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CHAPTER 26

A Long-Term Study of Eastern Box Turtles (*Terrapene c. carolina*) in a Suburban Neighborhood: Survival Characteristics and Interactions with Humans and Conspecifics

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Abstract—We report findings from over 125 animal-yr of adult Eastern Box Turtle (*Terrapene carolina carolina*) radio tracking in an urban forest/suburban neighborhood ecotone in Aiken, South Carolina (USA). Data gathered from 23 radiotelemetered adults over 15.5 yr (1989–2004) documented 10 deaths (7 associated with human activities). Constant annual adult survival probability estimated for radiotelemetered turtles was 0.932 ± 0.021 (SE). Although a model of gender-specific adult survival was not as strongly supported as a constant survival model, evidence pointed to females experiencing lower survival than males. A model that included time spent in suburban neighborhoods also performed nearly as well as a constant survival model, suggesting that greater time spent in suburban habitats tended to reduce survival. In a separate analysis derived from opportunistic marking and recapture of 86 adult turtles not used in the radiotelemetry study, a model of constant survival and constant capture probability proved the most parsimonious, with annual apparent survival probability estimated as 0.954 ± 0.036. Estimated annual capture probability was low (0.085 ± 0.019), but a gender-specific capture probability model suggested that the encounter rate for females was higher than for males, even though the population was male-dominated (male:female = 2.1:1). Survival estimates indicated that average life-span (after attaining adulthood) ranged from 14 to 21 yr. Coincidental human encounters with radiotelemetered turtles took place mostly within developed suburban areas, peaking in June–July, and suggested that females may have been more attracted to developed habitats than males (e.g., females were more likely than males to be encountered crossing streets). In contrast, conspecific interactions among Box Turtles were reported more frequently in forest than in developed habitats. Our study suggests that adult Box Turtles can persist in urban forest/suburban neighborhood ecotones with survival rates not differing greatly from those of adults in more natural habitats. However, movements of adult females from forested habitat into adjacent suburban neighborhoods, especially during the nesting season, may result in these human-altered habitats acting as ecological traps, possibly impacting long-term population viability.

Key Words — Behavioral Interactions, Eastern Box Turtle, Habitat Use, Mortality Sources, Suburban Habitats, Survival Estimation, *Terrapene c. carolina*

As urban/suburban development continues throughout eastern North America, mature eastern deciduous forests and their adjacent grassland-meadow-farmland ecotones are among the most frequently altered. Development of such areas has centered on their conversion to suburban housing developments (Budischak et al. 2006) and has resulted in fragmentation of many remaining natural areas. These impacts present diverse challenges to wildlife populations that require relatively large complex landscapes of varying habitats.

Of all the North American herpetofauna found within these natural and altered habitats, probably none is as visible and familiar as the Eastern Box Turtle (*Terrapene c. carolina*: Pope

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1949; Ernst et al. 1994; Dodd 2001). As a long-lived species with life spans commonly exceeding 50 yr (Dodd 2001), Box Turtles often exist within suburban/exurban neighborhoods and may be encountered regularly by their residents. Frequent observations of Box Turtles in suburban neighborhoods may lead to the impression that sustainable populations persist in residential areas. Without assessments of population survival rates, reproduction, and recruitment, however, the continued persistence of viable populations of Box Turtles in human-altered areas cannot be assured.

Our objective was to use radiotelemetry to evaluate the consequences to adult Eastern Box Turtles of living in or adjacent to an urban forest/suburban neighborhood ecotone. Specifically, we investigated the possibility that, although Box Turtles are commonly seen in some suburban neighborhoods, such habitats may be ecological traps (Gates and Gysel 1978) for the species and threaten long-term population viability. This information is needed to make more informed management decisions about translocating turtles out of such habitats or possibly using these areas for releasing turtles following removal from other locations. Our specific objectives were to estimate survival of adult turtles and identify specific causes of mortality. We related the survival of individual turtles to the frequency and circumstances of the turtles' use of the different habitat types available, and recorded the interactions of these turtles with the human residents of the neighborhood in which they were found. Although detailed information on reproduction and an analysis of movements and home range characteristics will eventually be available from this study, these data are not included here and will be published separately.

MATERIALS AND METHODS

We initiated a study in March 1989 using radiotelemetry to collect long-term data for individual adult turtles living in and around an urban forest/suburban neighborhood ecotone. We calculated annual adult survival probabilities with population parameter estimation techniques that are seldom used in studies of turtle demography. Sources of mortality identified for radiotelemetered turtles through 1 August 2004 are also reported. Adult survival was independently estimated from the opportunistic marking and recapture of additional non-telemetered turtles. Finally, we describe the circumstances surrounding encounters both between turtles and humans and between conspecifics.

Study Area — Our study was conducted within and adjacent to the southwestern limits of the city of Aiken (population 27,000) in west-central Aiken County, South Carolina. This region is characterized by long hot summers ($\bar{x}$ temperature = 27°C, with a frost-free period of approximately 240 days) and mild winters ($\bar{x}$ = 9°C). Mean annual rainfall is 120 cm, with the least rain falling in November ($\bar{x}$ = 5.9 cm) and the most ($\bar{x}$ = 13.1 cm) in March (Workman and McLeod 1990).

We studied Box Turtles in an ecotone between an 810-ha urban forest preserve (Hitchcock Woods) and an adjacent housing subdivision (Aiken Estates). Aiken Estates consists of single-family dwellings built on 0.7–1.0 ha lots that were largely developed in late 1955–early 1956. Additional development, particularly of lots bordering on the wooded preserve, was not completed until the mid–late 1960s. Most streets within the subdivision are two-lane with a 40 km/h speed limit. The curbs of most of these streets are sloping and can be easily traversed by even young Box Turtles. Traffic is generally limited to automobiles and light trucks. The neighborhood has restrictions prohibiting fences that are visible from the street, but some lots have fenced backyards that could impact movements of adult Box Turtles. Most yards are well-manicured and irrigated; many are landscaped with exotic ornamental plants, particularly border grass (*Liriope*) and perennial shrubs including rhododendron (*Azalea*), mountain laurel (*Kalmia*), and holly (*Ilex*). Small (≤ 0.1 ha) areas of unmanaged vegetation or woodlots are found along some unmowed backyard property lines. These areas are dominated by honeysuckle (*Lonicera*), wild grape (*Vitis*) and catbrier (*Smilax*) and occasionally form narrow, ≤ 0.5-km long segments of relatively undisturbed habitat extending through the neighborhood. Mature overstory trees include bull bays (*Magnolia*), pines (*Pinus*), oaks (*Quercus*), hickorys (*Carya*), and tulip trees (*Liriodendron*). These largely reflect the composition of the adjacent urban forest, as many trees were not removed during housing construction. A detailed description of the vegetation of the Hitchcock Woods is given by Jones (1979).

Hitchcock Woods has been maintained as an urban forest preserve since the early 20th century and is now a State of South Carolina Heritage Preserve. The forest is located within the Carolina Sandhills region of the upper Coastal Plain (Wilds et al. 1998). Use of the preserve is restricted to recreational pedestrian and equestrian activities with forest management under the direction of the Hitchcock Foundation Board of Trustees. After 60 yr of fire suppression, an active forest management plan was implemented in the late 1990s (Wilds et al. 1998). The current forest management plan includes limited selective timbering and controlled burning to promote fire safety, control disease outbreaks, enhance forest habitat diversity, and maintain trails.

Most of our data were collected within a 215.9-ha study area (Fig. 1) that included an ecotone between the southern boundary of Hitchcock Woods and the adjacent Aiken Estates subdivision. Approximately 56.5 ha (26.2%) is forest habitat, including 33.2 ha of the Hitchcock Woods and 23.3 ha divided among four isolated patches in the southern portion of the study area (Fig. 1). The remaining 159.4 ha (73.8%) includes developed residential lots (134.6 ha), portions of two golf courses (12.6 ha; one of which surrounds a 4.3 ha patch of remnant forest), and paved street (12.2 ha). Although no quantitative demographic data are available for the human residents of our study area, the general impression of those familiar with the area is that the majority of residents are older

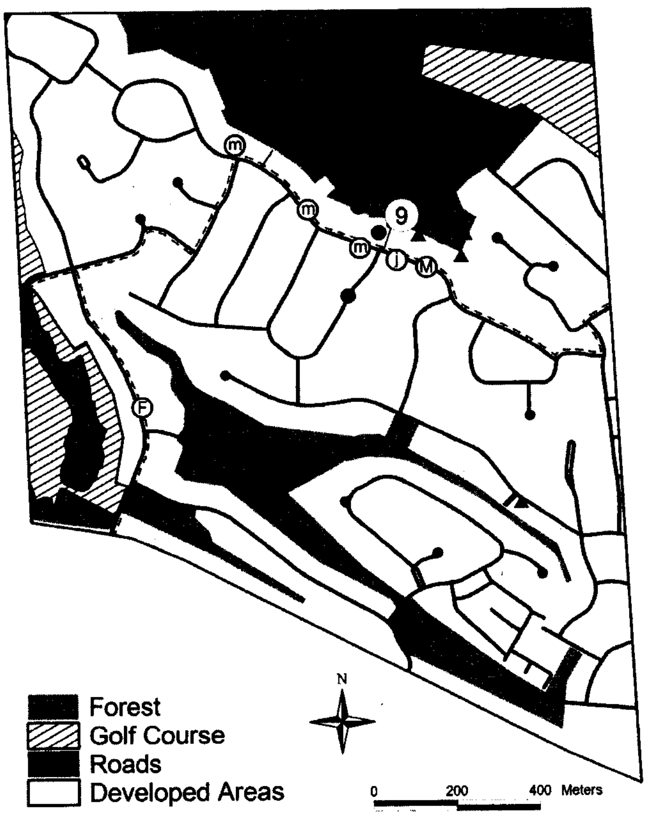

Fig. 1. Map of the area used to study the movement, behavior and survival of 22 radiotelemetered adult Eastern Box Turtles (*Terrapene c. carolina*) in an ecotone between an urban forest (Hitchcock Woods) and a housing subdivision (Aiken Estates) in the city of Aiken, SC. Gray-shaded areas represent natural forest habitat, and non-shaded areas represent areas of residential housing lots. Cross-hatching represents golf courses, and heavy dark lines indicate paved two-lane streets. Original capture locations of individual turtles are indicated by black triangles (males) and circles (females). The white circle with the number "9" indicates an area where additional male (n = 5) and female (n = 4) turtles were originally captured. Circled letters M, F and J indicate locations where adult male, adult female, and juvenile, respectively, turtles were found killed on the street by motor vehicles. Circled upper and lower case letters designate turtles that were or were not carrying radio transmitters, respectively. Streets paralleled with a dashed line indicate routes often used by non-resident vehicular traffic passing through the neighborhood (often at increased rates of speed) to avoid more congested traffic areas outside the study area. Other streets are mostly used only by local residents and deliveries servicing homes within the study area. An additional female turtle was studied in a similar area about 1.9 km northwest of the study area (see text).

retired individuals with only a minority of families having smaller (school-age or younger) children. Many of the residents who became familiar with our turtles during the course of this study indicated that they would like their grandchildren, who were not resident in the neighborhood, to see the radio-telemetered turtles and learn more about our study.

Traffic flow on the streets of our study area was mostly limited to the travel of local residents to and from their homes. One exception, however, was a frequently-used corridor comprised of several neighborhood streets (Fig. 1; solid and dashed line) which had become familiar to many non-residents of the area as a route to avoid traffic congestion and a number of traffic signals in locations outside of our study area. Traffic on these streets therefore traveled at a generally greater rate of speed than that on the other streets, many of which terminated in dead-end cul-de-sacs (Fig. 1).

Some radio tracking data were also collected for a female May 2000–October 2003 in an area about 1.9 km NW of our primary study area. During this period, this turtle also ranged within an ecotone formed at the southern boundary of Hitchcock Woods and another housing subdivision (Foxchase).

Study Animals and Radiotelemetry — Adult Box Turtles were collected opportunistically between March 1989 and July 2000. Attempts to estimate age by counting scute growth annuli (Wilson et al. 2003) were made at the initial capture and at several subsequent recaptures of each turtle. Turtles used in the radiotelemetry study were fitted with Telonics MOD-080 transmitters measuring 32 × 18 × 21 mm. These were attached to the rear of the carapace and weighed 16–17% of the turtle's body mass. Radio transmissions were in the 163–164 MHz range and could usually be detected at distances ranging from 50–500 m, depending on whether the turtle was active on the surface or buried, and on the density and moisture of the vegetation and litter. Turtles were brought into the laboratory biennially, just before and immediately after winter dormancy, to replace transmitters. Turtles were then released at their capture locations generally within 48 h. Radiotelemetered turtles were located visually at least once per month; turtles located during the last week of a month were not located again until at least 2 weeks later.

Throughout the study, we documented dates, locations and circumstances of encounters between radiotelemetered turtles and neighborhood residents. In earlier years of the study, we attached contact information to the radio transmitter. In the latter years of the study however, the movements and habits of turtles in neighborhood habitats became sufficiently known to residents that including such information was no longer necessary. Encounters not involving use of the radiotelemetry equipment were also documented between radiotelemetered turtles and researchers involved in the study. These two sets of observations were used to estimate a minimal frequency of turtle encounters with humans (i.e., an encounter reporting rate < 1.0 was assumed).

During the study, other non-radiotelemetered Box Turtles were also captured and recaptured opportunistically by residents and researchers in the study area. There was, however, no systematic effort to locate non-radiotelemetered turtles as a part of this study. Previously unmarked turtles were permanently marked by unique combinations of small holes drilled in the marginals, and were typically released at their capture locations within 48 h. Gender was determined for adult turtles from external morphology. Encounter histories from these non-telemetered individuals were used in survival estimation procedures described below. Occasionally, turtles were observed in close proximity to conspecifics. We defined these presumed social encounters between turtles (with or without radio transmitters) as including any two turtles found ≤ 0.5 m apart, and such that there was no doubt that each turtle was aware of the other's presence.

Statistical Analyses — Deaths of radiotelemetered turtles were categorized as either human-related or natural, with the latter including turtles that were found dead with no apparent cause. To determine whether turtle survival was related to time spent in forest habitat versus developed areas (i.e., neighborhoods or golf courses), a habitat use index (HUI) was calculated from a subset of all first monthly locations for turtles with ≥ 500 days of radiotracking data. In sampling turtle locations for calculating HUI, an additional restriction was imposed such that no two successive locations were used if they were < 2 wks apart, even if they were in different months. Each HUI value was calculated as the fraction of all first monthly locations of each turtle during April–October in which the turtle was located in developed habitat of the study area (Fig. 1). HUIs were thus continuously distributed between 0 (always in forested habitat) and 1 (always in developed habitat).

Survival rates of adults were estimated independently for the radiotelemetered turtles and the non-radiotelemetered turtles that were located opportunistically over the course of the study. Sixteen encounter occasions (yr) yielded 15 intervals over which survival could be modeled. In all survival analyses, we used only those encounters that occurred between April and October. We used the Cormack-Jolly-Seber (CJS) model for open populations (from program MARK version 4.2, White and Burnham 1999) for analysis of capture-recapture data from non-radiotelemetered turtles. For radiotelemetered turtles, we conducted analyses using the known-fates model within MARK. It is important to distinguish between survival estimates generated from these two types of data. Because it is impossible to differentiate between mortality within a population and emigration of individuals from the area, only apparent survival (Φ) can be estimated from capture-recapture data. In contrast, known-fates data from radiotelemetry studies imply knowledge of the true status of individuals (alive or dead), with the exception of lost contact with radiotelemetered animals, which may require censoring on those occasions. For a given population, therefore, the survival estimate from a known-fates model (S) is typically higher than that derived from a capture-recapture model if emigration occurs. We were interested in estimating survival probabilities of radiotelemetered adult Box Turtles while considering the effects of gender and relative use of natural versus suburban habitats as estimated by their HUI values. We therefore modeled effects of gender and habitat-use in separate survival analyses to maximize our use of the available data, with potential gender effects tested/eliminated first to maximize sampling size for subsequent HUI comparisons. We constructed sets of candidate models from which the most appropriate model was chosen using an information-theoretic approach (Burnham and Anderson 2002) to select the best-fitting and most parsimonious model. Following model selection, population parameter estimates, standard errors, and 95% confidence intervals were generated.

The CJS model used for encounter histories of non-radiotelemetered turtles estimated both apparent survival probability (Φ) and capture probability (p) in the presence of a group (g) parameter for potential gender effects and a time-specific parameter (t) for potential annual survival differences. We chose not to include t for use with p because there was no systematic annual search for marked turtles over the course of the study. Thus, all encounters with turtles (by researchers without the use of telemetry equipment and by non-researchers) coincided with other activities and all annual capture probabilities were assumed to be equally low. Our global model in this analysis was denoted as $\Phi(g^*t)p(g)$, and included an interaction between group effects and time for the Φ parameter. We performed a goodness-of-fit test following initial construction of the global model using program RELEASE version 3.0 in which we examined potential over- and/or under-dispersion of the data (Burnham et al. 1987). Reduced models were then constructed for comparison using variants of Akaike's Information Criterion (AIC; Akaike 1973), and we included models that constrained Φ by removing gender effects, time effects, or both, and constrained p by removing the gender effect.

The first known-fates model analysis used data from radiotelemetered turtles and estimated survival (S) while considering the effect of time and a gender group effect. In this case, the global model included the interaction of these two primary effects. Reduced models were constructed and compared using AIC variants, constraining S by removing g, t, or both as above.

The second known-fates model analysis used data from radiotelemetered turtles and estimated survival (S) while considering both time effects and group effects (here representing a potential response to differences in HUI). Turtles were classified as having a "high" (HUI ≥ 0.50) or "low" (HUI < 0.50) occupation of developed areas. The global model in this analysis included the interaction of main effects, and reduced models were constructed and compared as above.

To determine whether conspecific social encounters occurred randomly with respect to the sex ratio of the population, we used a χ^2 test of independence to compare the observed frequencies of paired-participant encounters with those expected by chance. The population sex ratio was estimated from sex determinations of all adult turtles captured in the study area during the study, including those not equipped with transmitters. We also used χ^2 tests of independence to compare observed numbers of conspecific encounters and encounters between humans and turtles with numbers expected if turtles were distributed relative to the areas of forested and developed habitats described above (Fig. 1).

Results

We radiotracked 23 adult turtles (12 males, 11 females) within a 15.5-yr period between 30 March 1989 and 1 August 2004, totaling over 125 animal-yr (Table 1). Counts of scute growth annuli suggested that most of our radiotelemetered turtles were at least 30 yr old, and some were probably considerably older. Therefore, some (perhaps many) of these radiotelemetered turtles undoubtedly hatched in undeveloped forest habitat that was subsequently replaced by the present neighborhood and golf course developments. During our study period, we documented the deaths of 10 individuals (4 M, 6 F; Table 1). Deaths attributable to the activities of

Table 1. Summary of radiotelemetric observations of adult Eastern Box Turtles (*Terrapene c. carolina*) in an urban forest/suburban neighborhood in Aiken, South Carolina. The date on which it was determined that the turtle had either died since the previous location attempt (ca. 1 month earlier) or the date of the last visual observation of surviving turtles (final date) and total days of radiotracking (total days) are indicated, with the total number of times located during this tracking period (times located) being given in parentheses. Habitat Use Index (HUI) is the proportion of a sampling of locations that were in developed suburban neighborhood or golf course habitat. The sample of locations for each turtle was drawn from the total number of locations listed in the previous column, such that the time between selected locations was ≥ 14 d, that no more than one location per month was used, and that locations were restricted to the period of Apr–Oct annually. The number of sampled locations used to calculate HUI (relocations used) is given in parentheses. HUI was not calculated (NC) for turtles tracked < 2 yr. Data collection for this study ended 1 Aug 2004, although (ongoing) turtles continue to be monitored.

Turtle	Sex	Final Date	Total Days (Times Located)	Habitat Use Index (Relocations Used)	Fate/Cause of Death
Surviving turtles					
HW-22	M	30 Jul 1989	43 (6)	NC	Lost radio contact
HW-37	M	7 Jun 1995	71 (0)	NC	Transmitter removed
HW-42	F	19 Apr 2003	1005 (43)	0.583 (12)	Transmitter removed
HW-41	M	18 Apr 2001	1450 (111)	0 (24)	Transmitter removed
HW-36	F	18 Sep 1998	1556 (133)	0.950 (20)	Lost radio contact
HW-40	M	18 Apr 2001	2000 (163)	1 (31)	Transmitter removed
HW-34	M	18 Apr 2001	2082 (204)	0.061 (33)	Transmitter removed
HW-33	M	18 Apr 2001	3105 (347)	0.082 (49)	Transmitter removed
HW-32	M	1 Aug 2004	4376 (386)	0.397 (68)	Ongoing
HW-38	F	8 Jan 2004	3136 (307)	0.188 (48)	Transmitter removed
HW-30	F	1 Aug 2004	4068 (519)	0.506 (79)	Ongoing
HW-25	F	1 Aug 2004	4334 (471)	0 (82)	Ongoing
HW-26	M	1 Aug 2004	5427 (406)	0 (78)	Ongoing
Total =			**32653 (3096)**	**Median = 0.188**	
Mortalities					
HW-28	M	28 Jul 1990	308 (22)	NC	Burning plant litter
HW-23	M	7 Nov 1990	420 (20)	NC	Unknown – natural
HW-31	F	20 Apr 1993	684 (147)	0.636 (11)	Power mower
HW-24	M	15 May 1992	975 (102)	0.333 (12)	Unknown – natural
HW-27	F	9 Aug 1992	1051 (85)	0.235 (17)	Burning plant litter
APS-1	F	29 Oct 2003	1251 (15)	0.308 (13)	Power mower
HW-35	F	22 May 1998	1484 (212)	0.600 (25)	Drowned in artificial pond
HW-39	F	7 Jul 1999	1488 (141)	0.087 (23)	Motor vehicle
HW-29	M	5 Aug 1994	1767 (248)	0.542 (24)	Motor vehicle
HW-21	F	27 Oct 1999	3863 (348)	0.068 (59)	Unknown – predator?
Total =			**13291 (1340)**	**Median = 0.321**	

humans were more than twice as frequent as those apparently due to natural causes (Table 1). Deaths associated with human activities and habitat modification included: entrapment in wire fences or under leaf litter during backyard burning by homeowners (n = 2); being struck by powered lawnmowers (n = 2) or by vehicles (n = 2), and drowning in an ornamental pond (n = 1).

We omitted from survival estimation procedures the data from two radiotransmittered males: one for which radio contact was lost after only 43 days and one for which the radio transmitter was removed after 71 days (Table 1). After 1,556 d of tracking, radio contact was lost permanently with female HW-36, a turtle with a well-established home range in two neighborhood backyards. The survival record for this turtle was censored beyond the time of the last visual contact. Transmitter failures for 4 other turtles caused temporary loss of contact for periods up to 21 months, after which each turtle was recaptured and provided a new transmitter. In 3 of these cases, periods of lost contact were short enough (< 14 months) that contact was still made within April–October of each of the years in question, so survival estimation was made on the basis of known continuing survival through the periods when these turtles were not carrying operable transmitters. For the individual with 21 months of lost contact however, we censored the period while this turtle could not be located.

Nineteen turtles were radio tracked for ≥ 500 d, and the number of locations used to calculate HUIs for these individuals ranged from 11 to 82 (Table 1). The 11 surviving individuals tended to be located less often in suburban neighborhood habitats (median HUI = 0.188) than the 8 that died (median HUI = 0.321; Table 1), but these differences were not significant either overall (Mann-Whitney U test: tied $Z = -0.744$, P = 0.457), for females (Mann-Whitney U test: tied $Z = -0.183$, P = 0.855), or for males (tied $Z = -1.006$, P = 0.314). Median HUI values for surviving males (n = 6) and females (n = 5) were 0.072 and 0.506, respectively, but these differences were also not significant (Mann-Whitney U test: tied $Z = -0.921$, P = 0.357). Among turtles that died during the study, median HUIs for males (n = 2) and females (n = 6) were 0.438 and 0.272, respectively. Again, these differences were not significant (Mann-Whitney U test: tied $Z = -0.667$, P = 0.505).

Between April–October throughout the study, there were 127 encounters reported with 86 Box Turtles (63 males, 23 females) that did not carry radio transmitters. In our demographic analysis of encounter histories for these individuals, an initial goodness-of-fit test of the global model $\Phi(g{*}t)p(g)$ indicated that overdispersion of the data was not a problem ($\hat{c}$ = 0.36; TEST 2 and TEST 3 in RELEASE yielded a combined $\chi^2 = 12.95$, df = 36, P > 0.999). However, we acknowledge that insufficient data likely contributed to an apparent underdispersion of the data (i.e., $\hat{c} < 1$). The subsequent model selection process provided more support (73%; Table 2) for models with constant survival than for models with time- or gender-specific survival. However, in the presence of constant survival, models with constant capture probability and gender-specific capture probability performed equally well (ΔAICc ≤ 2; Table 2).

Annual adult Box Turtle survival (Φ) estimated from capture-recapture data was 0.954 (SE = 0.036; Table 3). As expected, capture probability estimates (p) were low, with a constant capture probability model estimate of 0.085 and gender-specific capture probabilities of 0.081 for males and 0.096 for females (Table 3).

In known-fates modeling of data from 21 radiotelemetered turtles that explored potential gender effects on survival (S), the greatest support (70%; Table 4) was for a model with constant survival. However, models with constant survival and gender-specific survival both performed well (ΔAICc ≤ 2; Table 4). Annual adult survival was estimated as 0.932 (SE = 0.021), with gender-specific survival estimated as 0.944 (SE = 0.027) and 0.921 (SE = 0.031) for adult males and adult females, respectively (Table 3).

Known-fates modeling of data from 19 radiotelemetered turtles that explored potential HUI effects on S again indicated the greatest support for a constant survival model (72%; Table 5). However, models with constant survival and HUI-specific survival both performed well in terms of describing

TABLE 2. Alternative model selection for estimating apparent survival probability (Φ) and capture probability (p) parameters from Cormack-Jolly-Seber modeling for open populations (program MARK version 4.2; White and Burnham 1999). The modeling used capture-recapture histories for 86 carapace-marked adult *Terrapene c. carolina* in Aiken County, South Carolina, 1989–2004. Model abbreviations include: (t) = time (yr)-specific parameters, (g) = group (gender)-specific parameters, (.) indicates that parameters are constant over time, and (*) indicates an interaction. We considered the most parsimonious model to be the one with the lowest AICc score. ΔAICc values ≤ 2 generally reflect equally well-fitting models. A goodness-of-fit test of the global model was not significant (TEST 2 + TEST 3; program RELEASE version 3.0, Burnham et al. 1987: $\chi^2 = 12.95$, df = 36, P > 0.999, $\hat{c} = 0.36$).

Model	AICc	ΔAICc	Weight	Number of parameters
Φ(.)p(.)	303.03	0.00	0.52	2
Φ(.)p(g)	304.88	1.86	0.21	3
Φ(g)p(.)	305.12	2.10	0.18	3
Φ(g)p(g)	306.58	3.55	0.09	4
Φ(t) p(.)	331.30	28.27	0	16
Φ(t)p(g)	333.67	30.65	0	17
Φ(g*t)p(.)	375.13	72.10	0	31
Φ(g*t)p(g)	377.45	74.43	0	32

TABLE 3. Estimates, standard errors (SE), and 95% confidence intervals (CI) of apparent survival probability (Φ) and capture probability (*p*) parameters using capture-recapture (Cormack-Jolly-Seber) data and survival probability (S) using radiotelemetry (known-fates) data with program MARK version 4.2 (White and Burnham 1999) for adult *Terrapene c. carolina* in Aiken County, South Carolina, 1989–2004. For the models represented, (g) indicates that parameters are group (gender)-specific, and (.) indicates that parameters are constant over time. Models presented within each study type may be considered equally representative of the data as determined in model comparisons shown in Tables 2 and 4.

Study type	Model	Parameter	Estimate	SE	95% CI
Capture-recapture	Φ(.)*p*(.)	1: Φ	0.954	0.0363	0.804–0.991
		2: *p*	0.085	0.0193	0.054–0.131
	Φ(.)*p*(g)	1: Φ	0.954	0.0364	0.803–0.991
		2: *p* ♂♂	0.081	0.0201	0.049–0.130
		3: *p* ♀♀	0.096	0.0325	0.049–0.182
Radiotelemetry	*S*(.)	1: *S*	0.932	0.0206	0.879–0.963
	S(g)	1: *S* ♂♂	0.944	0.0270	0.861–0.979
		2: *S* ♀♀	0.921	0.0309	0.835–0.964

a well-fitting and parsimonious model (Table 5). Constant adult survival was estimated as 0.944 (SE = 0.019), with HUI-specific survival estimated as 0.950 (SE = 0.022) for turtles located in developed habitats < 50% of the time and 0.932 (SE = 0.038) for turtles located in developed habitats ≥ 50% of the time (Table 6). Mean life-spans for Box Turtles (after attaining adulthood) that corresponded to our survival estimates (1/-ln[*S*]; Seber 1982; Brownie et al. 1985) ranged from 14 to 21 yr.

We documented 82 coincidental encounters between humans and radiotelemetered turtles during the course of this study. In two cases, human encounters were inferred when turtles were found at sufficient distances from their last known locations (in one case outside of the study area) that it would have been impossible for the turtles to have moved unassisted over those distances in the intervening time. Human encounters with female turtles (n = 53) were more frequent than expected (χ^2 = 5.25, df = 1, P = 0.022), based on the proportional number of transmitter animal-days of females (23,920; expected encounters = 42.7) versus males (22,024; expected encounters = 39.3). Coincidental turtle encounters while researchers were radiotracking other individuals occurred 16 times (62.5%) in forest habitat, with the remaining 10 (38.5%) in developed habitats; based on the proportional sizes of these habitats, coincidental researcher encounters with turtles were different than expected by chance (χ^2 = 16.86, df = 1, $P \leq 0.0001$) due to a greater proportion of encounters with researchers occurring in the forest than expected. In contrast, encounters of neighborhood residents with turtles were more likely to occur in developed areas than expected by chance (χ^2 = 8.64, df = 1, P = 0.003); of 56 encounters, 51 (91.1%) were in developed habitats versus 5 (8.9%) in forest habitat. Of the 61 encounters within developed habitats (including those by researchers and neighborhood residents), 45 (73.7%) were in

TABLE 4. Alternative model selection for estimating the survival probability (S) parameter from known-fate modeling (program MARK version 4.2; White and Burnham 1999) using radiotelemetry data from adult *Terrapene c. carolina* in Aiken County, South Carolina, 1989–2004. For each model where noted, (t) indicates that parameters are time (yr)-specific, (g) indicates that parameters are group (gender)-specific, (.) indicates that parameters are constant over time, and (*) indicates an interaction. The most parsimonious model is generally considered the best for describing the data, and is identified as the model with the lowest AICc score. Models with ΔAICc values ≤ 2 are generally not distinguishable in their fit of the data.

Model	AICc	ΔAICc	Weight	Number of parameters
S(.)	75.23	0.00	0.70	1
S(g)	76.96	1.73	0.30	2
S(t)	89.18	13.95	0	15
S(g*t)	119.61	44.39	0	30

TABLE 5. Alternative model selection for estimating the survival probability (S) parameter from known-fate modeling (program MARK version 4.2; White and Burnham 1999) using radiotelemetry data from adult *Terrapene c. carolina* in Aiken County, South Carolina, 1989–2004. For each model where noted, (t) indicates that parameters are time (yr) specific, (g) indicates that parameters are group (HUI)-specific, (.) indicates parameters are constant over time, and (*) indicates an interaction. The most parsimonious model is generally considered the best for describing the data, and is identified as the model with the lowest AICc score. Models with ΔAICc values ≤ 2 are generally not distinguishable in their fit of the data.

Model	AICc	ΔAICc	Weight	Number of parameters
S(.)	63.82	0.00	0.72	1
S(g)	65.69	1.87	0.28	2
S(t)	79.76	15.94	0	15
S(g*t)	112.19	48.37	0	30

TABLE 6. Estimates, standard errors (SE), and 95% confidence intervals (CI) of the survival probability (S) parameter from program MARK version 4.2 (White and Burnham 1999) using radiotelemetry data from *Terrapene c. carolina* in Aiken County, South Carolina, 1989–2004. For the models represented, (g) indicates that parameters are group (HUI)-specific and (.) indicates that parameters are constant over time. Models presented may be considered equally representative of the data as described in Table 5. Low HUI values indicate more frequent turtle association with forested habitat and high HUI indicates more frequent turtle association with developed neighborhood habitat.

Study type	Model	Parameter	Estimate	SE	95% CI
Radiotelemetry	*S*(.)	1: *S*	0.944	0.0191	0.893–0.972
	S(g)	1: *S* Low HUI	0.950	0.0218	0.885–0.979
		2: *S* High HUI	0.932	0.0380	0.809–0.978

residential lots, 12 (19.7%) were on streets, and 4 (6.6%) were on golf courses (3 of which were with the same female). Again, based on the proportional sizes of these areas, encounters differed from those expected by chance (χ^2 = 11.6, df = 2, P = 0.003), with encounters on streets being much more frequent than expected.

Coincidental encounters between neighborhood residents and radiotelemetered turtles ranged from one (initial capture only; 9 individuals) to 12 per turtle. For turtles that were radiotracked > 1 yr (n = 20) this represented a range of minimal encounter rates of 0.11–3.74 encounters/yr. Encounter rates of neighborhood residents with radiotelemetered turtles tended to increase as turtles increased their use of developed habitat (HUI; Fig. 2). On the other hand, encounter rates of researchers with turtles (without the aid of radiotracking equipment) tended to be independent of habitat-use patterns. Coincidental researcher encounters with turtles also involved a greater number of radiotelemetered turtles but lower encounter frequencies with most individuals (Fig. 2). Thus, researchers and neighborhood residents did not perceive similar segments of the population in the same way with regard to how individual turtles used the two habitat types in the study area.

Coincidental encounters of radiotelemetered turtles with neighborhood residents and researchers were not uniformly distributed throughout the year, and there were apparent turtle gender differences in monthly encounters (Fig. 3). Encounters occurred during March–November and the highest frequencies of encounters with females occurred during the period of egg-laying (June–July). Frequencies of encounters with males gradually increased throughout the active period, peaking in September–October (Fig. 3).

Conspecific social encounters (n = 40) were more frequently observed in forested areas (75%) than expected from the relative proportions of forest and developed habitats in the study area (χ^2 = 49.3, df = 1, P < 0.001). In 25 of these encounters, non-radiotelemetered turtles were discovered interacting with radiotelemetered individuals. In 9 other cases, radiotelemetered turtles were found interacting with each other, and in 6 cases, two turtles without transmitters were discovered interacting. Of the 40 total encounters, 16 were between two males and almost always suggested some form of dominance/aggression. The remaining 24 encounters were between a male and a female, and 11 of these involved courtship and/or attempts by the male to copulate. We observed no female-female social encounters. Based on an estimated population sex ratio from all adult turtles captured within the study area (n = 105; 67.6% male), the expected numbers of random male-male, male-female, and female-female encounters in the study area were estimated as 18.3, 17.5, and 4.2, respectively. Encounter frequencies differed significantly from random expectations (χ^2 = 6.90, df = 2, P = 0.032), and resulted from greater than expected numbers of male-female encounters, the absence of female-female encounters, and fewer than expected male-male encounters.

DISCUSSION

Annual survival probabilities estimated for adult Box Turtles in our study (0.932–0.954) were similar to the only other two such estimates known for Eastern Box Turtle populations. Annual survival probabilities of Box Turtles in a natural wooded area in Indiana were 0.93–0.94 (calculated from mor-

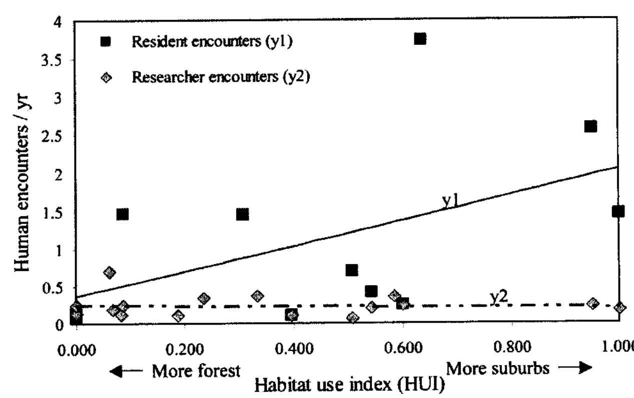

Fig. 2. Rates of reported human encounters with radiotelemetered adult *Terrapene c. carolina* inhabiting an urban forest/suburban neighborhood ecotone in Aiken, South Carolina. Encounter rates were classified as those with residents of the neighborhood (black squares) or with researchers without the use of the radiotelemetry equipment (gray diamonds). Each point represents a turtle described in Table 1 (some points are hidden) and is plotted according to that turtle's habitat-use index (HUI, see Table 1). Encounter rates are calculated as the total number of times that each turtle experienced each of the two kinds of encounters, divided by the total number of yr which that turtle carried a radio in the study area ("Total Days" in Table 1). Regression y1 represents the best linear fit to data for resident encounters, and y2 represents the best linear fit to data for researcher encounters.

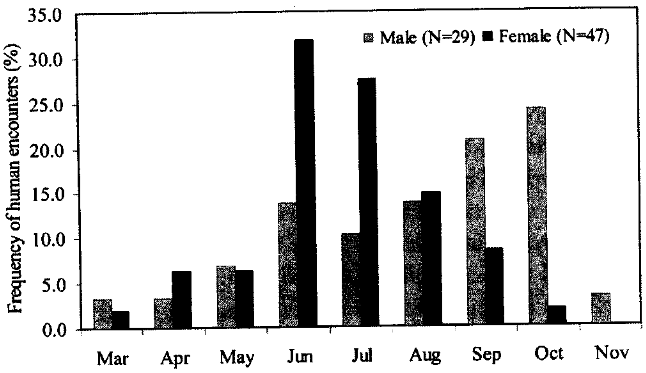

Fig. 3. Monthly (March–November) distributions (percent) of human encounters reported with dates for radiotelemetered male (black bars) and female (gray bars) adult *Terrapene c. carolina* in an urban forest/suburban neighborhood ecotone in Aiken, South Carolina. Encounters were recorded from 30 Mar 1989 through 1 Aug 2004, and included those with residents of the neighborhood and with researchers without the use of radiotelemetry equipment.

tality rates reported by Williams and Parker 1987). Annual survival probabilities were also calculated as 0.85–0.94 for Box Turtles inhabiting forest habitat in Maryland (Frazer et al. 1990; calculated using data from Stickel 1978). A mean annual survival probability of 0.97 was estimated for *T. ornata* inhabiting an area that had been fragmented and isolated by human activity (Bowen et al. 2004). However, the 95% CI (0.85–1.0) of this latter estimate almost completely overlapped those calculated in our study (capture-recapture 95% CI = 0.804–0.991; radiotelemetry 95% CI = 0.879–0.963), as well as the other survival estimates reported for this species. Thus, simple comparisons with other estimates would not suggest any general decrease in overall survival as a result of the turtles in our study inhabiting an urban forest/suburban neighborhood ecotone.

Most reported survival estimates for Box Turtles, including our own, are equal to or higher than those reported for some species of freshwater turtles. These include means of 0.70–0.95 for all age classes of *Sternotherus odoratus* and 0.63–0.94 for all age classes of *Chrysemys picta* in Virginia (Mitchell 1988) and 0.84 and 0.81 for male and female *Trachemys scripta*, respectively, in South Carolina (Frazer at al. 1990). The 95% CI's presented in this latter study did not overlap those of the Box Turtles in our study, suggesting a significantly higher rate of survival for Box Turtles than for these freshwater turtles.

Results from the CJS population modeling (Table 3) suggested that the capture probability of adult female turtles in the population was greater than that of adult males. Female Box Turtles seeking suitable nesting sites may be particularly attracted to the openness of urban/suburban developments and thus be exposed to a variety of uncharacteristic mortality sources including some that are (albeit unintentionally) human-induced. More frequent encounters of the radiotelemetered females with neighborhood residents, especially during June and July (Fig. 3), were undoubtedly related to nesting activities and suggested that female turtles either were nesting in developed neighborhood habitats or were forced to move through them to reach suitable nesting sites. Of 12 times that radiotelemetered turtles were encountered on streets, nine (67.7%) involved females, and on the only two occasions when females found in streets were x-rayed (Gibbons and Greene 1979), they were both confirmed to be carrying shelled eggs. Similarly, radiotelemetered female HW-39 was confirmed by radiography to be gravid on two of three occasions she was encountered on golf course habitat; she was ultimately killed while crossing a street (Table 1) near a golf course, carrying a clutch of four shelled eggs.

Survival probabilities from known-fates models (*S*) using radiotelemetered animals should be higher than those derived for the same population from capture-recapture models because losses from radiotelemetry studies should only be due to deaths or equipment failure, without additional losses from emigration that can occur in capture-recapture studies. In our study however, survival probabilities for radiotelemetered turtles were actually lower. However, the confidence intervals for these two estimates were sufficiently large that the differences were likely not significant. In only one case did we note a potential impact of radio transmitters on survival. Female HW-35 drowned in an ornamental pond (Table 1), and the extra weight of the transmitter may have shortened the amount of time that the turtle was able to stay afloat. However, because the pond was surrounded by vertical ornamental rockwork, this turtle would have been prevented from climbing out even without the added weight of a radio transmitter. The masses of the radio transmitters and attachment materials used in our study exceeded the general guideline of 10% of the total body mass proposed for reptiles and amphibians (ASIH, HL and SSAR 1987). However, Box Turtles carrying extrinsic loads of up to 150% of their body mass have not exhibited significantly reduced locomotor performance (Marvin and Lutterschmidt 1997).

Although the positioning of our transmitters just above the rear marginals of the carapace would seem to hinder mounting and copulation, there is reason to believe that successful copulation and fertilization could still occur. Some of our females carried transmitters continuously for as long as 10 yr, yet still produced fertile clutches, and it is unlikely that viable sperm could have been stored this long from inseminations occurring prior to transmitter attachment. We therefore do not believe that the transmitters carried by our turtles had any significant detrimental effects on their movement, behavior, or survival during the course of this study.

Deaths related to human activities were more frequent than those that were not. Considering the known importance of road-crossing mortality in turtle populations (Stickel 1978; Goodman et al. 1994; Keller et al. 1998; Steen and Gibbs 2004; Gibbs and Steen 2005), it is surprising that vehicle deaths of radiotelemetered Box Turtles did not represent a higher proportion of the human-related mortality we observed. With an average road density of 6.8 km/km^2, our study area far exceeded the level (1.5 km/km^2 of landscape) that Steen and Gibbs (2004) suggested was sufficient to produce male-biased sex ratios in two species of freshwater turtles due to disproportionate female road-kill mortality. In our study, two other sources of mortality, burning of backyard debris and powered lawn mowers, each resulted in the same number of deaths as road-kills (Table 1). Several authors have suggested, however, that road mortality is most severe when new road construction occurs within established home ranges, crossing established paths of movement and/or when steep road edges result in turtles entering/falling into roadbeds and becoming trapped there (Stickel 1978; Goodman et al. 1994). Neither of these conditions existed in our study area; paved streets had been established for more than 50 yr and most all curbing was gently sloped, allowing easy traversal by even small juveniles and hatchlings. All turtles killed by vehicular traffic during our study died on streets that were frequently used by non-residents of the study area who tended to travel at higher rates of speed through the neighborhood in efforts to by-pass areas of traffic congestion outside of our study area (Fig. 1). Box Turtles killed by motor vehicles during our study were mostly males (4 vs. 1 vs. 1 unsexed juvenile) and were mostly killed along that portion of the more highly-traveled streets that closely paralleled the southern boundary of the Hitchcock Woods (Fig. 1). As might be expected, the majority of turtles we found killed on neighborhood streets did not carry transmitters (4 vs. 2).

Interestingly, the 2 telemetered turtles killed by vehicles in our study were not among those that spent the greatest proportion of their time in developed habitats. Female HW-39 in particular, based on 141 sampled locations, spent only 8.7% of her time in neighborhoods. As mentioned above, this turtle carried a clutch of four shelled eggs when she emerged from the woods surrounded by golf course habitat (presumably to nest) and was killed while crossing the first street encountered. Some long-surviving turtles, however, spent most or all of their time in developed habitats and crossed streets frequently without being killed or injured. Male HW-40, for example, was radio tracked for > 5 yr, and was always located in neighborhood habitat, and female HW-36 was located in neighborhoods on 95% of her sampled locations for > 4 yr (Table 1), suggesting the possibility that some turtles living in neighborhoods may adopt behavioral strategies for safely crossing streets. An example of such behavior was noted on 1–2 Aug 1992 when female HW-31 was observed to approach and cross one of the most traveled streets in the neighborhood. Starting at 0900 h on 1 Aug, the turtle moved directly toward the street over a distance of about 12 m in about 20 min. At this point, the turtle buried under pine straw where she spent the rest of the day and night < 5 m from the street curbing. The next morning, this turtle emerged and paced back-and-forth parallel to the street over a distance of nearly 60 m. At times, the turtle came to within about 1 m of the curb, while craning her neck toward the street and stopping for about 10–15 sec each time that a vehicle passed. At 0942 h on 2 Aug, the turtle abruptly turned toward the pavement and crossed to the other side within 90 sec, including a brief stop as a car passed over her (swerving so as to straddle the turtle). After crossing the 8 m of pavement, she then immediately buried herself within a border of English ivy and then moved away from the street the following day.

Other than mortality associated with motor vehicles and fires, human-related deaths of Box Turtles have not been widely described in the literature. Russell et al. (1999) reviewed the effects of natural fires and controlled burns on herpetofauna and supported the suggestion by Ernst et al. (1995), based on the examination of museum specimens, that Box Turtles likely survive fires by burying into forms (cavities pushed into forest litter and upper soil layers). One death in our study, however, resulted when a turtle was trapped above ground by a fence as it apparently attempted to flee burning backyard vegetation. In the other fire-related death we noted, the turtle was located within a large pile of leaves and pine straw that was burned by a homeowner. In both deaths we observed from powered mowers, the turtles seemed to have been buried shallowly into unmowed lawns, with the top of the carapace protruding no more than 2–3 cm above the soil. Under these conditions, they almost certainly could not have been seen by the lawnmower operators. Questioning afterward revealed that neither of the (highly remorseful) lawnmower operators had even been aware that they had killed a turtle.

Conspecific social encounters among Box Turtles in our study area generally reflected patterns found in previous studies, even though 25% of the 40 encounters we documented were within modified neighborhood habitat. A complete absence of female-female encounters in our study was similar to previous studies (Schwartz and Schwartz 1974; Stickel 1989) that described only male-male and male-female encounters in long-term studies of *T. carolina* in Missouri and Maryland, respectively. Similarly, in contrast to 560 observed male-male encounters among Wood Turtles (*Clemmys insculpta*), interactions among adult females were "infrequent" (Kaufmann 1992).

The pattern of monthly distributions of male-male and male-female social interactions we found in our study were similar to those reported in other studies (Schwartz and Schwartz 1974; Stickel 1989; Fig. 4). However, the month-to-month variation we observed was not as great, with no single month accounting for > 25% of our observations for either type of interaction. In previous studies, however, peak interactions occurred from late summer through early fall and included individual months with > 40% of the total interactions for the entire year (Fig. 4). Such dissimilarity in the degree of monthly variation may be due to climatic differences between the more southerly latitude of our study area and the other two study sites where winter-like conditions earlier in the year likely compel earlier turtle dormancy. In contrast, turtles in our area remained active well into the fall, undoubtedly prolonging mating opportunities. One of the more important aspects of our data on Box Turtle interactions was that they were reported significantly more often in forested areas.

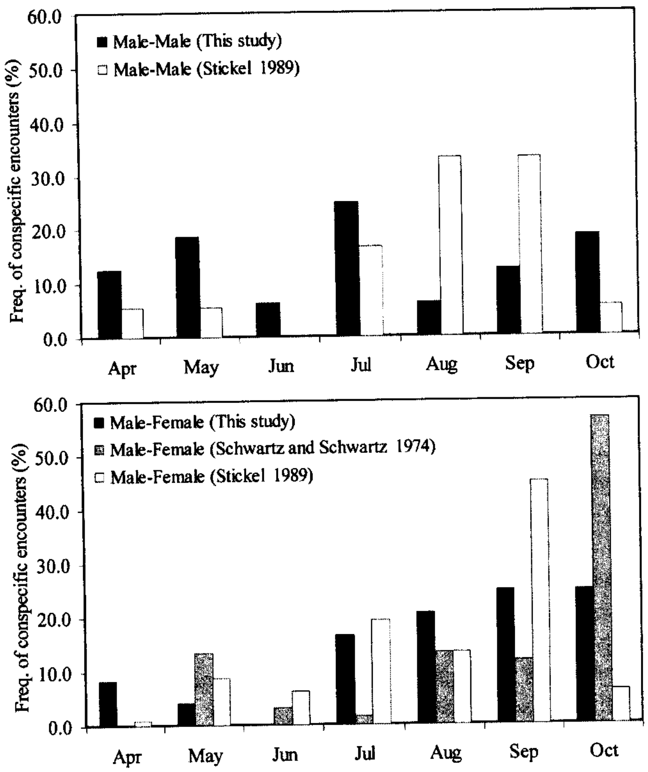

Fig. 4. Monthly (April–October) distributions (percent) of male-male (MM; top) and male-female (MF; bottom) conspecific social interactions between adult *Terrapene c. carolina* from this study (black bars, n = 16 MM and 24 MF) and as reported by Schwartz and Schwartz (1974; gray bars, n = 60 MF) and Stickel (1989; unshaded bars, n = 18 MM and 113 MF). Schwartz and Schwartz (1974) recorded only 4 MM interactions and did not report their monthly distribution.

Although forest comprised only 26.2% of our study area (Fig. 1), fully 75% of the observed social interactions were in that habitat.

In conclusion, our data suggest that adult Box Turtles can survive in an ecotone between a developed suburban neighborhood and a residual urban forest at rates comparable to if not greater than those reported for populations occurring in purely forested habitats. Adult Box Turtles are almost completely protected by their size and shell from mortality by domestic cats and all but the largest dogs — predators that inflict significant losses on smaller species of herpetofauna such as lizards in urban/suburban habitats (Koenig et al. 2002). Further, our adult Box Turtles, like the *T. ornata* studied by Bowen et al. (2004), did not appear to be as vulnerable to the effects of suburban habitat fragmentation and would not be expected to be impacted by the consequential isolation of wetlands as was the case with the more aquatic Blanding's Turtles (*Emydoidea blandingii*) studied by Rubin et al. (2001). Radiotelemetered turtles did indeed die from human-related causes more often than from natural causes. However, these combined mortality sources were apparently not sufficient to adversely affect overall survival of adult turtles, as determined independently from analyses of both radiotelemetered and carapace-marked turtle data. This suggests that trade-offs may be associated with living in ecotones between natural and human-altered habitats, in which increases in human-related mortality are offset by reductions in some forms of natural mortality associated with life in purely natural areas.

Relatively high rates of adult survival and associated longevity are not sufficient to insure long-term population viability without adequate reproduction and recruitment of younger age classes. Anecdotal observations of nesting by both radiotelemetered and non-radiotelemetered females, accompanied by radiography identifying gravid females, confirmed successful reproduction in our study area, and the capture of younger turtles ranging in age from hatchlings to older subadults indicated that some level of recruitment into the adult age class was almost certainly occurring. However, adequate quantitative data concerning these population parameters are lacking and should be a high priority for future studies of this and similar suburban Box Turtle populations.

Finally, it is important to note that encounters of radiotelemetered turtles with residents of the neighborhood in our study area were almost always viewed in a positive light. For the turtle deaths we documented in residential areas, the involved homeowners expressed both dismay and the intention to take actions to prevent such accidental deaths on their property in the future (e.g., by adding a wire mesh ramp to the backyard pond where one of our turtles drowned). On only two occasions in more than 15 yr of study did residents express negative attitudes about the turtles. In one instance, a homeowner asked that a turtle be removed from her yard because she was sure that it could "sting" her, and another resident voiced his desire that turtles be moved (without harming them) out of his garden plot where they damaged low-growing vegetables. With these two exceptions, all other residents with whom we had contact were not only tolerant of Box Turtles using their lawns and gardens but enjoyed finding them and reporting their activities to researchers. In many cases, residents developed a genuine interest/affection for individual turtles they encountered regularly and often inquired about their welfare. It is important to remember, however, that our data show that reports of Box Turtle encounters from neighborhood residents may not be comparable to reports of encounters from experienced researchers working in the same study area.

As noted by Brisbin (2002), contacts between neighborhood residents and researchers served to portray the study's sponsors/funding agencies in a very positive light. Personalized accounts of turtles that used residents' own backyards clearly helped to educate them as to how common activities, such as burning yard debris and mowing lawns, if not done carefully, could negatively impact this species of growing conservation concern. By thus embodying the conservation message in a tangible form, studies of Box Turtles in suburban neighborhoods may serve as an effective means of public outreach/education for the conservation of other forms of urban herpetofauna as well as for wildlife conservation in general.

Acknowledgments — We appreciate the many expressions of interest and support of this work that have been received over the years from the residents of the Aiken Estates and Foxchase neighborhoods. Without their help in finding and reporting the activities of radiotelemetered and otherwise marked or unmarked turtles much of the information reported in this paper would have remained unknown. Deserving of special mention are Mr. and Mrs. Bruce Eberhard, Dr. and Mrs. Jim Hill, Ms. Margaret Marion, Dr. Ken Perrine, Mr. and Mrs. Dennis and Natalie Taylor, Mr. and Mrs. Jim Samsel, Dr. and Mrs. Carl, and Christopher Strojan. Support for portions of this work and particularly manuscript preparation was provided by the U.S. Department of Energy under Award Number DE-FC09-*07SR22506II* to the University of Georgia Research Foundation. Support from Chicago State University allowed for a sabbatical leave for ELP. Significant supplemental funding for equipment was provided by donations made by and through the congregation of the First Presbyterian Church of Aiken, South Carolina, the Trinity Presbytery of the Presbyterian Church (USA) and that denomination's National Office of Environmental Justice. An additional equipment grant was provided by an award to the Aiken Preparatory School from the Aiken-Augusta Audubon Society. Warren Stephens provided assistance in changing equipment for battery refurbishment. Permission to conduct this research in Hitchcock Woods was given by the Board of Trustees of the Hitchcock Foundation. Our manuscript was greatly improved by editorial review and comments provided by Don Church, an anonymous reviewer and the editors of 2008. All procedures were approved by the University of Georgia Institutional Animal Care and Use Committee under IACUC #A2003-10013-m1.

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