Natural History of *Terrapene carolina* (Box Turtles) in an Urbanized Landscape

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Abstract - Urbanization and other anthropogenic factors are often implicated in turtle population declines, yet limited research on the natural history of turtles in urban areas has been conducted. To assess the effects of urbanization and to help develop proper conservation strategies for *Terrapene c. carolina* (Eastern Box Turtles), we conducted a mark-recapture study in the vicinity of Davidson, NC, from 1999 to 2004. We made 354 turtle captures, 42 of which were recapture events. We evaluated meristic characters, body condition, activity patterns, population structure, and growth rates, and then examined relationships among these variables and the amount of anthropogenically-modified habitat within 100 m of each turtle's collection location. Males and females had different patterns of seasonal activity and body condition indices. Growth rates decreased with turtle age and varied between developed and forested habitats. More turtles over the age of 20 were found in areas with extensive forest cover than in areas that were developed. Although box turtles may persist in urbanized landscapes and may grow more quickly there, they suffer higher mortality in these habitats compared to forested landscapes.

Introduction

Recent research suggests that reptiles are declining worldwide and these declines are often credited to anthropogenic causes, including exploitation and habitat alteration (Gibbons et al. 2000, Mitchell and Klemens 2000). Urbanization and other human impacts may increase pollution levels, fragment habitats, further the spread of disease, and introduce dangers such as roads and household pets (Belzer and Steisslinger 1999; Dodd et al. 1989; Kornilev et al., in press; Mitchell and Klemens 2000; Wilcove et al. 1986; Wilcox and Murphy 1985; Williams and Parker 1987). Turtle life history characteristics, such as delayed sexual maturity, may put them at an increased risk and slow population recovery following declines (Klemens 2000). Effective conservation planning requires knowledge of the natural history of the species of interest (Congdon et al. 1994). For example, studies of the life history characteristics of *Emydoidea blandingi* Holbrook (Blanding's Turtles), *Chelydra serpentina* Linnaeas (Common Snapping Turtles), and other long-lived animals have demonstrated that harvesting such species is not sustainable (Congdon et al. 1993, 1994).

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Terrapene carolina carolina Stejneger and Barbour (Eastern Box Turtles) regularly live longer than 50 years (Stickel 1978). Because box turtles are long-lived organisms that rely on relatively high juvenile survivorship and low adult mortality to maintain stable populations (Congdon and Gibbons 1990, Hall et al. 1999, Klemens 2000), the full extent of anthropogenic effects that negatively impact recruitment may not be immediately evident (Congdon et al. 1994, Garber and Burger 1995, Hall et al. 1999). Previous long-term studies of box turtle populations have documented significant population size and density declines in areas experiencing only moderate anthropogenic impacts (Schwartz and Schwartz 1974, Stickel 1978, Williams and Parker 1987). Long-term studies of turtle natural history and ecology in habitats undergoing various levels of anthropogenic influence are needed to estimate the effects of urbanization on turtle populations and to develop conservation strategies for these animals (Congdon et al. 1993, 1994; Garber and Burger 1995; Hall et al. 1999).

In this study, we evaluated data from a 6-year mark-recapture study of Eastern Box Turtles in the vicinity of Davidson College, Davidson, NC. We examined meristic characters, body condition, activity patterns, population structure, and growth rates, and then examined the relationships between these variables and the amount of anthropogenically-modified habitat near each turtle's collection location. Our study provides information on box turtle natural history in the eastern United States and increases understanding of the potential impacts of urbanization.

Study Area

We studied box turtles in the western Piedmont of North Carolina, within Mecklenburg, Iredell, Rowan, and Cabarrus Counties. Our study area, which is approximately 20 km north of Charlotte, NC, has undergone rapid urban growth and large-scale changes in land use, including a significant decrease in the amount of forested land, during the last 30 years (Griffith et al. 2003). A large fraction of turtles collected for this study were from the Davidson College Ecological Preserve (DCEP) and local residential areas (Hester et al., in press). The DCEP is an approximately 89-ha area of mostly forested, protected land adjoining the Davidson College campus and it accounted for 35% of the total captures.

Methods

A box turtle mark-recapture study was initiated at Davidson College in May 1999. The final date of data collection for this study was 1 September 2004. Students and faculty of Davidson College and members of the surrounding communities accounted for a large portion of our collection effort (Hester et al., in press). All box turtles were captured opportunistically and taken to the Davidson College Herpetology Laboratory to be marked and measured.

We marked the turtles by filing three notches in their marginal scutes, corresponding to an alphabetical coding system (Gibbons 1968, Sexton 1959). We determined gender on the basis of coloration intensity, tail length, plastron concavity, and carapace depth (Palmer and Braswell 1995). Juveniles included all animals whose gender could not be determined morphologically (most turtles under age 6, carapace length [CL] aprox. 33–82 mm). We approximated the age of each turtle by counting the lines of arrested growth of carapace scutes, although the validity of this technique has been questioned (Wilson et al. 2003). A second researcher verified each count of arrested growth lines, and both researchers agreed upon a degree-of-confidence integer ranking between 0 and 3, with 3 representing relatively high confidence in the accuracy of their count (Sexton 1959). This age-confidence scale was used because growth rings on older turtles can be difficult to count due to wear and other factors (Dodd 2001, Stickel 1978).

We used a top-loading balance to determine the mass of each turtle to the nearest 0.1 g. To rehydrate potentially dehydrated turtles, all turtles were placed in a container with approximately 3 cm of water for at least 3 hours before weighing. We measured shell dimensions, including straight-line carapace length, straight-line plastron length, maximum shell width, and maximum shell depth, to the nearest 1 mm with calipers. If the front hinged flap was angled or closed, the plastron length was measured as the sum of the lengths of the two plates. We recorded additional comments, and digital images of each turtle were taken to aid in recapture identification and to document physical condition. We returned each turtle to its collection site, typically within 2 days of collection, and recorded the geographic coordinates (UTM, NAD 83) for the location (± 3 m) using a Garmin Handheld GPS unit or online topographic maps and aerial photographs taken in 2002 (1 pixel = 0.5 m).

We used all available data, but our records for each turtle were not always complete. For example, we have no mass data for turtles when only an empty carapace was collected. Thus sample sizes vary among analyses and reflect these missing data. An experiment-wide significance level was set at $\alpha = 0.05$. We examined correlations between carapace length and other size and age measurements for males, females, and juveniles using linear regression. Mass was log transformed before this analysis. We also compared meristic characters between males and females using one-tailed t-tests. Age distributions were tested for gender differences using one-tailed t-tests and included only the age at first capture for recaptured turtles.

To examine age-specific growth rates, we grouped turtles into four 5-year age groups. These groupings serve to minimize the effects of inaccurate growth ring counts and assume that one ring was added each year (Wilson et al. 2003). Because of the difficulty associated with estimating the age of older turtles by counting marginal scute rings (Dodd 2001, Stickel 1978), all turtles > 20-yr old were classified in one age group termed "older." We examined our ability to confidently estimate the age of a turtle relative to that turtle's age group using a chi-square test. For each 5-year group, we analyzed the relationship between age and carapace length using linear regression. The slope of each age group's regression line was calculated to estimate a growth rate for that group. To test if the growth rates differed from zero we determined if zero was within the 95% confidence intervals of the growth rate of each group.

To assess the condition of the turtles, we calculated the residuals of a linear regression with mass because mass does not scale 1:1 with size (i.e., larger turtles weigh more per unit of carapace length than smaller turtles; Shine et al. 2002). This method allowed us to compare individual turtle masses to the average mass for their size. We treated this condition index as the dependent variable and collection month as the independent variable for months with at least 4 captures (May through October) to study seasonal variation in condition. We used separate single-factor analyses of variance to determine if condition varied seasonally for males or for females. Tukey-Kramer tests were conducted separately for each sex to determine if condition differed among individual months. We used two-factor analysis of variance to compare the monthly condition distributions of males and females. We conducted additional Tukey-Kramer tests to test for significant condition differences between the sexes for individual months.

Capture locations were plotted using a Geographical Information System (ArcGIS ver. 8.3, ESRI, Redlands, CA). We added 100-m circular buffers around each location and visually estimated the relative amounts of developed, open field, and forested land within the buffer to the nearest 10% using aerial photographs taken in 2002 (1 pixel = 0.5 m). Since locations were classified based on local cover type, we could not distinguish between clusters of suburban trees and expanses of forest. Because forest is the preferred habitat of box turtles (Dodd 2001) and forest coverage has decreased significantly in the vicinity of Davidson during the last 30 years (Griffith et al. 2003), we examined the relationship between percent forest and condition (by gender) and age using linear regression. By classifying turtles into two groups (those from > 50% forest and those from < 50% forest), we determined if turtle size (carapace length) differed by amount of forest for each age group using two-tailed t-tests with a modified alpha value due to multiple comparisons (adjusted $\alpha = 0.05/4 = 0.0125$). Additionally, we examined the influence of forested habitat on age-specific growth rates by calculating the slopes of the relationship between turtles' ages and carapace lengths for each 5-year age group. Since we only had one age-specific growth rate for each habitat type (low or high forest cover), we could not perform any statistical analysis to compare the growth rates (i.e., our df = 0).

Results

Meristic and population characteristics

From May of 1999 until September 2004, we collected 365 turtles, 342 of which were alive. Forty-three turtles were recaptured, five of which were captured three times over the 6-year period. We captured slightly more females than males and few juveniles (Table 1). Approximately one-third of the total captures were found on the DCEP. Males had significantly longer carapaces ($t = 6.15$, $df = 328$, $p < 0.01$), shallower shell depths ($t = 3.59$, $df = 320$, $p < 0.01$), and shorter plastrons ($t = 14.7$, $df = 327$, $p < 0.01$) than females , but both sexes had similar shell widths ($t = 0.03$, $df = 324$, $p = 0.49$) and masses ($t = 0.11$, $df = 311$, $p = 0.46$; Table 2). The carapace lengths of the largest male, largest female, and smallest juvenile captured alive in this study were 145 mm, 142 mm, and 26.8 mm, respectively. In general, carapace length and other body measures were positively correlated in adults (R^2 ranged from 0.57 to 0.92) and were highly positively correlated for juveniles (most $R^2 > 0.92$; Table 3). Because carapace length was highly correlated with other shell dimension measurements in adults, it was used as a measurement of overall turtle size in all subsequent analyses.

Age distributions of both males and females were skewed towards older ages, with the number of turtles > 20 yrs exceeding that of all single-year age groups (Fig. 1). Older turtles were significantly more difficult to age with a high degree of confidence ($\chi^2 = 46.6$, $df = 8, 326$, $p < 0.0001$), and no turtles of

Table 1. Capture data for *T. carolina* (Eastern Box Turtles) in the Piedmont of North Carolina from May 1999 to September 2004. Empty carapace shells account for most of the turtles of unknown gender.

	Captures	Recaptures	Total individuals
Male	134	9	125
Female	204	34	170
Juvenile	16	0	16
Unknown	11	-	11
Total	365	43	322

Table 2. Meristic data, by sex, for all living and dead Eastern Box Turtles (*T. carolina*) collected in the vicinity of Davidson, NC. Data are presented as means ± 1 SE. Sample sizes are given below each mean. Asterisks (*) indicate a significant difference between males and females determined by one-tailed t-tests ($\alpha = 0.05$).

	CL* (mm)	PL* (mm)	Width (mm)	Depth* (mm)	Mass (g)	Age* (yr)
Females	119.2 ± 0.8	118.5 ± 0.8	100.0 ± 4.1	61.8 ± 0.5	363.2 ± 7.0	16.5 ± 0.3
	198	198	196	195	189	193
Males	126.2 ± 0.7	100.0 ± 1.0	99.9 ± 1.0	59.1 ± 0.5	362.2 ± 5.8	17.5 ± 0.4
	132	131	130	127	124	124
Juveniles	54.6 ± 4.5	52.4 ± 4.6	47.1 ± 3.5	26.8 ± 2.1	35.7 ± 6.8	2.9 ± 0.5
	16	16	16	16	16	16

Table 3. Correlation coefficients (r^2) of linear regressions of carapace length and other meristic measurements from Eastern Box Turtles collected near Davidson, NC.

	Females	Males	Juveniles
Age	0.40	0.55	1.00
Plastron length	0.92	0.91	1.00
Carapace width	0.90	0.76	1.00
Shell depth	0.79	0.57	0.92
Log(mass)	0.76	0.67	0.97

the two youngest age groups received the lowest confidence rating (Fig. 2). Relatively more females of intermediate ages (15–18) were found than males of the same ages. Average age of males was significantly higher than that of females ($t = 1.97$, df = 315, $p = 0.02$). Turtles showed age-specific growth rates with relatively rapid growth from ages 0–4 yr (2.78 mm/yr) and from 5–9 yr (2.26 mm/yr, Fig. 3). After age ten, the mean growth rate decreased to 0.63 mm/yr and slowed even further after age 15 (0.05 mm/yr; Fig. 3).

Activity and condition

The active season for box turtles in the Davidson area began in April and continued through October, although a few individuals were active in March, November, and December. From May through October, male and female turtles exhibited different seasonal patterns of captures ($\chi^2 = 21.0$, df = 5, $p < 0.01$; Fig. 4). A significantly larger fraction of females than males

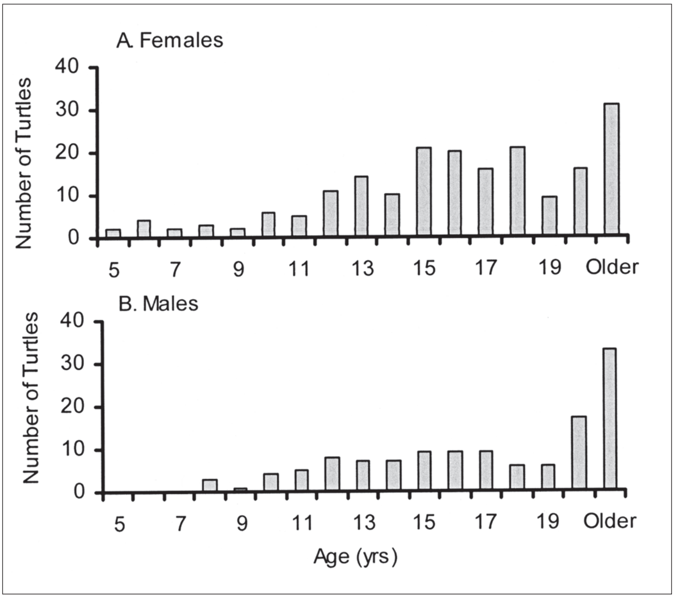

Figure 1. Ages of female (A) and male (B) Eastern Box Turtles (*T. carolina*), including only age at first capture for recaptured turtles.

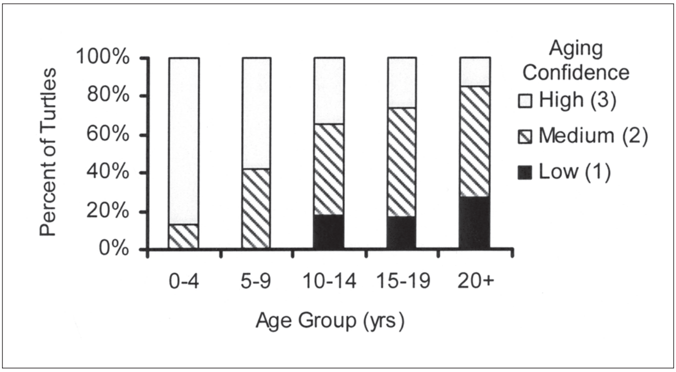

Figure 2. The distribution of aging confidence scores for 5-year age spans show the increasing difficulty of accurately aging of older turtles.

were collected in June ($\chi^2 = 4.34$, df = 1, p = 0.04). The trend towards male-biased captures in August approached significance ($\chi^2 = 3.10$, df = 1, p = 0.08), and a significantly larger fraction of males than females was collected in September ($X^2 = 9.81$, df = 1, p < 0.01).

Female turtle condition varied among months (ANOVA: F = 2.42, df = 5, 148, p = 0.04), although monthly condition did not differ seasonally for males (ANOVA: F = 0.48, df = 5,105, p = 0.79; Fig. 5). Collection month (F = 1.36, df = 5,5, p = 0.24), sex (F = 0.58, df = 1,1, p = 0.45), and the combined effect of month and sex (2-way ANOVA: F = 0.71, df = 5, 253, p = 0.62) had no detectable effects on turtle condition. Neither the condition of males nor females differed significantly between any two consecutive months (t-tests, adjusted $\alpha = 0.05 / 5$ pairs = 0.01, all p's > 0.01). Condition did not differ significantly between males and females for any individual month (t-tests, adjusted $\alpha = 0.05 / 6$ pairs = 0.008, all p's > 0.008).

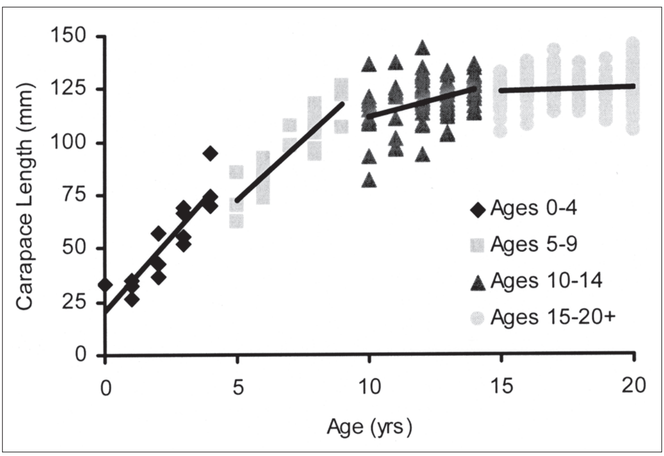

Figure 3. Age-specific growth rates for box turtles in the western Piedmont of North Carolina, as determined by the distribution of carapace lengths (mm) in relation to age at first capture. Least squares best-fit lines for 5-year age spans were added to depict the decreasing growth rate of older turtles.

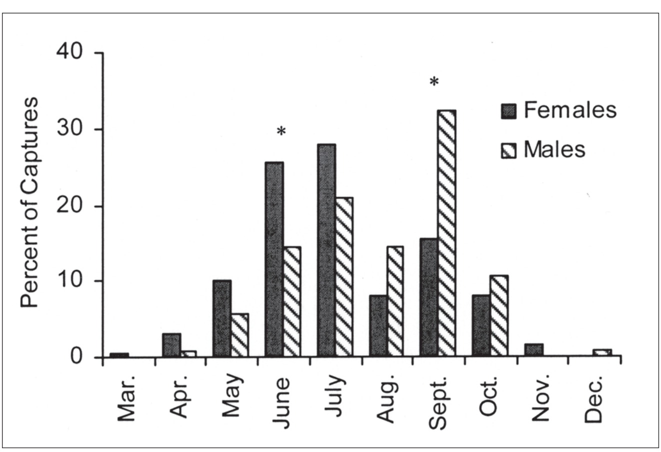

Figure 4. Monthly variation in the sex ratio of captures suggest differences in activity patterns between male and female box turtles. Asterisks indicate significant differences between sexes when compared using χ^2 tests (α =0.05).

Impacts of urbanization

Turtle age and percent of forest cover for males or females were not highly correlated ($R^2 = 0.03$ and 0.08, respectively). However, older turtles tended to be found more often in highly forested areas (Fig. 6). Approximately 54% of the turtles > 20 years old were collected in areas with 90–100% forest cover within a 100-m radius of their capture location. Areas with greater than 90% forest cover also accounted for the largest fraction of turtles in the 15–19 yr age group (34%). Mean carapace lengths for all four age groups did not differ between low and high forest cover areas (t-tests, p values > 0.0125; Fig. 7). Growth rates, however, varied by age and amount of forest cover (Fig. 8). We detected no effect of the amount of forested habitat on the body condition of male ($R^2 < 0.01$) or female ($R^2 < 0.01$) box turtles.

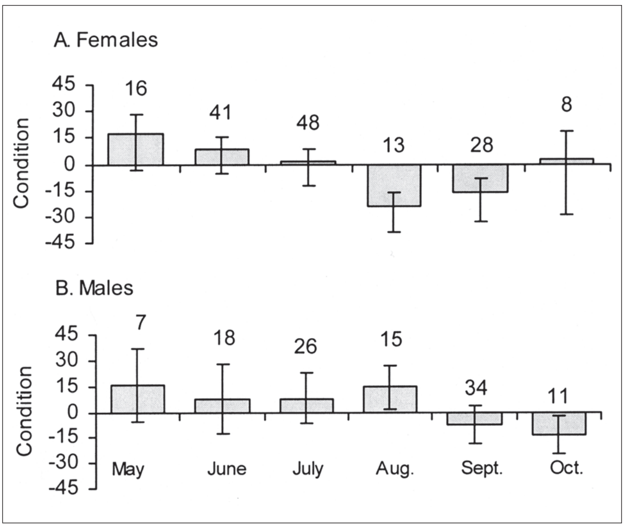

Figure 5. Monthly variation in condition, measured by the residual of the mass to carapace length ratio, for female (A) and male (B) box turtles. Sample sizes are indicated above columns. Bars represent ± one standard error.

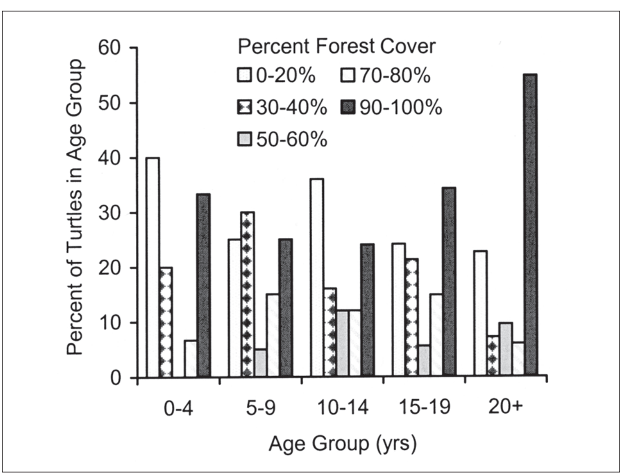

Figure 6. The percent of box turtles in 5-yr age groupings captured in locations with varying amounts of forest cover. Forest cover was determined by visually estimating the percent forest within 100 m of each turtle's capture location using aerial photographs.

Discussion

This study provides information about the sex ratio, age distribution, condition indices, and activity patterns of the Davidson, NC, Eastern Box Turtle population. These data can be used as a baseline for comparison with future results of this ongoing study to monitor this population. In this region, box turtles seem to be persisting even in highly developed areas, although we suspect that their life-spans, growth, and population density may be negatively affected by urbanization.

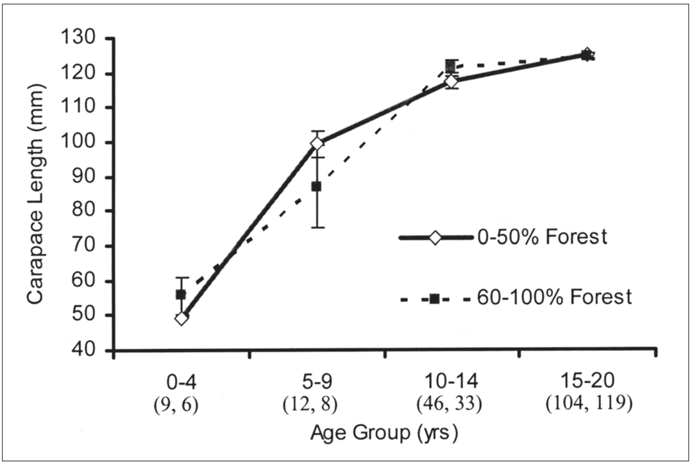

Figure 7. Mean carapace lengths (mm) for 5-year age groups divided into low forest cover and high forest cover categories. Average carapace length did not differ significantly by amount of forest cover for any age group. Numbers below age groups indicate (0–50% forest, 60–100% forest) sample sizes. Vertical bars show ± one standard error.

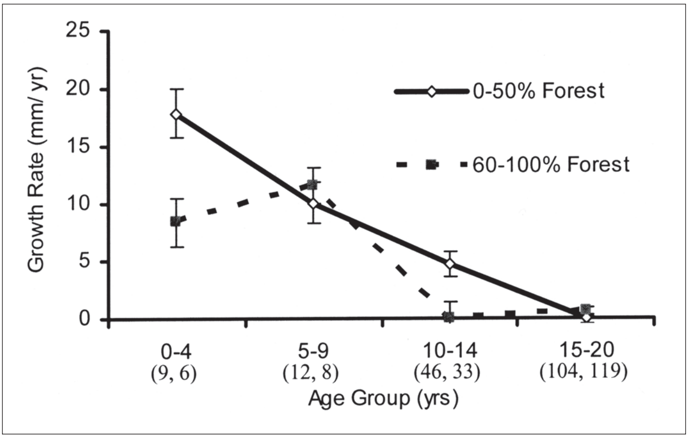

Figure 8. Differences in growth rates of box turtles captured in locations with low (0–50%) and high (60–100%) forest coverage. Growth rates represent the slope of linear regression lines fitted to age-vs.-carapace-length data for 5-year age groups. Numbers below age groups indicate (0–50% forest, 60–100% forest) sample sizes used to calculate the growth rate. The growth rate ± one standard error is shown for each 5-year age group.

Meristic and population characteristics

Size and age distributions for box turtles in this population were similar to those reported in other box turtle studies (Stickel 1950, Stickel and Bunck 1989, Stuart and Miller 1987). Minor differences among studies may be partially due to the difficulty of accurately aging turtles, the use of different sampling methods, and different systems of classifying juvenile and slow-growing, older turtles. In our study, as turtles grew and matured, correlations between age and meristic characters decreased, indicating increased variability among individuals. The lower correlation coefficients between carapace length and mass could be due to differences in hydration and stomach content. The decrease in growth rate that we documented as turtles aged was consistent with Stickel and Bunck (1989), who found that Eastern Box Turtle growth rates neared zero by age 16. Similar decreases in growth rates with age have been documented for *T. c. triunguis* Agassiz (Three-toed Box Turtles; Schwartz 2000) and additional turtle species including *Chrysemys picta* Schneider (Painted Turtles; Gibbons 1968). We found no differences in growth rates between males and females. However, other studies that tracked individual turtles over time found that male box turtles grew at a faster rate than female box turtles (Stickel and Bunck 1989).

Male turtles had longer carapaces and shorter plastrons than females, which is consistent with the pattern of sexual dimorphism noted in other Eastern Box Turtle populations (Brown 1971, Dodd 1997, Palmer and Braswell 1995, Stickel and Bunck 1989). Although males were longer than females, we did not detect any difference in mass between males and females, which also agrees with previous research (Dodd 1997, Stickel and Bunck 1989).

The box turtle population near Davidson, NC appears to be composed of mostly adult turtles, a trend common to most other box turtle populations that have been studied (Brown 1974, Schwartz and Schwartz 1974, Stickel 1950). However, juvenile turtles were likely underrepresented in our study because they are notoriously difficult to find (Langtimm et al. 1996, Stickel and Bunck 1989, Stickel 1950). The abundance of adult turtles is not surprising because turtles are long-lived and rely on a life-history strategy of high adult survival (Congdon and Gibbons 1990, Hall et al. 1999, Klemens 2000).

Contrary to previous research (Dodd 1997, Hall et al. 1999, Henry 2003), we collected more females than males. This could be due in part to uneven sampling effort and the seasonal activity differences between genders. We did, however, find fewer females over 20 years old than males, suggesting that the survival of adult females may be lower than males. Hall et al. (1999) suggested that the movement patterns and habitat selection (e.g., nesting in fields) of females may make them more vulnerable to the effects of urbanization such as being killed by lawn mowers and vehicles.

Activity and condition

Turtles are more likely to be encountered when they are active, assuming detection probabilities and sampling effort are constant throughout the year. Although we cannot justify these assumptions, we cautiously interpret seasonal variation in capture frequency to reflect variation in activity levels (Ford and Moll 2003). The primary active season for box turtles in North Carolina is reported to be May through August (Palmer and Braswell 1995). Our data indicate that a considerable amount of activity also occurs during September and October. We found that female turtles were more active during the earlier part of the active season, a pattern corroborated by radio-telemetric studies (J. Hester, unpubl. data) and that males were more active during the early fall. Females of other turtle species—e.g., *Sternotherus odoratus* Latreille in Sonnini and Latrielle (Common Musk Turtle)—have been shown to be active earlier in the year than males, possibly allowing females to accumulate energy reserves in preparation for producing eggs (Ford and Moll 2003). Dodd et. al (1994) detected no seasonal differences in activities between male and female box turtles, suggesting that regional differences in climate or resource availability may affect activity patterns.

Box turtles utilize overlapping home ranges to find mates and commonly undertake forays in search of females during the mating seasons (Dodd 2001). Box turtles have been reported to mate during the entire active season (Palmer and Braswell 1995, Williams and Parker 1987), but most mating events have been reported in the spring (Allard 1935, Dodd 2001, Legler 1960, Minton 1972, Palmer and Braswell 1995). A second mating season in the fall apparently occurs in some localities (Dodd 2001, Legler 1960, Minton 1972). The fall peak in male activity we documented suggests that early fall may be the primary mating season for box turtles in our area.

The seasonal variation in condition we documented is likely due to the reproductive condition and corresponding activity patterns of these animals. Female box turtles in North Carolina typically lay their eggs in June and July (Allard 1935, Palmer and Braswell 1995), which coincides with the dramatic decrease in female condition we observed between June and August for the Davidson population. The decrease we observed in male body condition during the fall, although not statistically significant, corresponds to the time when males were most active (Ford and Moll 2003, Legler 1960) and is likely due to energy expenditure during mate-searching activity. Other studies have shown that males reduce feeding during courtship (Rosenberger 1936), which may contribute to their lower condition during the fall mating season.

Impacts of urbanization

Our results indicate that although box turtle populations can persist in developed areas, they may have higher adult survivorship in forested areas, or at least in areas with a high proportion of tree cover. Decreased survivorship for turtles in urban environments near Davidson may be due to several factors, including habitat degradation, pollution, increases in the number of anthropogenically-subsidized predators, and mortality due to automobile traffic (Belzer and Steisslinger 1999, Dodd et al. 1989, Mitchell and Klemens

2000, Stickel 1978, Wilcove et al. 1986, Wilcox and Murphy 1985, Williams and Parker 1987). Adult Eastern Box Turtles may be especially susceptible to road mortality. A study in Alabama showed that box turtles accounted for 85% of the turtles killed on a series of roads (Dodd et al. 1989).

Growth patterns of turtles from highly-forested areas and areas with low forest cover show different trends. First, although the difference was not statistically significant, turtles of ages 0–4 from forested areas tended to be larger than those from areas with less forest. Turtles in areas with less forest, however, showed higher initial growth rates than those from areas with greater than 50% forest cover. Lastly, growth in turtles from forested areas slowed to almost zero mm per yr for the 10–14 yr old age group, whereas turtles from 10–14 yrs old from the less forested areas continued to grow until approximately age 15. All turtles reached similar sizes by ages 15–20, suggesting that turtles in forested areas may reach their adult size sooner. Eastern Box Turtles are opportunistic omnivores, so turtles in less forested areas, such as in suburban neighborhoods, may benefit from food sources, such as gardens and dumpsters, not available to those in more natural habitats (Dodd 2001; M. Dorcas, pers. observ.). Turtles inhabiting forested habitats reach adult size earlier than those in areas with < 50% forest cover, which may allow them to mate earlier and/or provide the safety benefits of adult turtle size (Dodd 2001).

For long-lived species with characteristically low adult mortality, decreased adult survivorship or delayed maturity may lead to long-term population declines (Congdon and Gibbons 1990, Hall et al. 1999, Klemens 2000). Road networks and urbanized areas in the western Piedmont of North Carolina and in many other regions of the eastern United States are increasing rapidly (Griffith et al. 2003). Urbanization is suspected to decrease juvenile recruitment and adult life-span, but long-term effects may not be immediately evident due to the secrecy of juveniles, delayed sexual maturity, and longevity of adults (Congdon and Gibbons 1990, Congdon et al. 1993, Garber and Burger 1995). Lower population densities are also suspected in urban areas and may have reproductive consequences for species, like box turtles, that rely on chance encounters for breeding (Belzer and Steisslinger 1999, Stickel 1950). Although the Davidson box turtle population appears to be persisting despite increasing levels of urbanization, more long-term data are needed to truly assess the health of populations of this and other long-lived species.

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Literature Cited

Allard, H.A. 1935. The natural history of the box turtle. The Scientific Monthly 41:325–338.

Brown, W.S. 1971. Morphometrics of *Terrapene coahuila* (Chelonia, Emydidae), with comments on its evolutionary status. Southwestern Naturalist 16:171-184.

Brown, W.S. 1974. Ecology of the Aquatic Box Turtle, *Terrapene coahuila* (Chelonia, Emydidae) in northern Mexico. Bulletin of the Florida State Museum, Biological Sciences 19:1-67.

Belzer, B., and M.B. Steisslinger. 1999. The box turtle: Room with a view on species decline. The American Biology Teacher 61:510–513.

Congdon, J.D., A.E. Dunham, and R.C. van Loben Sels. 1994. Demographics of Common Snapping Turtles (*Chelydra serpentina*): Implications for conservation and management of long-lived organisms. American Zoology 34:397–408.

Congdon, J.D., and J.W. Gibbons. 1990. The evolution of turtle life histories. Pp. 45–54, *In* J.W. Gibbons (Ed.). 1990. Life History and Ecology of the Slider Turtle. Smithsonian Institution Press, Washington, DC.

Congdon, J.D., A.E. Dunham, and R.C. van Loben Sels. 1993. Delayed sexual maturity and demographics of Blanding's Turtles (*Emydoidea blandingii*): Implications for conservation and management of long-lived organisms. Conservation Biology 7:826–833.

Dodd, Jr., C.K. 1997. Population structure and the evolution of sexual size dimorphism and sex ratios in an insular population of Florida Box Turtles *Terrapene carolina bauri*. Canadian Journal of Zoology 75:1495–1507.

Dodd, Jr., C.K. 2001. North American Box Turtles: A Natural History. University of Oklahoma Press, Norman, OK. 231 pp.

Dodd, Jr., C.K., K.M. Enge, and J.N. Stuart. 1989. Reptiles on the highways in north-central Alabama, USA. Journal of Herpetology 23:197–200.

Dodd, Jr., C.K., R. Franz, and L.L. Smith. 1994. Activity patterns and habitat use of Box Turtles (*Terrapene carolina bauri*) on a Florida Island, with recommendations for management. Chelonian Conservation Biology 1:97–106.

Ford, D.K., and D. Moll. 2003. Sexual and seasonal variation in foraging patterns in the Stinkpot, *Sternotherus odoratus*, in southwestern Missouri. Journal of Herpetology 38:296–301.

Garber, S.D., and J. Burger. 1995. A 20 year study documenting the relationship between turtle decline and human recreation. Ecological Applications 5:1151–1162.

Gibbons J.W. 1968. Population structure and survivorship in the Painted Turtle, *Chrysemys picta*. Copeia 1968:260–268.

Gibbons, J.W., D.E. Scott, T.J. Ryan, K.A. Buhlmann, T.D. Tuberville, B.S. Metts, J.L. Greene, T. Mills, Y. Leiden, S. Poppy, and C.T. Winne. 2000. The global decline of reptiles, déjà vu amphibians. BioScience 50:653–666.

Griffith, J.A., S.V. Stehman, and T.R. Loveland. 2003. Landscape trends in mid-Atlantic and southeastern United States ecoregions. Environmental Management 32(5):572–588.

Hall, R.J., P.F.P. Henry, and C.M. Bunck.1999. Fifty-year trends in a box turtle population in Maryland. Biological Conservation 88:165–172.

Henry, P.F.P. 2003. The Eastern Box Turtle at the Patuxent Wildlife Research Center 1940s to the present: Another view. Experimental Gerontology 38:773–776.

Hester, J.M., S.A. Budischak, and M.E. Dorcas. In press. The Davidson College box turtle mark-recapture program: Urban herpetological research made possible by citizen scientists, *In* R.E. Jung and J.C. Mitchell (Eds.), Urban Herpetology: Ecology, Conservation and Management of Amphibians and Reptiles in Urban and Suburban Environments. Herpetological Conservation Vol 3. Society for the Study of Amphibians and Reptiles, Salt Lake City, UT.

Klemens M.W. (Ed.). 2000. Turtle Conservation. Smithsonian Institution Press, Washington, DC. 334 pp.

Kornilev, Y.K., S.J. Price, and M.E. Dorcas. In press. Between a rock and a hard place: Responses of Eastern Box Turtles (*Terrapene carolina*) when trapped between railroad tracks. Herpetological Review.

Langtimm, C.A., C.K. Dodd, Jr., and R. Franz. 1996. Estimates of abundance of Box Turtles (*Terrapene carolina bauri*) on a Florida island. Herpetologica 52:496–504.

Legler, J.M. 1960. Natural history of the Ornate Box Turtle, *Terrapene ornata ornata* Agassiz. University of Kansas Publication Museum of Natural History 11:527–669.

Minton, S.A., Jr., 1972. Amphibians and Reptiles of Indiana. Indiana Academy of Science Monographs 3. Indianapolis, IN. 346 pp.

Mitchell J.C., and M.W. Klemens. 2000. Primary and secondary effects of habitat alteration. Pp. 5–32, *In* M.W. Klemens (Ed.). 2000. Turtle Conservation. Smithsonian Institution Press, Washington, DC.

Palmer W.M., and A.L. Braswell. 1995. Reptiles of North Carolina. The University of North Carolina Press, Chapel Hill, NC. 412 pp.

Rosenberger, R.C. 1936. Notes on some habits of *Terrapene carolina* (Linne). Copeia 1936:177.

Schwartz, E.R. 2000. Update on permanent residency, persistence, and longevity in a 35-year study of a population of Three-toed Box turtles in Missouri. Chelonian Conservation and Biology 3:737-738.

Schwartz, C.W., and E.R. Schwartz. 1974. The Three-toed Box Turtle in central Missouri: Its population, home range, and movements. Terrestrial Series # 5. Missouri Department of Conservation, Jefferson City, Missouri. 28 pp.

Sexton, O.J. 1959. Spatial and temporal movements of a population of the Painted Turtle, *Chrysemys picta marginata* (Agassiz). Ecological Monographs 29:113–140.

Shine, R., R.N. Reed, S. Shetty, and H.G. Cogger. 2002. Relationships between sexual dimorphism and niche partitioning within a clade of sea-snakes (Laticaudinae). Oecologica 133:45–53.

Stickel, L.F. 1950. Populations and home-range relationships of the box turtle. Ecological Monographs 20:351–378.

Stickel, L.F. 1978. Changes in a box turtle population during three decades. Copeia 2:221–225.

Stickel, L.F., and C.M. Bunck. 1989. Growth and morphometrics of the box turtle, *Terrapene c. carolina*. Journal of Herpetology 23:216–223.

Stuart, M.D., and G.C. Miller. 1987. The Eastern Box Turtle, *Terrapene c. carolina* (Testudines: Emydidae), in North Carolina. Brimleyana 13:123–131.

Wilcove, D.S., C.H. McLellan, and A.P. Dobson. 1986. Habitat fragmentation in the temperate zone. Pp. 237–256, *In* M.E. Soule (Ed.). Conservation Biology: The Science of Scarcity and Diversity. Sinauer Publishers, Sunderland, MA.

Wilcox, B.A., and D.D. Murphy. 1985. Conservation strategy: The effects of fragmentation on extinction. American Midland Naturalist 125:879–887.

Williams, E.C., and W.S. Parker. 1987. A long-term study of a Box Turtle (*Terrapene carolina*) population at Allee Memorial Woods, Indiana with emphasis on survivorship. Herpetologica. 43:328–335.

Wilson, D.S., C.R. Tracy, and C.R. Tracy. 2003. Estimating age of turtles from the growth rings: A critical evaluation of the technique. Herpetologica 59:178–194.