17) does not contain the routes traveled on the days those locations were recorded. In the kernel illustration, however, the boundaries are expanded around these right-sided locations enough to include the majority of number 14's travel routes.

The kernel method is ineffective, however, at including all routes of travel between more distant locations within the home range. In the majority of the kernel illustrations (Fig. 17: turtles 2, 11, 13, 14, 20, 21, 23, 53), linear travel paths between widely separated points are not within the 95% probability boundaries. These illustrations depict more than one home range for the same individual, depending on the distance between patches. Stickel (1950) suggested that some turtles may have two home ranges and travel between them intermittently. This may be the case if home range is considered only those areas an animal uses regularly and/or intensively, as opposed to Burt's (1943) definition of home range as *any* "...area traversed by the individual in its normal activities." MCP's, however, do not discriminate between closely bunched and distant points and comply with the latter definition of home range, thereby including all of the areas an animal is familiar with (regardless of intensity of use) within its home range.

Despite their inherent differences, both MCP and kernel methods effectively portrayed the turtles' home ranges. The preferred method is largely dependent on the research questions and/or intended applications of the results. The MCP method is effective at delineating the total home range within the boundaries of known locational data, whereas the kernel method weights the intensity of use via probability estimators, often expanding beyond the peripheral locations that the MCP method uses as a boundary. With large enough sample sizes, the kernel method is more effective at depicting an animal's uneven home range use. Kernel estimators are therefore more pertinent to issues that this study addresses, such as intensity of wetland use and seasonal variation in home range.

Seasonal Variation in Home Range. – As in other emydid studies (Kaufmann 1995, Madden 1975), there was individual variability in the extent to which turtles seasonally used different areas. There seemed to be seasonal patterns of home range use, largely due to the exploitation of the temporary pond during the summer. Eight out of eleven turtles for which at least two weeks of spring and two weeks of summer trailing data were available remained in the pond for a portion of the summer. After leaving the water in the summer, many turtles returned to the same areas they had visited in the spring (Fig. 15).

Aside from the concentration of summer movements in and nearby the temporary pond for most trailed turtles, individuals in the fall generally returned to areas they had been in the vicinity of over the spring and/or summer (Figs.16, 20). For the turtle (#23) trailed from early June through December that did not visit either pond, there was little disparity between spring, summer, and fall home range use. Locations for all tracked turtles were much more contained in the fall than were those in the summer. Turtles remained within a smaller section of their home ranges as temperatures began dropping quickly after September. The total extent of movement from one form to another in the fall was unknown, however, since locational data was obtained only biweekly via radio transmitters (rather than trailing devices) during the fall.

Fall home range size, according to MCP analysis, increased more than 10% for two of the turtles tracked from spring or summer to hibernation (Table 5). Extended movement in search of valuable food resources would be to their advantage before falling temperatures force them into torpor. For the majority of turtles tracked until hibernation that had visited the pond during the summer, the minimal increase in their fall home ranges were extensions on the far edge of the ranges from the pond (Fig. 18). Summer ranges that are relatively close to the pond compared to fall ranges may lower the travel costs when high temperatures and low rainfall draw turtles to the water.

Hibernacula were located within the summer home range for 5 out of 6 of the turtles (Fig. 21). Stickel (1989) similarly reported Eastern box turtles' hibernacula within their normal summer ranges. Despite any venturing out of spring and/or summer home ranges in the fall, turtles chose hibernacula in areas which were perhaps more familiar.

Water Use

If *Terrapene* evolved from aquatic ancestors (Bramble 1974, Burke et al. 1996), it is not surprising that *T. c. carolina* has seasonal aquatic tendencies. The *carolina* group may have evolved physiological and behavioral mechanisms to cope with dessication that allows them to survive without access to wet areas, but apparently their preference for water during periods when the danger of dessication is highest is not lost among all of its members.

Although box turtle habitat use, home range, and a wide variety of behaviors have received substantial attention in the literature, there are surprisingly few accounts (and no thorough studies) of their aquatic tendencies. One possible explanation for the scarcity of information regarding box turtle water use may be their propensity to conceal themselves under mud, leaf litter, and/or crevices along the sides and bottom of pools and streams. While they have occasionally been seen swimming (Stickel 1950, Tyler 1979), they more commonly bury themselves, most likely to avoid predators (Bennett et al. 1970), while using the water for evaporative cooling (Stubaum 1982).

Of course, not all Eastern box turtles make use of wet areas despite relative proximity to them. Fifteen of the 20 turtles fitted with trailing devices were originally found in the woods, often quite far from the temporary pond and prior to any turtles visiting the pond that year. Six out of the fifteen did not visit either of the temporary ponds while they contained water from June through August. This is not to presume, however, that these six individuals did not visit any wet areas beyond the study site. One of the six turtles traveled 260 m in two days in July through a dried up streambed, well out of the delineated boundaries of the study site, until he was found resting in water further down the stream. Four of the of the six that were never found in the ponds were trailed for very short periods before they could not be located due to string breakage or trailing device detachment; it is unknown whether they traveled to other water sources. Only one turtle (# 23) tracked during the entire range of temporary pond use was known to not visit any wet areas.

Overall, access to water has been found to be extremely important to Eastern box turtles during periods of drought coupled with high temperatures. Core home ranges were centered around the temporary pond of 69% of the trailed turtles. Regular censuses throughout the summer of not only temporary ponds, but also a small stream and a creek in two separate wooded areas in Tennessee, have confirmed their predilection for water. Considering the velocity and cool temperature of the creek relative to those of the stagnant temporary ponds, the presence of turtles in side pockets along the creek was unexpected. The fact that they overcame the water velocity and the rocky substructure in order to reach a side crevice confirms the importance of water as a means of thermoregulation, and suggests that they may have more effective swimming abilities than what is generally assumed (Pritchard 1979).

Seeking out water to the extent found in this study may have profound implications that extend beyond the importance of behavioral regulation of body fluids and temperatures in periods of drought. The only turtle tracked that was known to not visit any wet areas through the active season (# 23) remained in forms longer and traveled significantly less during the summer than any other turtle (x=3.8 m). Perhaps by preventing dessication and replenishing vital fluids lost by summer heat, individuals that use wet areas have an advantage over those that do not. Weight loss in turtles (which occurs in hot environments) is indicative of water loss, and water is used for evaporative cooling (Stubaum 1982). Soaking and drinking opportunities may provide turtles the energy required for increased movement that facilitates food-finding and mating encounters before hibernation.

Home Range Relationship to the Temporary Pond. – Combining a home range analysis by means of trailing devices with a regular and frequent count of pond visitors has revealed the significant effect wet areas had on movement patterns and home ranges. For most individuals, spring home ranges were greatly expanded during the summer to include the pond (Fig. 15). This conclusion is based on the location of the pond within each home range and the turtles' obvious tendencies to move linearly towards the water from far distances in response to hot temperatures and no rainfall. Two turtles' (turtles # 2 and # 3) summer ranges did not increase because they regularly visited the pond in the spring as well, though never remaining more than a few hours before re-entering the woods. MCPs effectively illustrated that the pond was on the edge of turtles' home ranges, and also elegantly displayed the broad use of the habitat surrounding the entire pond (Fig. 18).

Given that that Figure 18 illustrates only the home ranges of ten of the 96 turtles that used the southern temporary pond, asserting that their home ranges overlap is an understatement. High densities and home range overlapping are essential for sufficient mating encounters among Eastern box turtles and undoubtedly many other turtle species (Stickel 1950, Calzohai and Chelazi 1991). Despite the high densities in the temporary ponds, however, mating was never witnessed. Other than an occasional swim, burrowing beneath water and mud, or coming to the surface to breathe, turtles seemed to generally remain motionless as they took advantage of their haven from the summer heat.

Illness

Although the histopathological tests on five of the seven turtles found dead or ill in or near the pond were inconclusive, the symptoms and laboratory findings strongly suggest respiratory disease. Nasal discharge and swollen eyelids on all seven ill turtles, and the swollen cheek of one, are common among turtles with respiratory infections (Gould 1998). Sick turtles were in close proximity within the temporary pond over the summer, and all remained in the water well after the others had left. Prolonged immersion in water is often a sign of illness (Belzer 1999b), though it is highly doubtful that they came to the pond because they were ill; symptoms did not appear until weeks after visiting the pond. Respiratory disease, which is not unexpected in areas of dense congregation (D.A. Bemis, D.V.M., pers. comm), was the likely cause of death.

The fact that the illness seemed to be correlated with close contact of the turtles within the small area of the pond has significant implications regarding aggregating behavior. It is not known how common dense congregation within a small wet area is among box turtle populations, or the effects it has on reproductive opportunities or disease transmission. Although water use by Eastern box turtles is not uncommon, the temporary ponds in this study may be somewhat unique due to the manner in which they were formed. Their small sizes relative to turtle concentration may result in closer contact among individuals than what appears in more spacious wet areas. It is important to note that in the northern temporary pond, which did not have quite as high turtle densities as the southern pond, no sick or dead individuals were found. While close contact for days to weeks at a time may increase the chances of contracting an illness from a sick turtle, it in no way suggests that turtle aggregations in water are a general danger to individuals.

Conservation Implications

Although box turtles were recently considered a common species, their rates are rapidly declining as a result of habitat loss and overcollection. Human impact not only results in fragmented habitats, but also causes habitat degradation. Curtin (1997) found degraded habitats created a cooler microclimate and shortened *Terrapene ornata* activity, causing them to emerge later from hibernation, thereby delay nesting. Because home range size is dependant on habitat quality (Madden 1975, Stickel 1978, Stickel 1989), degraded habitats increase home ranges (Curtin 1997), increasing the likelihood of turtles traversing heavily-used roads and encountering people. Since mating opportunities rely on chance encounters in the wild, the loss of each reproductive individual can be devastating to the population (Belzer 1999a).

Tens of thousands of North American box turtles are collected from the wild for the international pet trade despite their listing on Cites Appendix II, and there are no federal regulations on box turtle exports from the U.S. (Lieberman 1994). Most states require a permit for or forbid wild collection, though little is done to enforce this (Gould 1998). Their late onset of sexual maturity makes them commercially unprofitable animals to breed to marketable size. A ban on European tortoise importation in 1984 resulted in a dramatic increase on the importation of box turtles, particularly into the UK. The genus *Terrapene* accounts for the greatest number of imports of any wild turtles into Britain (Zug 1994).

In addition to rigorous enforcement of laws intended to reduce the collection of Eastern box turtles, habitat protection should include all areas of seasonal activity. Special attention should be given to resource areas where turtles aggregate, such as feeding sites as well as wet areas. In conservation management decisions, permanent or temporary creeks and ponds (with depths from a few cm up to 35 cm) should be included in the delineation of their seasonal habitat requirements. In assessing harvesting operations that would cause possible impact to wetland turtles such as wood turtles (*Clemmys insculpta*) and spotted turtles (*Clemmys guttata*), the Massachusetts Natural Heritage Program recommended mitigating timing of harvest and buffers around water bodies (Kittrede 1996). Because wet areas have been shown to have a significant effect on *Terrapene c. carolina* lifestyle, particularly in terms of movement and summer home range expansion to incorporate these water bodies, they should therefore be afforded similar consideration where appropriate.

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APPENDICES

Appendix A:

Tables

Table 1. Home range sizes reported for *Terrapene c. carolina.*

Author(s), year	Study Location	Home range			
		Method	Mean size (ha)	Mean size (m)	n
Strange, 1983	South-central Pennsylvania	Range-length[1]		167.0	33
Stickel, 1950	Near Laurel, Maryland	Range-length		106.7	55
Stickel, 1989	Near Laurel, Maryland	Adaptation of bivariate normal	1.17		103
Williams and Parker, 1987	Near Annapolis, Indiana	Range-length		173.7	109
Dolbeer, 1969	Knoxville, Tennessee	Range-diameter[2]		75.6	270
Davis, 1981	Knoxville, Tennesee	Minimum convex polygon[3]	0.38		4
Cook, 1996	New York	Bivariate normal[4]	9.77		53
Madden, 1975	Long Island, New York	Bivariate normal	6.96		23

[1]Maximum distance between extreme capture locations
[2]Diameter of smallest circle that includes all capture locations
[3]Area formed by connecting the outermost locations to create the smallest possible polygon
[4]Area of ellipse formed from a bivariate normal probabily distribution based on capture locations

Table 2. Individual *Terrapene c. carolina* measurements and records on tracking methods and temporary pond use. Sex, weight, and carapace length data on 166 turtles were collected from May 2 to August 22, 2000 in Loudon Co., Tennessee. Sex could not be determined for turtles with carapace lengths less than 9.5 cm. The 20 turtles fitted with a trailing device (T) were tracked from five to 106 days from May 3 to August 22. The six turtles subsequently fitted with a radio transmitter (R) were tracked for 98 days from September 8 until hibernation through December.

Turtle	Sex	Weight (g)	Carapace length (cm)	Tracking method	Use of temporary pond
1	M	390	13.2	T	+
47		320	12.4	T,R	+
		288	12.5	T,R	+
4	F	195	11.0	-	-
5	-	55	6.9	-	+
6	M	295	11.0	-	-
7	M	320	12.0	-	-
8	M	480	12.0	-	-
9	M	320	12.0	T	-
10	F	290	11.9	T	-
11	M	310	11.9	T,R	+
12	-	48	6.7	-	-
13	F	250	10.8	T	-
14	M	275	11.5	T,R	+
15	M	360	12.1	-	-
16	M	295	11.3	T	+
17	M	225	10.4	T	+
18	F	415	12.7	T	-
19	F	450	13.1	T	-
20	F	240	10.1	T	-
21	M	465	12.6	T	+
22	-	9	3.2	-	-
23	M	320	12.5	T,R	-
24	-	110	8.8	-	-
25	F	350	11.6	-	-
26	F	380	11.9	-	-
27	M	445	13.8	-	-
28	F	270	11.5	T,R	+
29	F	430	12.0	-	-
30	M	170	10.1	-	-
31	M	420	13.3	-	-
32	F	250	11.0	T	+
33	F	360	12.3	-	+
34	M	360	12.8	-	-
35	M	385	12.7	-	-

Table 2, continued

Turtle	Sex	Weight (g)	Carapace (cm)	Tracking Method	Use of Temporary Pond
36	M	465	12.4	-	+
37	M	295	11.5	-	+
38	M	362	13.0	T	+
39	-	165	9.4	-	+
40	M	315	11.1	-	+
41	-	65	6.9	-	+
42	M	410	12.6	-	+
43	M	372	13.2	-	-
44	M	305	11.5	-	-
45	-	170	9.2	-	+
46	F	455	12.0	-	+
47	M	245	11.0	-	+
48	M	205	10.3	-	+
49	M	335	12.1	-	-
50	-	120	9.0	-	+
51	M	320	12.3	-	+
52	F	385	12.6	-	+
53	M	482	13.4	T	+
54	M	300	12.1	-	+
55	M	397	12.5	-	+
56	M	465	13.4	-	+
57	-	140	8.5	-	+
58	M	470	14.4	-	+
59	M	450	13.5	-	+
60	F	310	10.6	-	+
61	F	240	10.4	-	+
62	F	390	12.0	-	+
63	F	375	11.6	-	+
64	F	420	12.8	-	+
65	-	150	9.2	-	+
66	M	210	10.7	-	+
67	M	355	11.4	-	+
68	F	355	11.6	-	+
69	F	435	11.7	-	+
70	-	185	9.3	-	+
71	F	465	13.0	-	+
72	F	330	11.8	-	+
73	F	430	12.4	-	+
74	F	225	11.2	-	+
75	F	182	9.5	-	+

Table 2, continued

Turtle	Sex	Weight (g)	Carapace (cm)	Tracking Method	Use of Temporary Pond
76	M	180	10.1	-	+
77	F	265	11.0	-	+
78	-	147	8.9	-	+
79	M	308	11.3	-	+
80	M	325	12.1	-	+
81	-	110	8.2	-	+
82	M	255	10.5	-	+
83	-	102	8.3	-	+
84	M	380	13.2	-	+
85	F	345	12.4	-	+
86	M	345	12.0	-	+
87	M	215	10.5	-	+
88	-	120	9.4	-	+
89	F	355	12.3	-	+
90	F	230	10.1	-	+
91	F	405	12.5	-	+
92	F	360	11.3	-	+
93	-	185	9.4	-	+
94	M	470	13.5	-	+
95	M	425	13.4	-	+
96	M	215	10.5	-	-
97	M	360	12.7	-	+
98	M	360	12.6	-	+
99	F	155	9.7	T	+
100	M	330	12.8	-	+
101	M	415	13.0	-	+
102	F	395	13.0	-	-
103	M	300	11.3	-	+
104	M	235	11.7	-	+
105	M	165	10.0	-	+
106	M	185	10.0	-	+
107	F	480	13.4	-	+
108	F	310	11.0	-	+
109	M	455	13.6	-	+
110	M	350	12.3	-	+
111	-	130	8.7	-	+
112	-	90	7.7	-	+
113	M	405	12.3	-	+
114	F	370	11.6	-	+
115	M	185	9.7	-	+

Table 2, continued

Turtle	Sex	Weight (g)	Carapace (cm)	Tracking Method	Use of Temporary Pond
116	M	225	11.0	-	+
117	M	305	11.5	-	+
118	M	300	11.8	-	+
119	M	285	11.9	-	+
120	F	315	11.6	-	+
121	M	320	11.5	-	+
122	M	360	12.6	-	+
123	M	265	12.5	-	+
124	M	355	10.6	-	+
125	F	160	9.7	-	+
126	M	372	13.0	-	+
127	M	350	11.7	-	+
128	M	285	12.4	-	+
129	-	65	6.7	-	+
130	M	340	12.5	-	+
131	F	205	10.0	-	+
132	M	410	12.5	-	+
133	F	430	11.0	-	+
134	F	230	10.5	-	+
135	-	115	8.5	-	+
136	F	260	10.8	-	+
137	M	305	12.1	-	+
138	M	400	13.0	-	+
139	M	440	13.0	-	+
140	F	275	11.5	-	+
141	M	460	12.5	-	+
142	M	365	11.6	-	+
143	-	120	8.4	-	+
144	M	380	12.3	-	+
145	M	360	11.8	-	+
146	F	150	9.7	-	+
147	-	110	8.3	-	+
148	-	120	8.6	-	+
149	-	105	8.1	-	+
150	M	250	10.8	-	+
151	M	380	13.0	-	+
152	F	480	13.4	-	+
153	M	345	12.3	-	+
154	M	405	12.6	-	+
155	M	260	11.5	-	-

Table 2, continued

Turtle	Sex	Weight (g)	Carapace (cm)	Tracking Method	Use of Temporary Pond
156	M	275	12.0	-	+
157	M	410	13.5	-	-
158	F	195	9.8	-	+
159	M	385	13.0	-	+
160	F	375	12.9	-	+
161	M	180	10.2	-	-
162	-	110	8.2	-	-
163	-	120	8.6	-	-
164	F	355	11.9	-	-
165	F	350	11.7	-	+
166	M	410	13.2	-	-

Table 3. Weather variables and activity records of trailed *Terrapene c. carolina* in five-day intervals from May through August, 2000. Precipitation data were taken from the NOAA meteorological station in Loudon Co., Tennessee. Temperature data were taken from a data logger at the Loudon Co. study site.

Dates	Total Precip-itation (mm)	Avg-erage Precip-itation (mm)	Avg. Max. Temp. (C)	Avg. Min. Temp. (C)	Turtles		
					Avg. Distance Traveled (m)	Avg. Number of Days in Pond	*n*
May 9-13	3	0.6	27.9	16.4	24.1	0	2
May 14-18	0	0	25.8	13.0	27.1	0	1
May 19-23	25.4	5.1	24.3	15.9	36.3	0.5	2
May 24-28	90.9	18.2	24.0	17.9	-	-	0
May 29-Jun 2	0	0	24.7	15.1	11.8	0	2
June 3-7	4.8	1.0	22.9	15.2	18.8	0	3
June 8-12	0	0	27.5	15.3	1.2	0	2
June 13-17	10.2	2.0	28.0	19.3	29.1	0	10
June 18-22	36.1	7.2	26.6	19.7	41.2	0.2	9
June 23-27	2.5	0.5	28.0	18.3	28.6	0	7
June 28-Jul 2	13.5	2.7	25.6	16.9	29.4	1.3	12
July 3-7	8	1.6	28.9	20.0	9.1	1.4	5
July 8-12	45.8	9.2	29.5	20.8	24.7	0.6	9
July 13-17	0	0	27.9	18.9	5.9	1.7	6
July 18-22	0.6	0.1	28.1	19.2	17.1	1.5	10
July 23-27	2.2	0.4	26.3	18.3	23.5	0.7	7
July 28-Aug 1	39.6	7.9	27.2	19.3	23.5	0.4	5
August 2-6	17.1	3.4	26.7	20.1	22.1	0	5
August 7-11	27.2	5.4	29.0	20.5	22.5	0	7
August 12-16	0	0	27.8	15.9	9.8	0.2	6
August 17-21	1.5	0.3	27.2	19.5	22.8	0	6

Table 4. *Terrapene c. carolina* activity with respect to the southern temporary pond[1] in Loudon Co., Tennessee.

Turtle	Sex	Furthest Distance from Pond (m)	Maximum Number of Consecutive Days in Pond	Number of times Visiting Pond
2	M	153	2	6
3	M	203	3	4
11	M	159	1	3
14	M	296	3	3
16	M	167	21	1
17	M	358	2	1
21	F	235	7	2
28	F	210	7	3
38	M	223	1	1
53	M	181	14	2
Average		219	6.1	2.3
Range		153-358	1-21	1-5

[1]All data included in the table were obtained from turtles fitted with trailing devices that remained in the pond for at least one day. Pond use for these turtles ranged from June 19 to August 17, 2000.

Table 5. Home range estimates (hectares) for *Terrapene c. carolina* using minimum convex polygon and fixed kernel methods. The 13 turtles fitted with trailing devices were followed 28 to 106 days during spring and/or summer 2000 in Loudon Co., Tennessee. "*n*" represents the number of turtle locations used to create the home range estimates based on trailing device data. *The 6 turtles subsequently tracked by radio transmitters (replacing trailing devices) were followed an additional 98 days (24 locations) from September until hibernation.

Turtle		Home Range Method			
		Minimum Convex Polygon		Kernel (95% probability)	n
#	Sex				
2*	M	1.32	1.33[1]	0.89	54
3*	M	1.13	1.16[1]	1.95	52
11*	M	1.89	1.90[1]	2.03	33
14*	M	4.24	4.71[1]	6.03	33
23*	M	0.36	0.80[1]	0.61	35
28*	F	0.62	0.84[1]	1.45[2]	24
17	M	1.91	-	6.30[2]	18
20	F	1.65	-	3.34[2]	14
21	F	2.74	-	2.73	41
13	F	6.50	-	9.90[2]	19
16	M	0.87	-	1.55	33
38	M	0.90	-	2.78[2]	17
53	M	0.28	-	0.90[2]	14
Average		1.88	1.74[1]	2.26	30

[1] Home range estimate subsequent to the addition of locational data obtained from the use of a radio transmitter.
[2] Due to the kernel estimator's sensitivity to sample sizes below 30, these values were not included in the kernel home range average.

Appendix B:

Figures

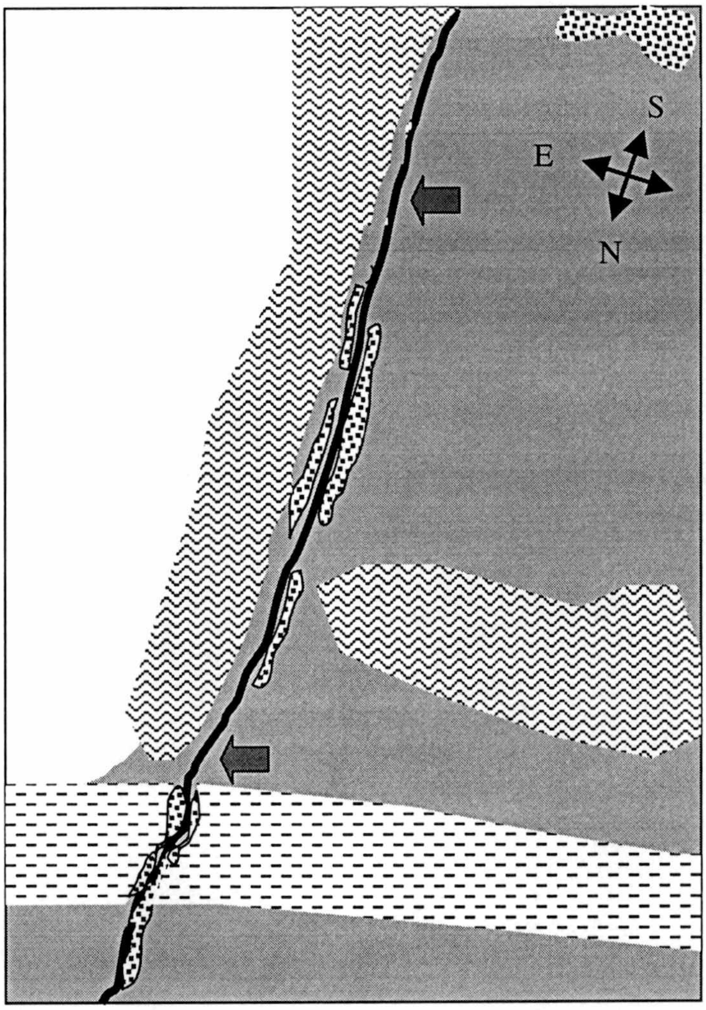


Figure 1. Map of the main site of a study in Loudon County, Tennessee, where a study of *Terrapene c. carolina* was conducted from May through December, 2000. The solid line running north to south through the map indicates the logging road, intermittently bordered by patches of blackberry bushes (represented by spotted contours). Arrows signify locations of two temporary ponds on the logging road. The shaded background mainly to the west of the road indicates areas of deciduous forest. The white area to the east of the road indicates pine forest, and the wavy figures represent mixed pine and deciduous forest. The dashed lines along the northern end of the study area indicates a cleared area (a power line right-of-way) overgrown with grasses.

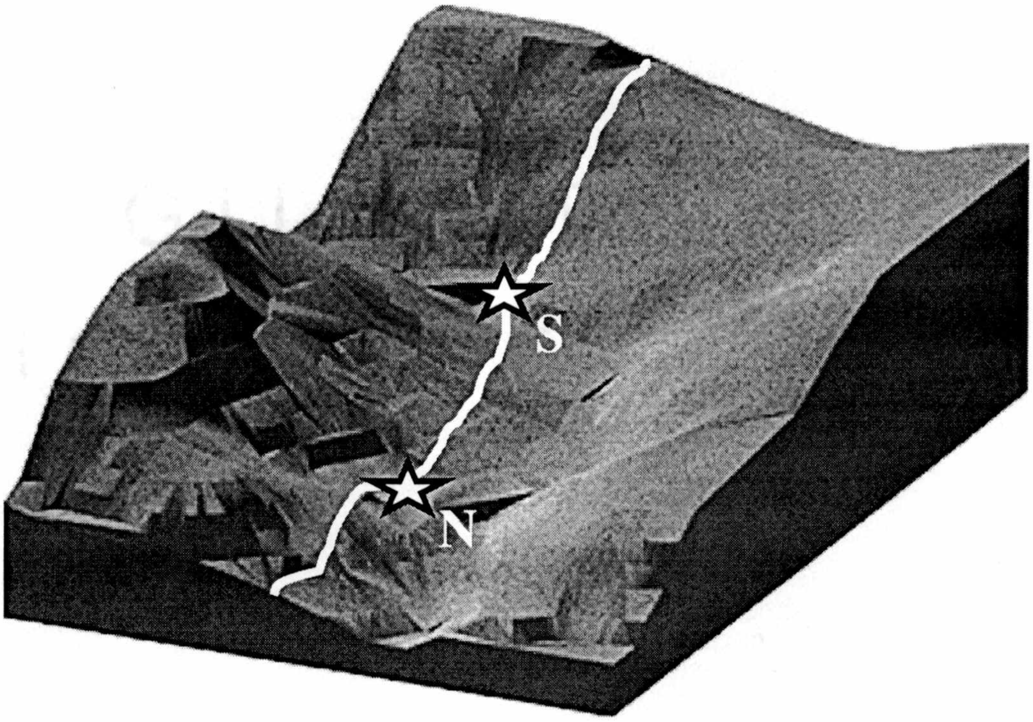


Figure 2. Topographical view of the site of a study of *Terrapene c. carolina* in Loudon County, Tennessee (not to scale). Stars represent locations of the northern (N) and southern (S) temporary ponds, and the curved line signifies the dirt logging road.

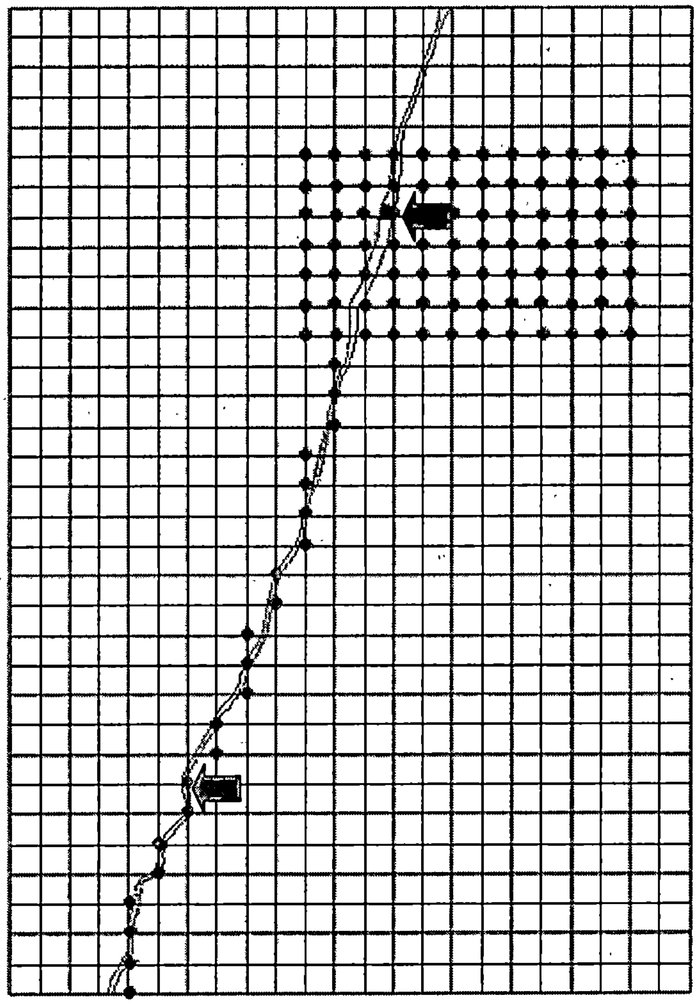


Figure 3. Grid of the main site of a study in Loudon Co., Tennessee, where a study of *Terrapene c. carolina* was conducted from May through December, 2000. The grid is 460 x 660 m; each box is 20 m on a side. Points represent labeled markers. The rectangle of points signifies the original study grid where the majority of turtles were found; points were later added along the road. The northern pond is indicated by the arrow towards the bottom of the grid along the dirt logging road; the arrow towards the top of the grid indicates the southern pond, also along the road.

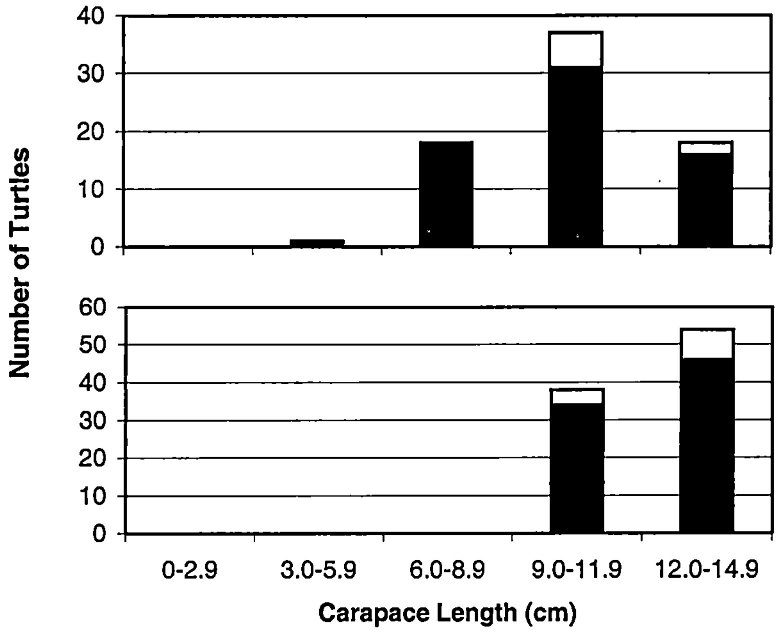


Figure 4. The number of female and juvenile (upper) and male (lower) *Terrapene c. carolina* found at the Loudon Co., Tennessee study area from May to August, 2000, separated into size classes based on carapace length. Juveniles are unsexed individuals with carapace lengths below 9.5cm. White areas indicate turtles for which movement data was obtained (via trailing devices and radio transmitters).

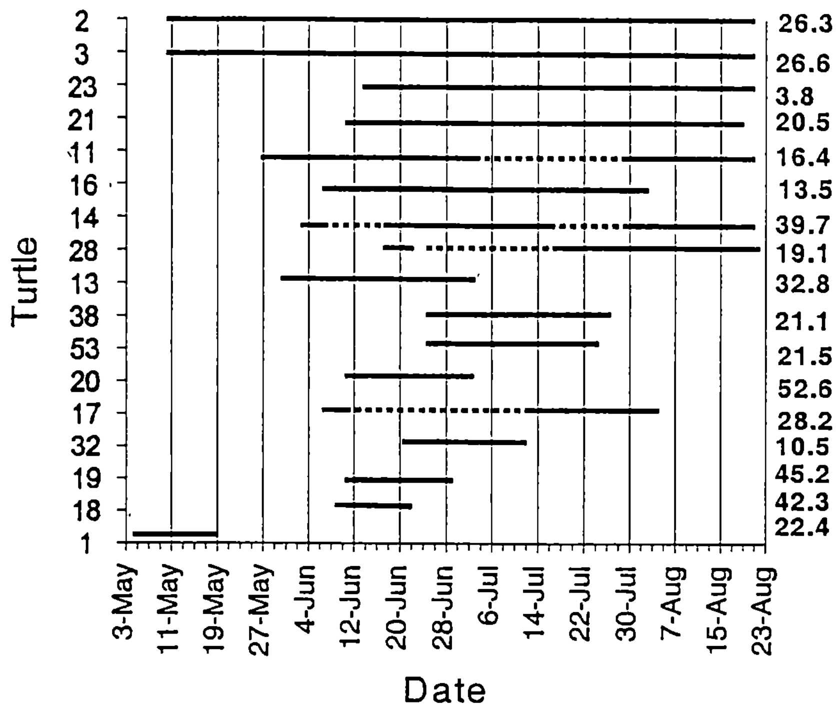


Figure 5. Periods of tracking *Terrapene c. carolina* with trailing devices and average distances traveled per day for 17 turtles. Data was collected in Loudon Co., Tennessee from May through August, 2000. Turtles trailed 14 to 106 days are included. Solid lines represent periods of continuous tracking. Dotted lines represent periods a turtle was not tracked.

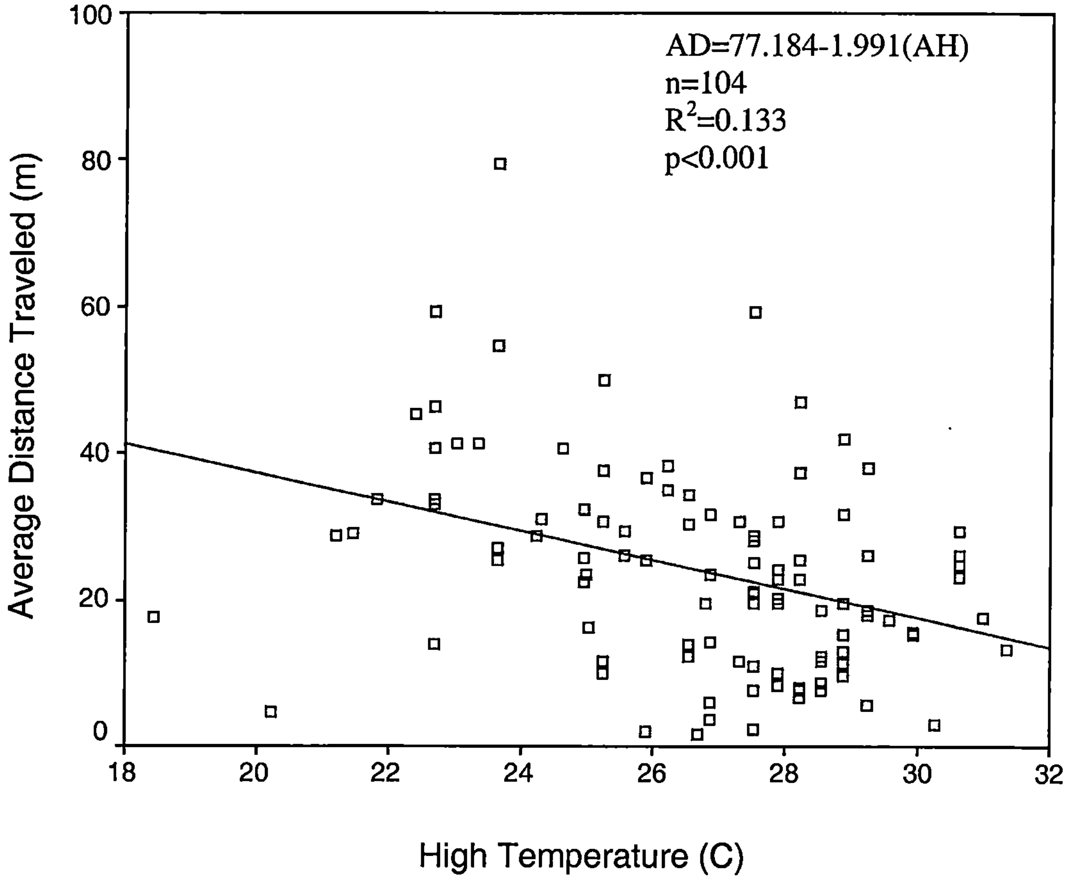


Figure 6. Average distance traveled per day (AD) and the average high temperature per day (AH) for 17 *Terrapene c. carolina* tracked a minimum of two weeks. Data were collected from May through August, 2000 in Loudon Co., Tennessee.

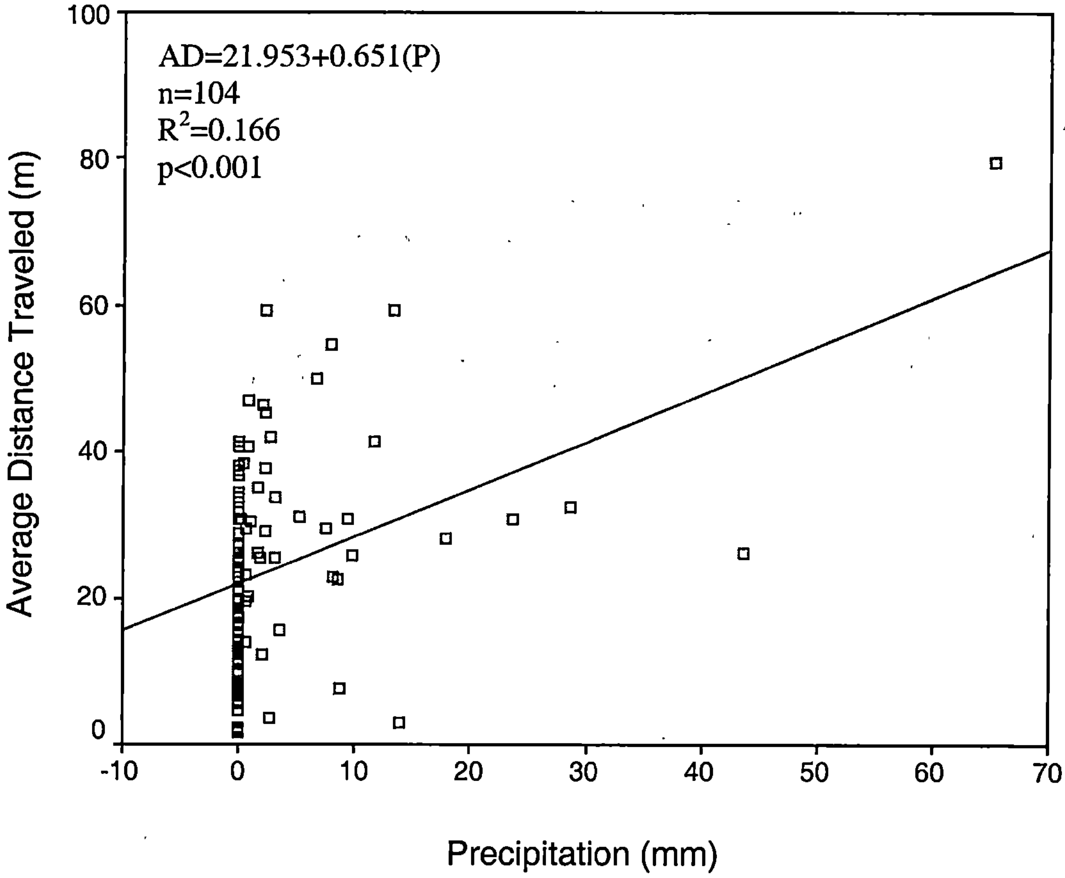


Figure 7. Average distance traveled per day (AD) and precipitation per day (P) for 17 *Terrapene c. carolina* tracked for a minimum of two weeks. Data were collected from May through August, 2000 in Loudon, Co., Tennessee.

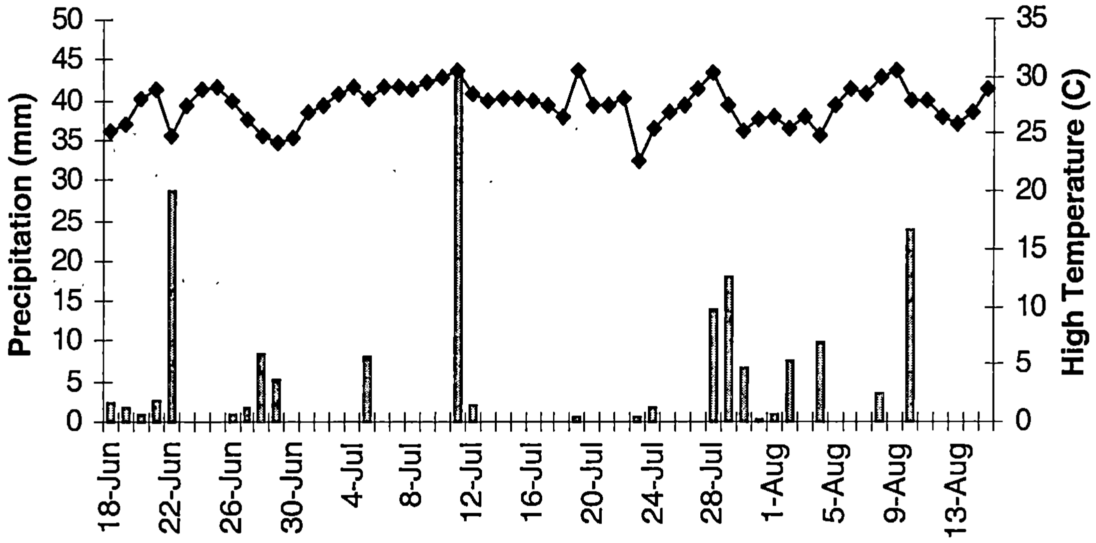


Figure 8. Daily precipitation (bars) and high temperature (diamonds) during the range of temporary pond use by *Terrapene c.carolina* in Loudon, Co., Tennessee. Data were taken from the NOAA meteorological station in Loudon Co., Tennessee in 2000.

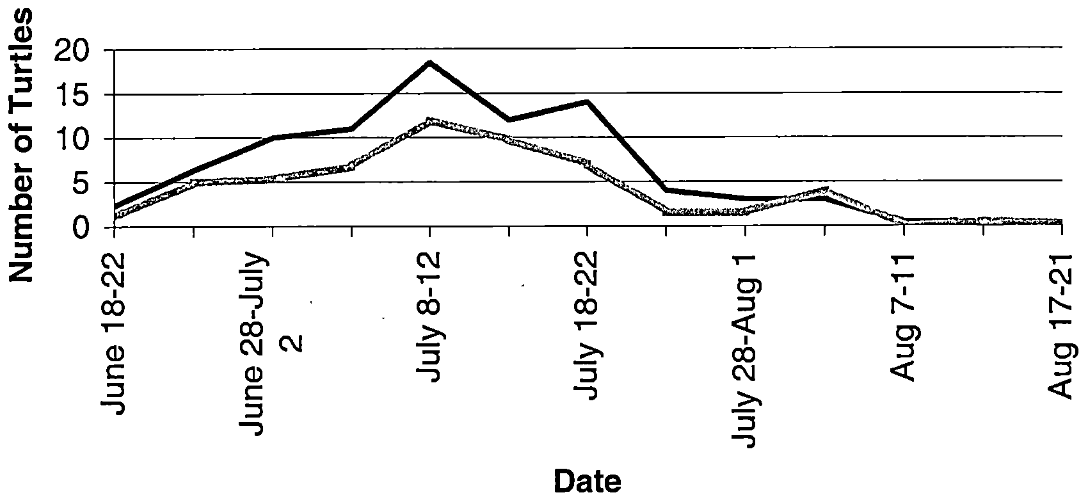


Figure 9. Numbers of male (dark line) and female (light line) *Terrapene c. carolina* found in the southern pond in Loudon County, Tennessee, averaged over five day intervals. Data on pond use were collected from June through August, 2000.

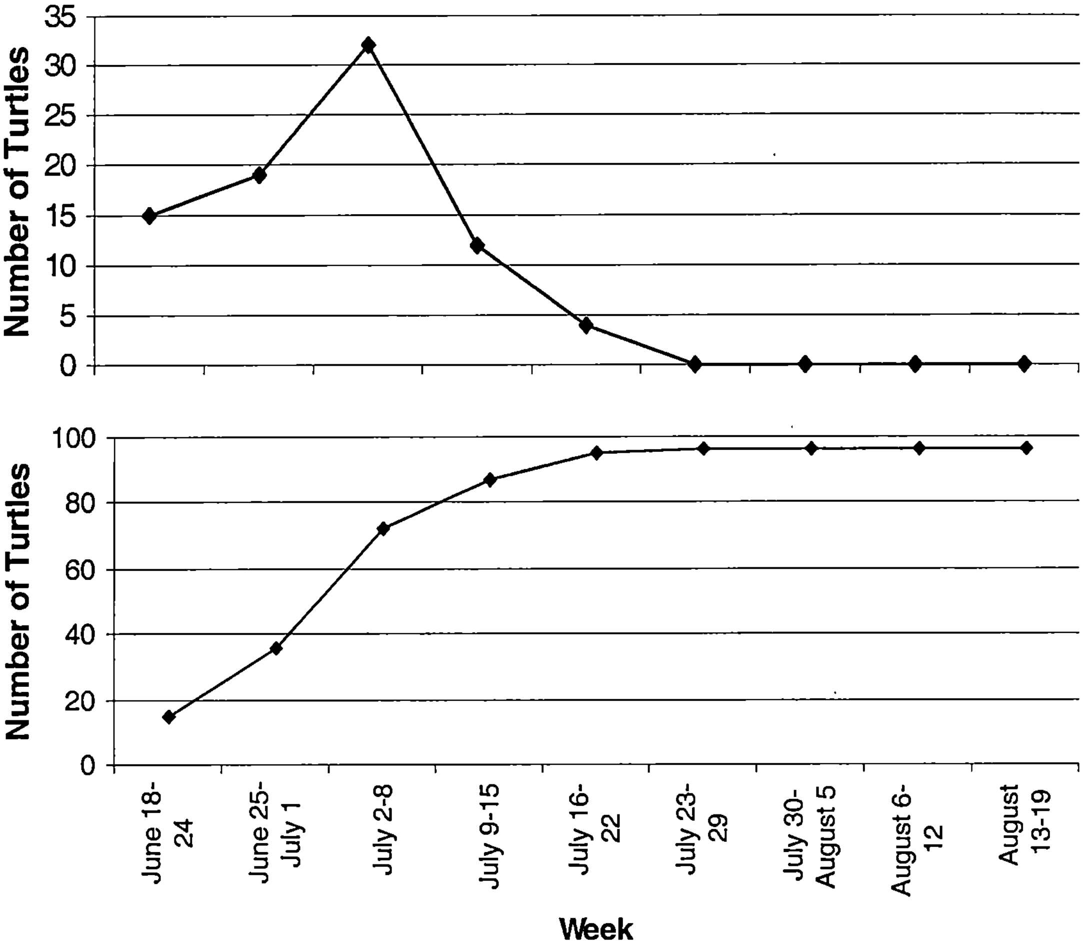


Figure 10. The number of *Terrapene c.carolina* found per week in the northern and southern temporary ponds in 2000 for turtles not previously found (upper) and the cumulative (lower) number of turtles. Recaptured turtles are not included. The ponds were located at the study site in Loudon Co., Tennessee.

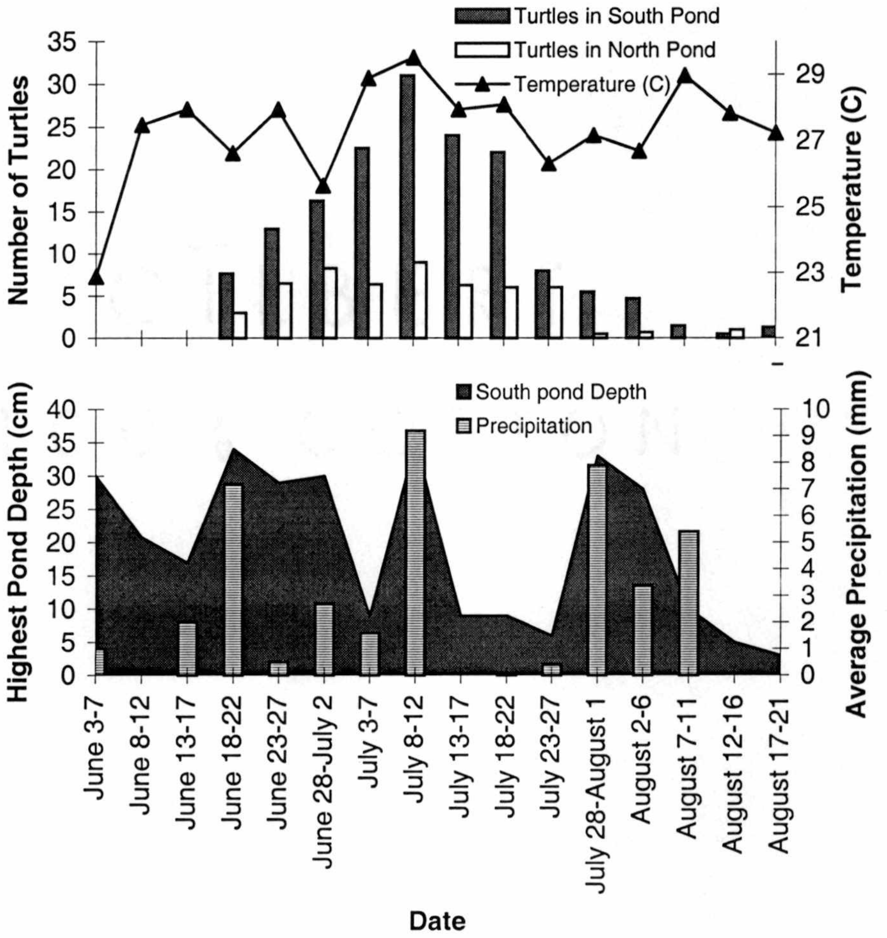


Figure 11. Five day intervals of (upper) the average number of *Terrapene c. carolina* in the temporary ponds relative to the average temperature and (lower) the highest pond depth relative to the average precipitation. Temperature and precipitation data were obtained from the NOAA meteorological station in Loudon County, Tennessee in 2000. Turtle densities in the ponds began rising during a period of increasing temperatures and low rainfall, and began dropping as temperatures dropped after the heaviest rain (and highest pond depth) of the season. At pond depths below approximately 8cm, the majority of the pond was mud.

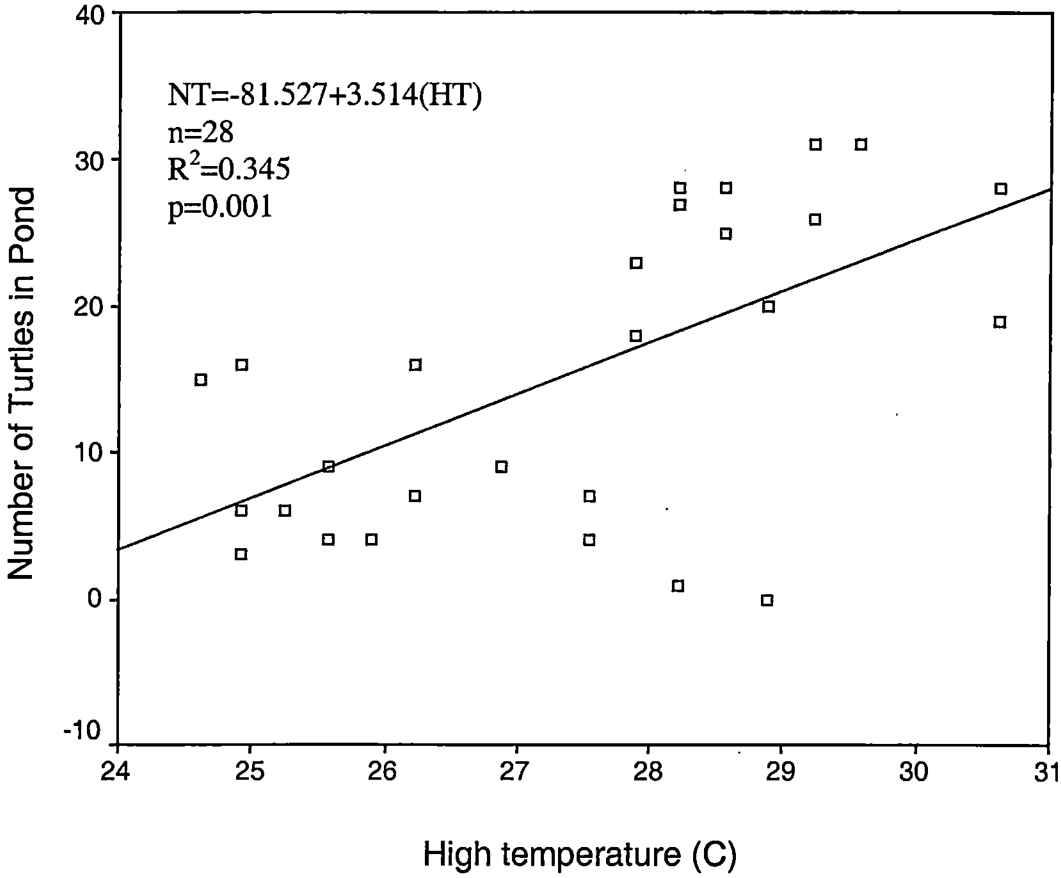


Figure 12. Number of *Terrapene c. carolina* (NT) in the southern temporary pond and high temperature (HT) at a study site in Loudon Co., Tennessee. Data were collected from the arrival of the first turtle to the pond in June until the pond contained no turtles in early August, 2000.

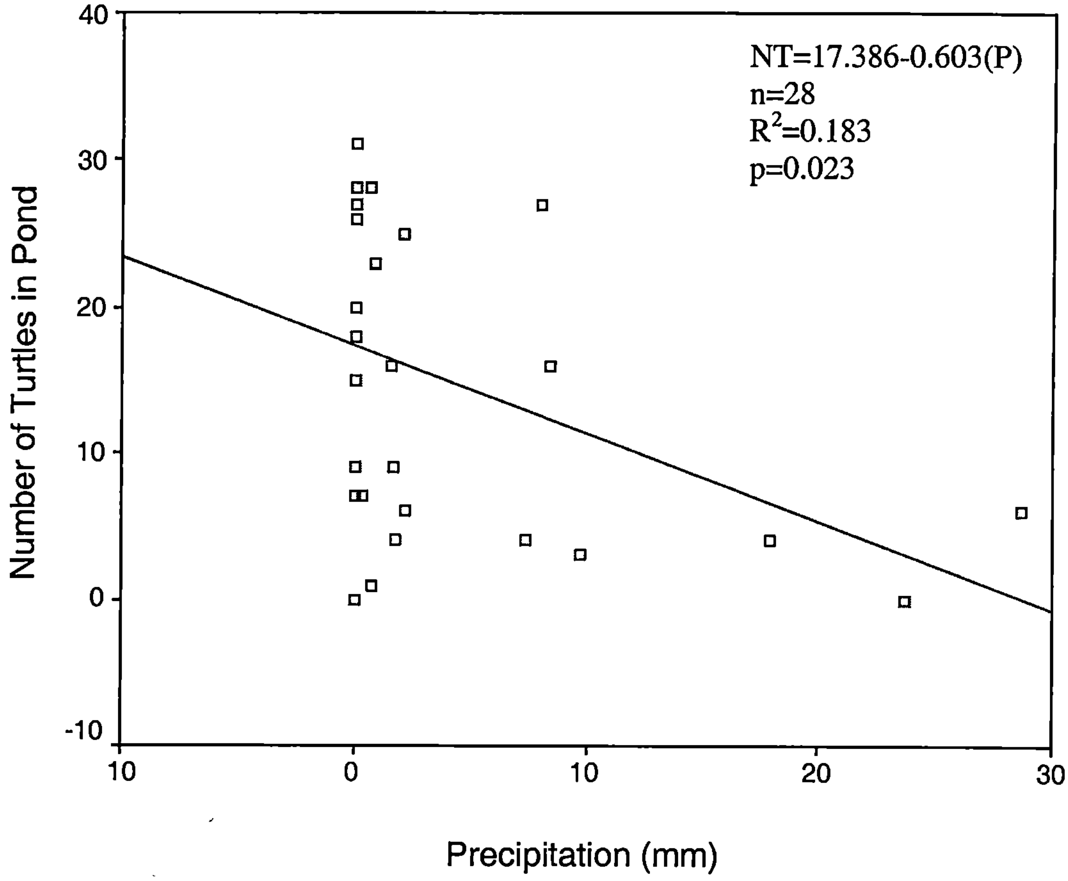


Figure 13. Number of *Terrapene c. carolina* (NT) in the southern temporary pond and precipitation (P). Data were collected at a study site in Loudon Co., Tennessee from June through early August 2000.

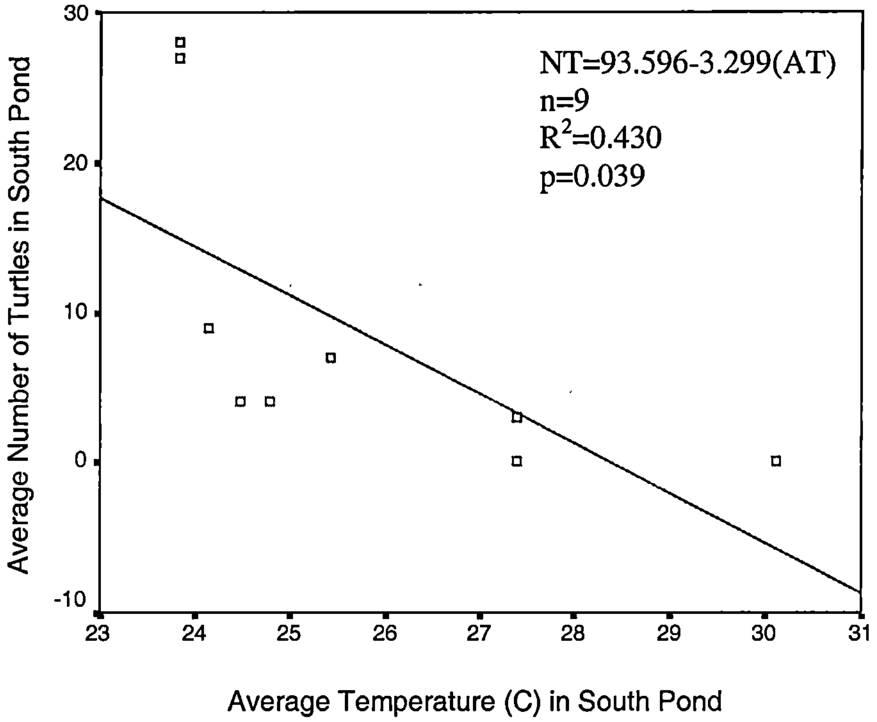


Figure 14. Average number of *Terrapene c. carolina* (NT) in the southern temporary pond and the average open water temperature (AT) of the southern temporary pond. Data were collected in Loudon Co., Tennessee from June through August 2000.

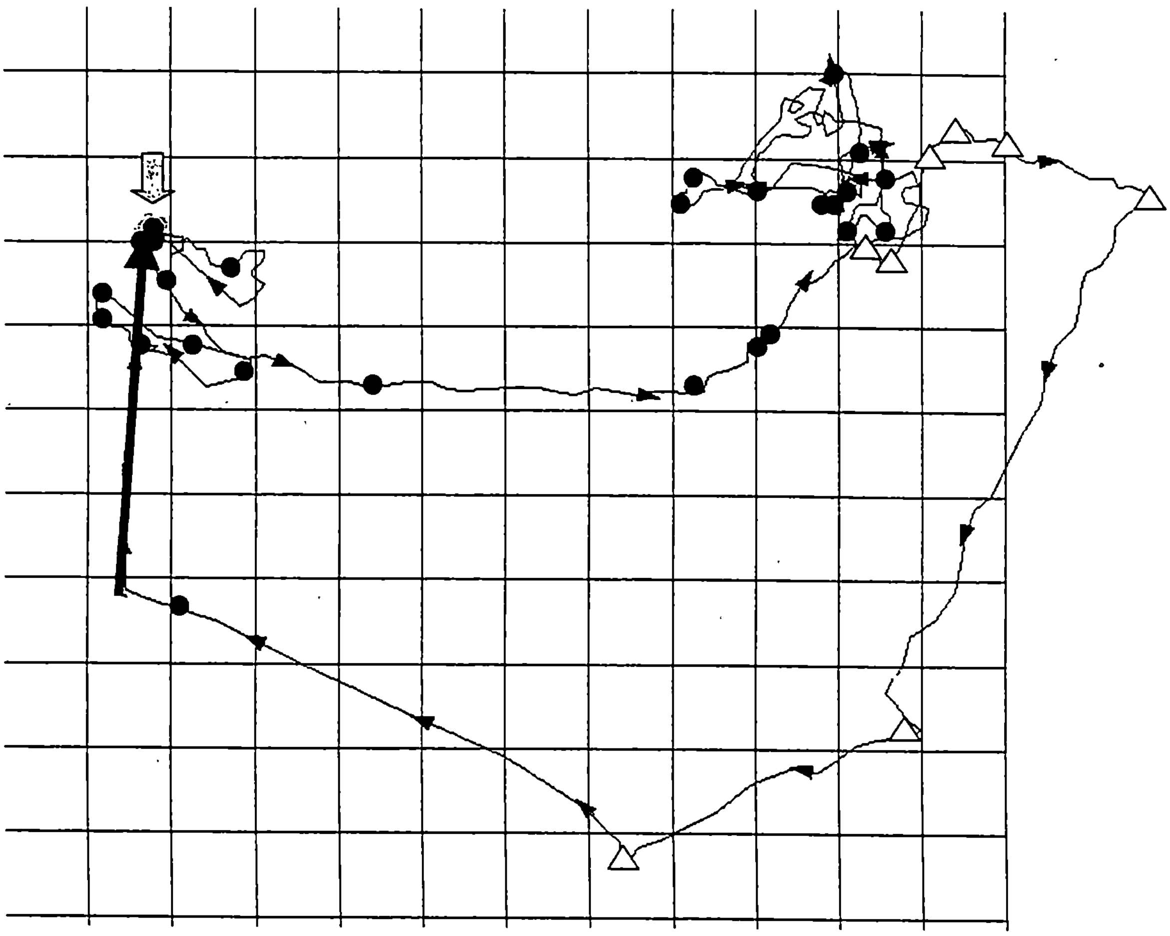


Fig. 15. Linear movement and seasonal use of home range of *Terrapene c. carolina* # 21 at the Loudon study site. Data for this turtle was first collected during late spring and continued through summer 2000. The short arrow indicates location of the temporary pond, and the long arrow replicates linear movement toward the pond on June 21. Triangles indicate spring locations and circles indicate summer locations. Each square is twenty m on a side.

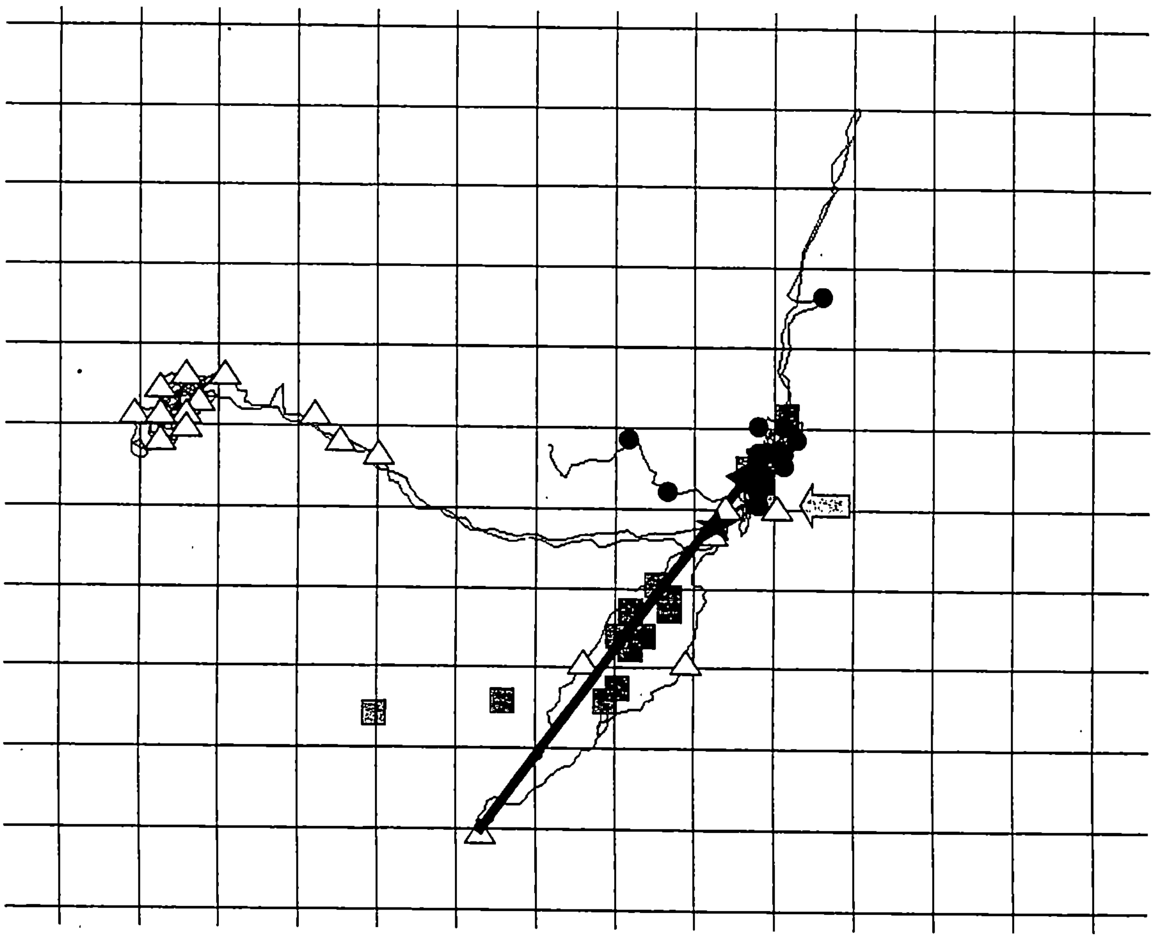


Fig. 16. Linear movement and seasonal use of home range of *Terrapene c. carolina* # 2 at the Loudon study site. Data for this turtle was collected from spring (May 9) until remaining in the hibernaculum for four weeks. The short arrow indicates location of the temporary pond, and the long arrow replicates linear movement toward the pond on May 16. Triangles indicate spring locations, circles indicate summer locations, squares indicate fall locations, and the star signifies hibernaculum location. Each grid square is twenty m on a side.

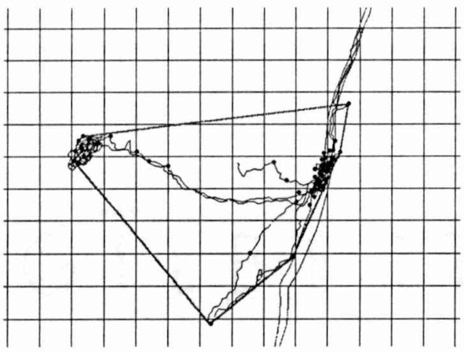
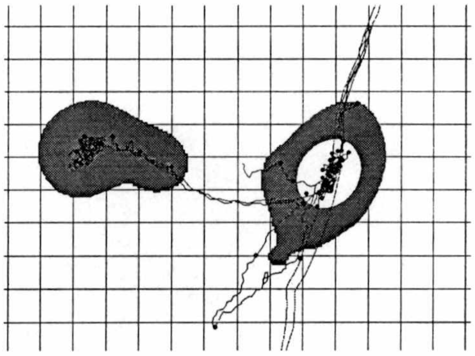
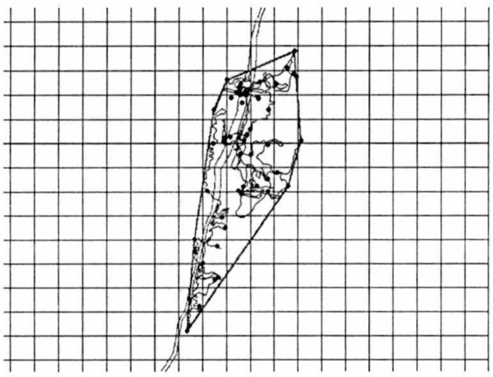
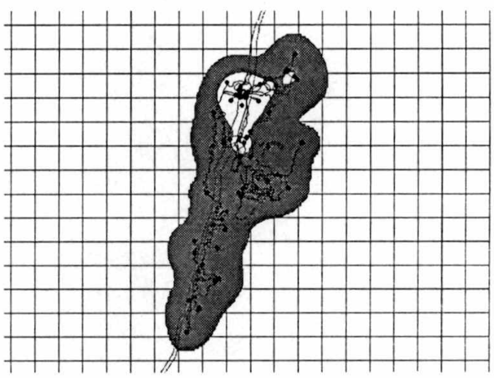
Turtle #	Minimum Convex Polygon	Kernel
		
2 (*n*=54)	home range=1.32 ha	home range=0.89 ha
		
3 (*n*=52)	home range=1.13 ha	home range=1.95 ha

Figure 17. Home ranges of 13 *Terrapene c. carolina* fitted with trailing devices and followed a minimum of 28 days. Data was collected in Loudon Co., Tennessee from May through August, 2000. Home ranges were calculated via minimum convex polygon and fixed kernel methods. Each square is 20 m on a side. Dots represent turtles' locations every two days; home range maps are constructed based on these locations. Daily routes of travel are included. Arrows indicate location of the temporary ponds; these lie on the dirt logging road that runs essentially vertically through each grid. Light areas of the kernel home ranges are based on a 50% probability; dark shaded areas are based on a 95% probability.

Figure 17, continued

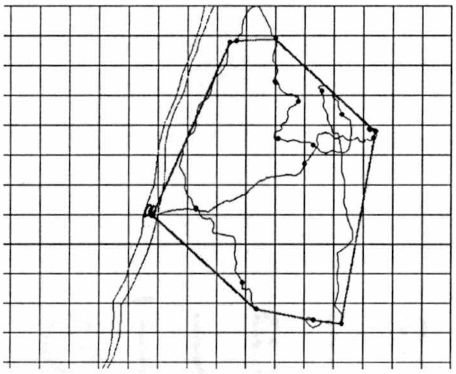
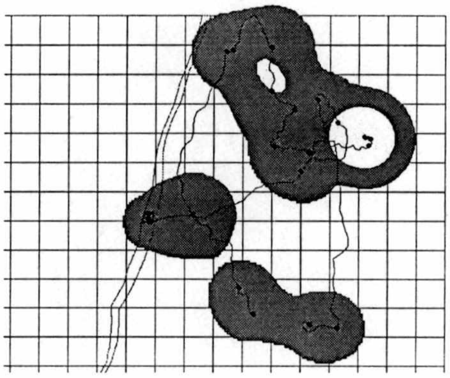
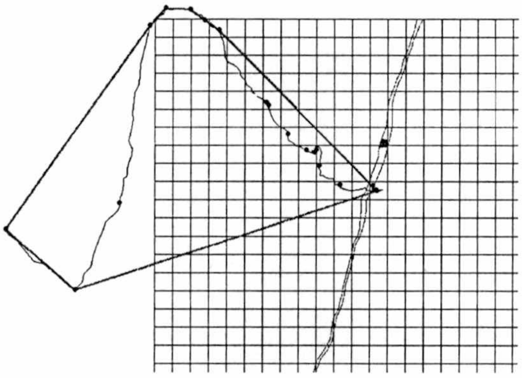
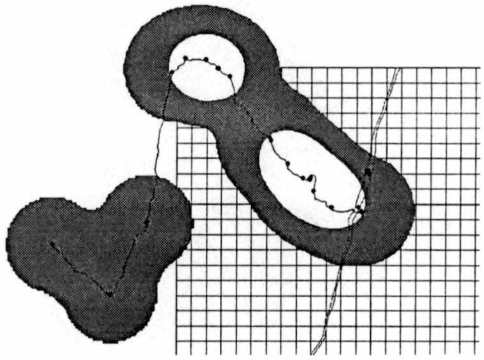
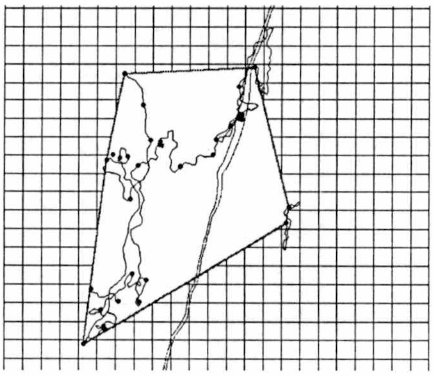
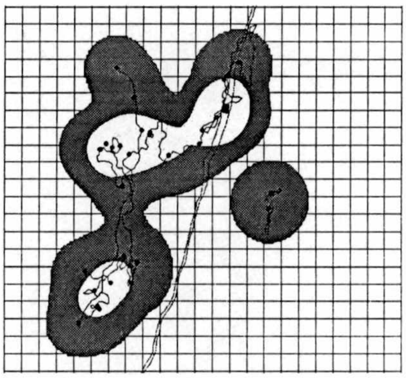
Turtle #	**Minimum Convex Polygon**	**Kernel**
11 (n=33)	 home range=1.89 ha	 home range=2.03 ha
13 (n=19)	 home range=6.50 ha	 home range=9.90 ha
14 (n=33)	 home range=4.24 ha	 home range=6.03 ha

Figure 17, continued

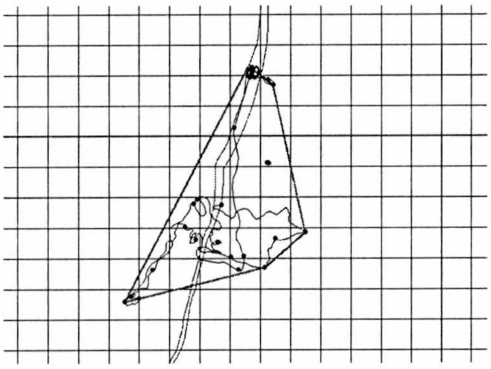
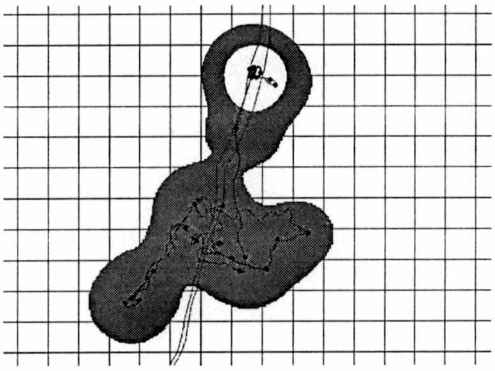
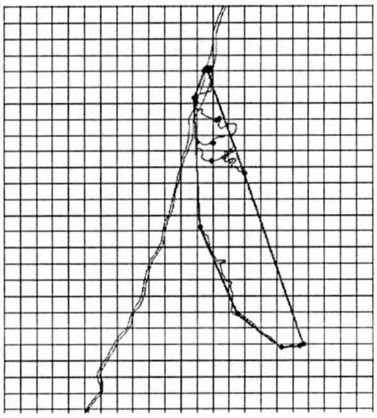
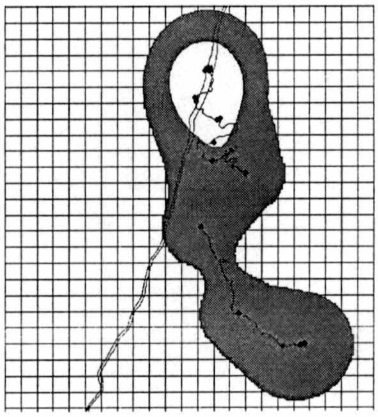
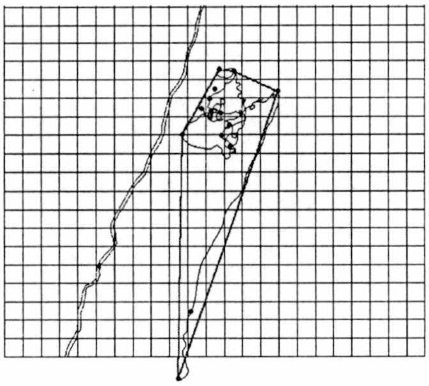
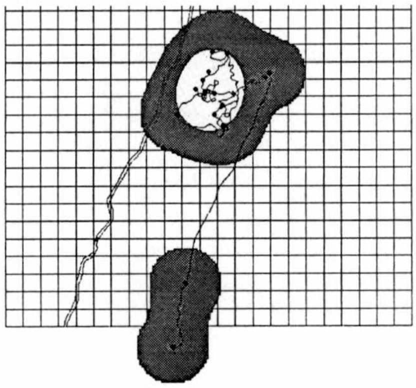
Turtle #	Minimum Convex Polygon	Kernel
16 (*n*=33)	 home range=0.87 ha	 home range=1.55 ha
17 (*n*=18)	 home range=1.91 ha	 home range=6.30 ha
20 (*n*=14)	 home range=1.65 ha	 home range=3.34 ha

Figure 17, continued

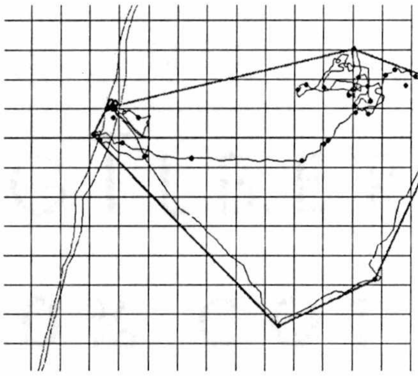
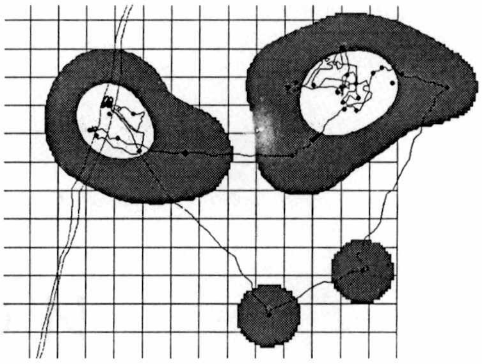
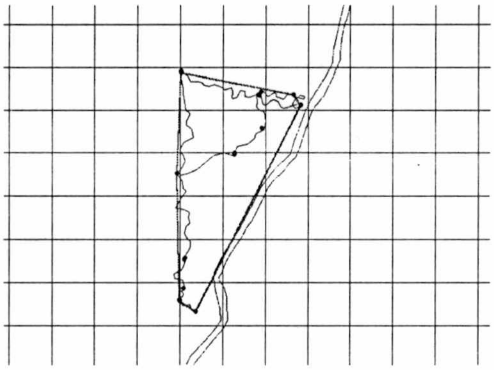
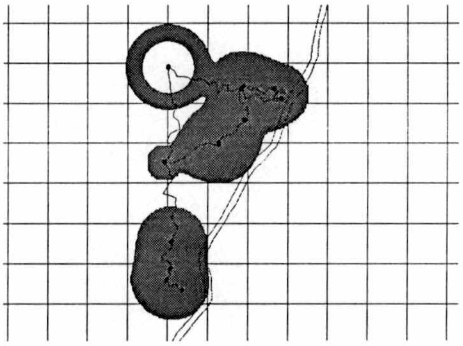
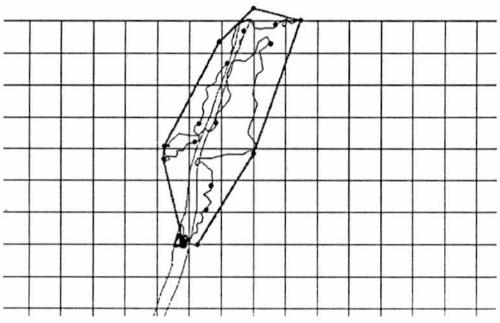
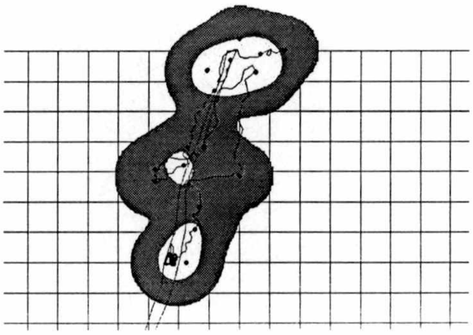
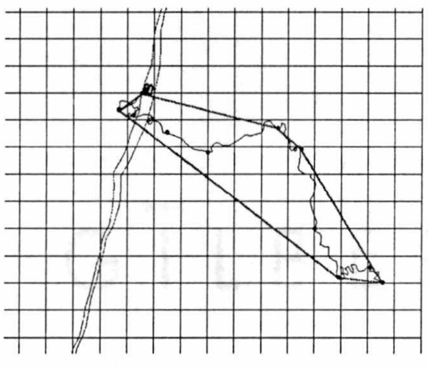
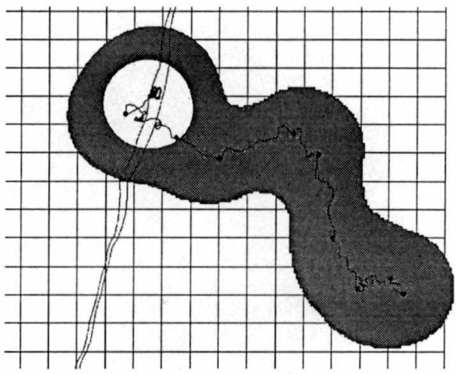
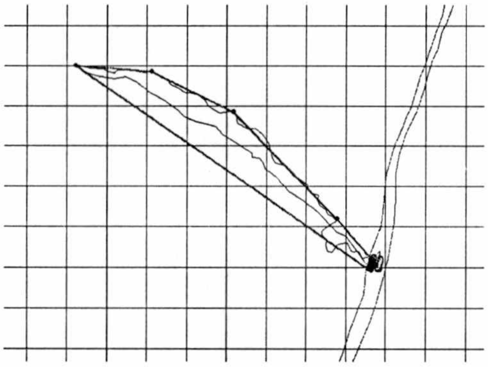
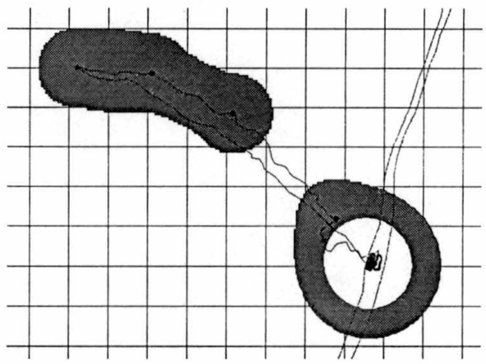
Turtle #	**Minimum Convex Polygon**	**Kernel**
21 (*n*=41)	 home range=2.74 ha	 home range=2.73 ha
23 (*n*=35)	 home range=0.36 ha	 home range=0.61 ha
28 (*n*=24)	 home range=0.62 ha	 home range=1.45 ha

Figure 17, continued

Turtle #	**Minimum Convex Polygon**	**Kernel**
38 (*n*=17)	 home range=0.90 ha	 home range=2.78 ha
53 (*n*=14)	 home range=0.28 ha	 home range=0.90 ha

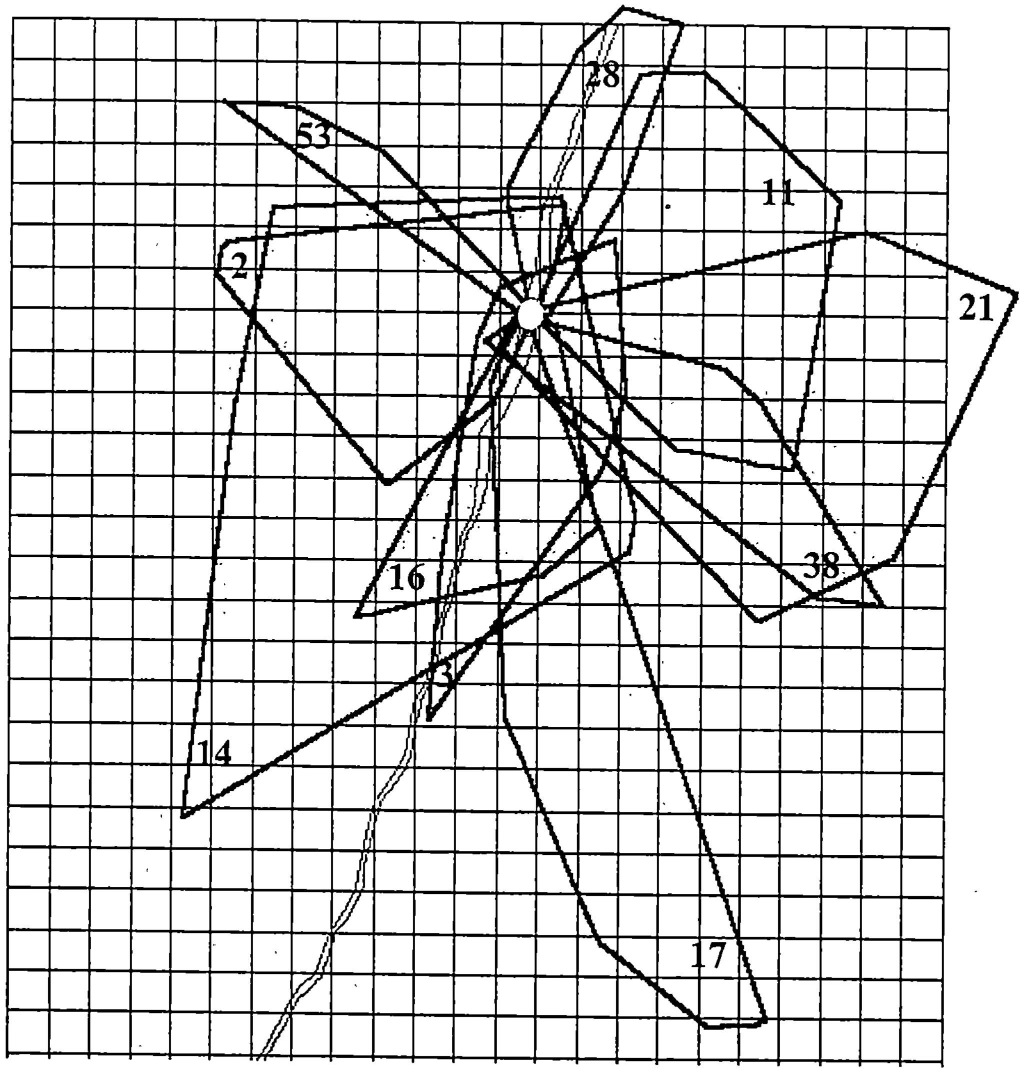


Figure 18. Minimum convex polygon home ranges of ten *Terrapene c. carolina* that used the southern temporary pond at the Loudon Co., Tennessee study site. Home ranges were based on string trailing data for turtles trailed a minimum of 4 weeks from May through August, 2000. Each square is 20 m on a side. The small white circle represents the southern temporary pond, which lies on the dirt logging road that runs roughly vertically through the map.

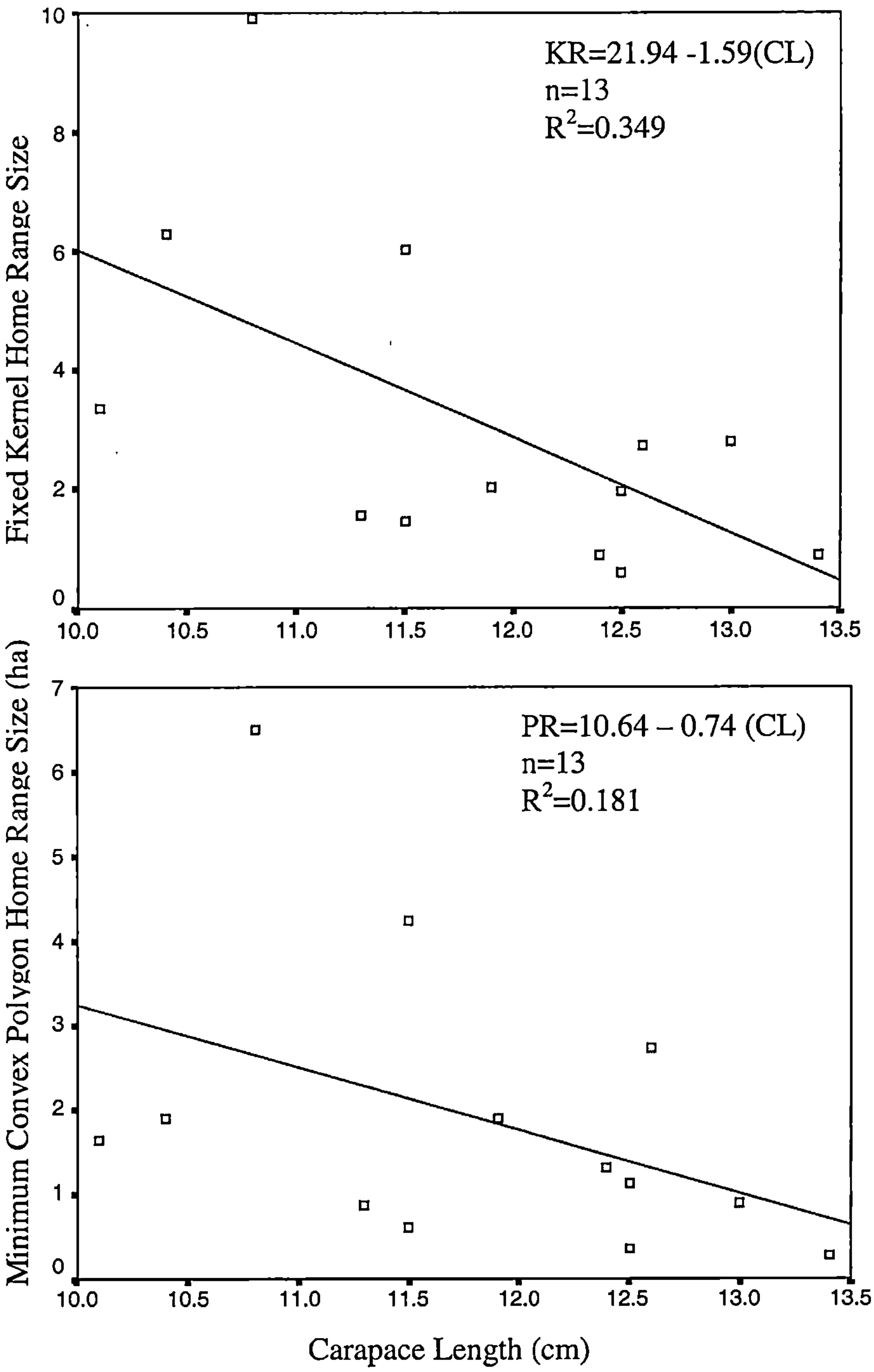


Figure 19. Home range size of *Terrapene c. carolina* and carapace length (CL), calculated by the kernel (KR) method (upper) and the minimum polygon (PR) method (lower). Data were collected daily from 28 to 106 days from May through August, 2000 in Loudon Co., Tennessee.

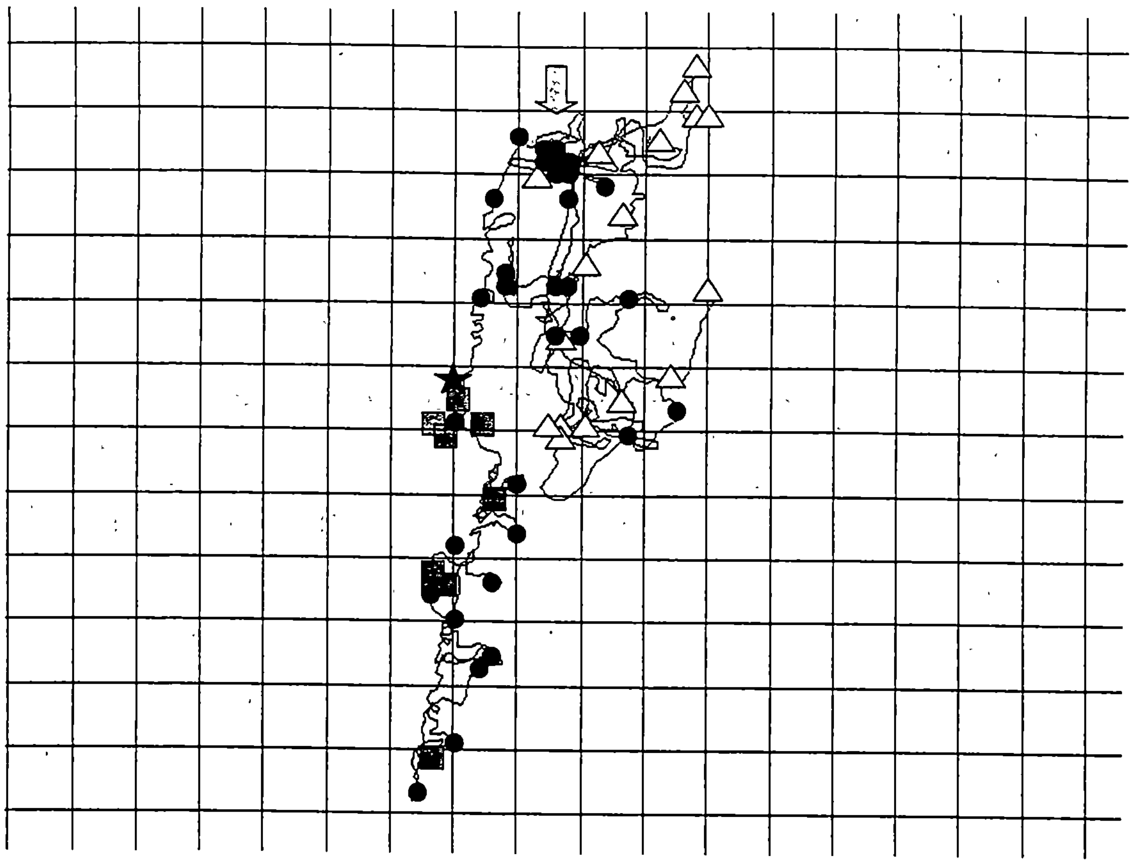


Fig. 20. Seasonal use of home range of *Terrapene c. carolina* # 3 at the Loudon study site. Data for this turtle was collected from spring (May 9) until remaining in the hibernaculum for four weeks. Triangles indicate spring locations, circles indicate summer locations, squares indicate fall locations, and the star signifies hibernaculum location. Each grid square is twenty m on a side.

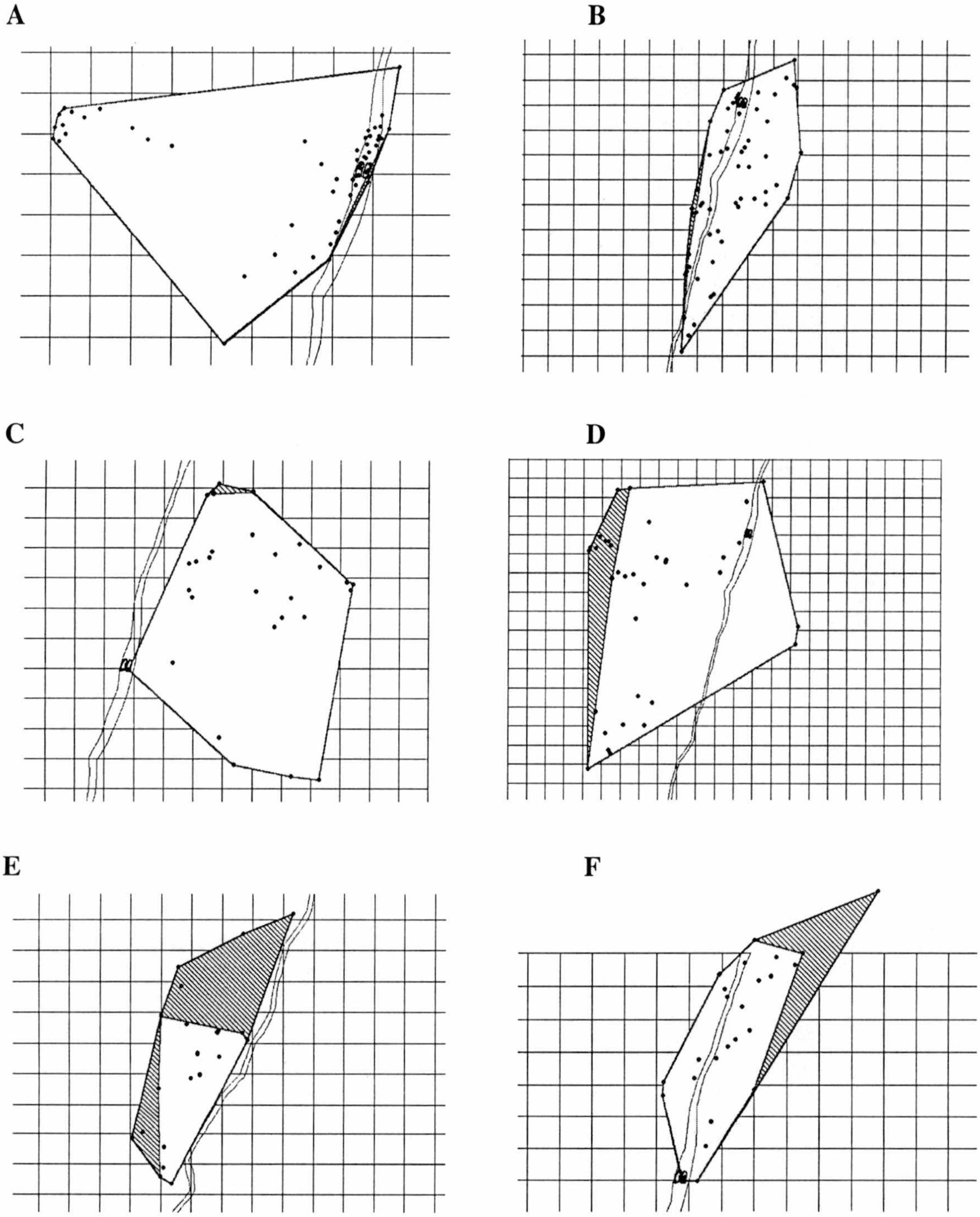


Figure 21. Minimum convex polygon home ranges and hibernation sites (indicated by stars) of the six *Terrapene c carolina* fitted with radio transmitters subsequent to trailing device removal. Hatched polygons represents home ranges derived from trailing device data from May through August, 2000. Transparent polygons represent home ranges derived from the additional 4 months of radio transmitter data from September through December, 2000. A = turtle # 2, B = turtle # 3, C = turtle # 11, D = turtle # 14, E = turtle # 23, F = turtle # 28

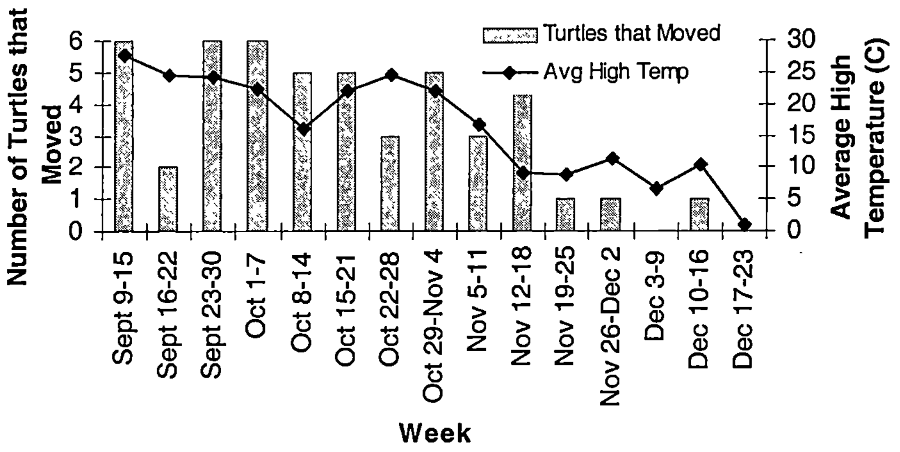


Figure 22. Average high temperature and number of *Terrapene c. carolina* that moved per week for the six turtles fitted with radio transmitters. Data were collected from September through mid January, 2000 at the Loudon Co., Tennessee study site. Turtles were located biweekly until they remained in hibernacula for 4 weeks.

VITA

Bridget Michelle Donaldson was born in Aurora, Illinois December 30, 1974. She attended primary education in the public system of Elkhorn, Nebraska, and completed her primary and secondary education in Cincinnati, Ohio. She graduated from high school in Cincinnati, Ohio in 1993. She then attended University of Colorado and received her Bachelor of Arts degree in Evolutionary, Populational, and Organismic Biology in May, 1997. She interned and worked for two years as a dolphin biologist and an environmental consultant prior to accepting a teaching assistantship at the University of Tennessee, Knoxville in August, 1998. She received a Master of Science degree in Ecology and Evolutionary Biology in May, 2001.