Herpetological Conservation and Biology 11:459–466.
Submitted: 27 March 2016; Accepted: 2 October 2016; Published: 16 December 2016.

Demographic Characteristics of the Eastern Box Turtle, *Terrapene carolina carolina*, in a Relictual, Suburban, Wetland Habitat of Middle Tennessee, USA

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***Abstract*.—The Eastern Box Turtle, *Terrapene carolina carolina*, is a species of concern in Tennessee, USA, due to population declines. These declines are primarily due to anthropogenic causes including, but not limited to, habitat fragmentation as a result of urbanization, road mortality, and disease. Demographic and natural history data are lacking for *T. c. carolina* populations in Tennessee and are much needed for conservation and preservation of the declining populations. We collected demographic data for monitoring a *T. c. carolina* population in a relictual, suburban, wetland habitat in Murfreesboro, Tennessee, USA. The demographic characteristics we recorded included population density, age class, sex ratio, and body size measurements. We estimated the population density to be approximately 14.0–15.5 turtles per ha. The age class structure of located turtles was negatively skewed and leptokurtic, with most turtles falling within the middle age class (10–14 y). The sex ratio of located turtles from both 2013 and 2014 was 1.26 male:1 female. For body size, the only variable that differed between males and females was straight-line carapace length, with males exhibiting a longer carapace length than females. The data collected herein will be important for monitoring and conserving this and other box turtle populations.**

Key Words.—age class; body size; conservation; population density; reptile; sex ratio

Introduction

The Eastern Box Turtle, *Terrapene carolina carolina*, is one of six subspecies of box turtles belonging to the family Emydidae and is currently in decline across its range. It is considered to be Vulnerable by the International Union for the Conservation of Nature (IUCN), is on the Red List of Threatened Species (2013; *Terrapene carolina*. Available from www.iucnredlist.org [Accessed 1 March 2015]), and is a Species of Greatest Conservation Need (SGCN) in Tennessee (Tennessee State Wildlife Action Plan Team 2015), USA. *Terrapene c. carolina* numbers are in decline mainly due to habitat fragmentation caused by urbanization (Budischak et al. 2006), vehicle mortality (Stickel 1978; Gibbs and Shriver 2002), and ranaviral infection (Allender et al. 2006; Allender et al. 2011). Few studies have analyzed demographic characteristics of *T. c. carolina* populations in Tennessee, and yet this information is critical for monitoring and conservation efforts, not only in Tennessee but for the entire geographic range of the species (Weiss 2009). Because of the status of *T. c. carolina* as a species of concern in Tennessee, it is even more important to have baseline demographic characteristics so that populations in Tennessee can be assessed for demographic variation among populations and monitored for demographic changes within populations.

Population density estimates for *T. c. carolina* are quite variable: 9.9–12.4 per ha in Maryland, USA, (Stickel 1950), 8.9–10.5 per ha in Indiana (Williams 1961), USA, 18.8–22.7 per ha in east Tennessee (Dolbeer 1969), and 2.7–5.7 per ha in Indiana, with a decline occurring across a > 20 y span from 1960–1983 (Williams and Parker 1987). Therefore, it would be hard to predict what the population density of turtles in any particular field site would be. However, it is important to have estimates of population densities so that these numbers can be monitored for decline over subsequent years and appropriate conservation actions can be taken if necessary. It is also important to understand the structure (e.g., age, sex ratio) of the population in question.

Age class structure can be an important indicator of many life-history traits including recruitment, survivorship, and mortality (Hall et al. 1999; Budischak et al. 2006). Because turtles, including *T. c. carolina*, are a long-lived species (Gibbons 1987), adults typically have a high survival rate (Stickel 1978; Hall et al. 1999; Budischak et al. 2006). However, urbanization can negatively impact adult survival and growth rates (Hall et al. 1999; Budischak et al. 2006). In addition, juvenile turtles typically make up a small portion of population counts due to their high mortality rates and reclusive nature (Dodd 2001). A stable population of box turtles should approximate a normal distribution of age classes (Dodd 2001).

Sex ratios of adult box turtles are often male-skewed (Dolbeer 1969; Schwartz and Schwartz 1974; Stickel 1989; Dodd 1997; Hall et al. 1999). However, in a natural population, the sex ratio should approximate 1:1 (Fisher 1958), which is also quite common for *T. c. carolina* (Stickel 1950; Williams and Parker 1987; Stickel 1989; Weiss 2009). Sex ratio estimates can fluctuate depending on several factors including age and size at which sexual maturity is reached, temperature-dependent sex determination (TSD), sampling methods, sampling bias, and anthropogenic influence (Dodd 1997). Several studies have indicated that nest site selection may be the most influential factor affecting sex ratio in *T. c. carolina* (Dodd 1997; Dodd 2001; Weiss 2009). *Terrapene c. carolina* exhibit TSD, where male box turtles develop in cooler temperature conditions (22.5–27.0° C; Ewert and Nelson 1991), typical of internal forest habitat, which is often the habitat of choice for Eastern Box Turtles (Dodd 1997; Weiss 2009). However, nesting may occur outside of the shady, forest habitat, either in open fields (Flitz and Mullen 2006) or in sunny clearings within the forest (Congello 1978), resulting in a more even mix of sexes, or possibly more females. In addition, it is typical for male box turtles to have a longer straight-line carapace length (SLCL) but a shorter carapace height than females (Legler 1960; Stickel and Bunck 1989; Dodd 1997; Weiss 2009).

Ultimately, all of the aforementioned demographic characteristics are important and useful for understanding population structure, monitoring populations, and implementing conservation and preservation practices when and where necessary. With declining populations in mind, the general purpose of our study was to obtain demographic data for *T. c. carolina* in a relictual (McIntyre and Hobbs 1999), suburban, wetland habitat of Middle Tennessee. Because this species is a SGCN, it is important to have baseline demographic data for monitoring.

Materials and Methods

Field site and study organism.—We studied a population of *T. c. carolina* in a relictual, suburban, wetland habitat, Nickajack Trace and Black Fox Wetlands (Nickajack), in Murfreesboro, Tennessee, USA. Nickajack is a 23.5 ha forested, wetland habitat that is cut into two sections by a residential road, and it is almost completely surrounded by a suburban housing community. The edges of Nickajack are made up of horse fields and the backyards of the surrounding community, and it is only a small patch of remaining forest with few connections to other forested areas. This site is described as relictual because < 10% of the original habitat remains (McIntyre and Hobbs 1999). One side of the road contains a small pond fed by Black Fox Spring, and is 3.5 ha in size (U.S. Army Corps of Engineers 2000). The area on the other side of the road is 20 ha and has a creek (Lytle Creek) running through the interior of the forest (U.S. Army Corps of Engineers 2000). Nickajack is predominantly a Hardwood Forest with large areas of Palustrine Emergent and Forested Wetlands (U.S. Army Corps of Engineers 2000). It is also heavily invaded by privet (Ligustrum spp.; U.S. Army Corps of Engineers 2000). Nickajack is home to many forms of wildlife, including various fish species, small and large mammals, various herpetofauna, and a diverse array of birds (U.S. Army Corps of Engineers 2000). Based on previous monitoring efforts at our field site (Rachel Singer, pers. comm.), we expected the population density of *T. c. carolina* to be relatively high.

Mark-recapture.—We captured *T. c. carolina* opportunistically by walking through the field site from April to October in both 2013 and 2014. This study was done in conjunction with another study analyzing seasonal hormone profiles of box turtles, which led to us capturing the majority of turtles during the spring (May), summer (July-early August), and fall (late September-October) sampling periods and from 0800–1430. During the seasonal sampling periods, we searched for and captured turtles on a near daily basis. During the months in between each seasonal sampling period, we still captured turtles regularly, but not on a daily basis. In addition, we gave more time to the 20 ha side of the field site than the smaller 3.5 ha side because it was more common to find turtles on the larger side. However, we still searched and sampled regularly the 3.5 ha site. We used a modified version of the notching system by Cagle (1939) to mark turtles by notching three marginal scutes with a triangular file using a unique three letter code corresponding to the chart from Somers and Matthews (2006). If a turtle was already marked with a three letter code, we recorded it as a recapture. We processed each turtle at the site of encounter and then released it.

Population density.—Using 2013 and 2014 monthly data, we estimated population size using the POPAN model (variation of Jolly-Seber model) in the program MARK (on-line program). The POPAN model is used as a submodule in MARK to estimate the entire population, or Super Population, and it assumes equal survival and catchability among the individuals of the population in question (Wagner et al. 2011). Also, using yearly data, we estimated the population size using the Lincoln-Petersen Index (Pollock et al. 1990). The equation for the Lincoln-Petersen Index is

$$\widehat{N} = \frac{n_1 n_2}{m_2}$$

where $\widehat{N}$ is population size; n_1 is the number of individuals marked and released in the first population sample; n_2 is the number of individuals captured in the second population sample; and m_2 is the number of marked individuals from the first sampling period (n_1) recaptured during the second sampling period (Pollock et al. 1990). The two sampling periods used for the Lincoln-Peterson Index were 2013 and 2014. After population size was calculated, we then calculated population density by dividing the population size by the size of the study site, 23.5 ha, to estimate the number of turtles per ha.

Age class and sex ratio.—We estimated age by counting the annular rings on the pleural scutes (Ewing 1939) and assigned each turtle to an age class: 0–4 y, 5–9 y, 10–14 y, 15–19 y, 20+ y (Budischak et al. 2006; Weiss 2009). Growth rings (Germano and Bury 1998) were counted on three to four pleural scutes to obtain the best overall estimate of age for placement in the appropriate age class. When analyzing age class structure, we combined 2013 and 2014 captures, and we used each turtle only once, even if it was recaptured multiple times.

We determined sex primarily by eye color and plastron concavity, where males typically have red eyes and a concave plastron and females typically have brown eyes and a flat plastron (Elghammer et al. 1979; Somers and Matthews 2006). When calculating sex ratio, we combined 2013 and 2014 data using each turtle only once and we compared 2013 and 2014 sex ratios separately.

Body size and supplemental information.—We measured mass to the nearest 1 g using a 1,000 g spring scale (Pesola, Forestry Suppliers, Jackson, Mississippi, USA). We used digital calipers (203 mm, Neiko Tools, Homewood, Illinois, USA) to obtain shell measurements to the nearest 0.1 mm, including straight-line carapace length (SLCL), carapace width, carapace height, length of hinge, length anterior to hinge (LAH), and length posterior to hinge (LPH). After recording body size measurements, we took photographs of shell pattern and any abnormalities of each turtle. In addition, we recorded GPS coordinates (Garmin Etrex 30, Olathe, Kansas, USA) at the location of each captured turtle.

Statistical analyses.—We combined 2013 and 2014 data for body size measurements. We compared male and female body size measurements and mass using the Welch *t*-test (Welch 1938, 1947) to control for unequal variances and unequal sample sizes. The sample sizes change between variables due to missing or inaccurate measurements on some individual turtles. We also calculated skewness and kurtosis for the age class distribution. Lastly, we used a chi-square analysis to determine if our calculated sex ratios differed significantly from a 1:1 sex ratio.

For recaptures that were only captured on two occasions, we tossed a coin to indicate which data point would be used for analyses. For any recaptures that were captured on more than two occasions, we used the RANDBETWEEN function in Microsoft© Excel to randomly select which data point would be used for analyses. We did not include any turtles with undetermined sex in analyses. Also, we did not include juveniles (< 190 g and/or < 7 y) in body size analyses. We used the Shapiro-Wilk normality test (Shapiro and Wilk 1965; Rose et al. 2015) to test that all datasets were normally distributed. For all statistical tests, we set alpha to 0.05. We present data as means ± SD. We completed all statistical analyses in IBM SPSS Statistics 22 (Armonk, New York, USA).

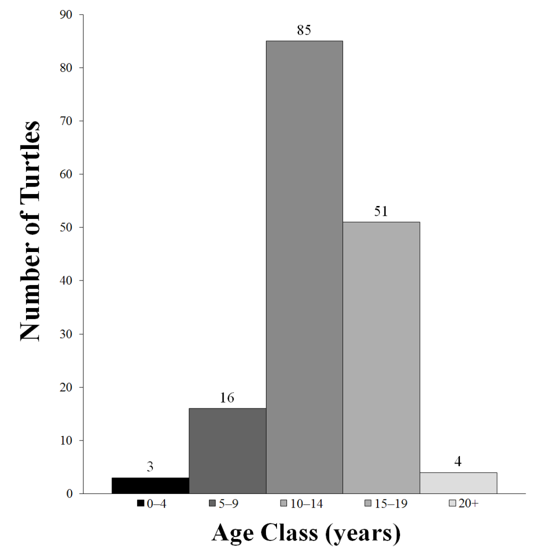

Figure 1. Age class structure of the sampled Eastern Box Turtle (*Terrapene carolina carolina*) population at Nickajack wetlands in middle Tennessee, USA. The numbers above the bars indicate number of turtles in that age class.

Results

In 2013, we caught 111 turtles, and in 2014 we caught 83 turtles of which 55 turtles were new captures and 28 recaptures. We caught some individuals multiple times across both years. Using the POPAN model in MARK, we estimated the population size at Nickajack to be 363 turtles (SE = 56.4, 95% CI: 268.1–491.3). Using the Lincoln-Peterson Index, we estimated the population size to be 329 turtles. These estimates equate to densities of 15.5 and 14.0 turtles per ha, respectively.

Age class structure was non-normal ($P < 0.001$), and the data was negatively skewed (skewness = -1.97) with a leptokurtic distribution (kurtosis = 1.67). Most of the turtles (53%, n = 85) were within the middle age class (10–14 y; Fig. 1). There were only three turtles in the youngest age group (0–4 y, 2%) and four turtles in the oldest age group (20+ y, 3%; Fig. 1).

We successfully identified 77 male and 61 female adult turtles across the 2013 and 2014 active seasons, which equates to a sex ratio of 1.26 male:1 female and did not differ significantly from a 1:1 sex ratio (χ^2 = 1.86, P = 0.173). When analyzing the years separately, the 2013 sex ratio was 1.12:1 (n = 48 males and 43 females) and the 2014 sex ratio was 1.66:1 (n = 48 males and 29 females). The 2013 sex ratio did not differ from a 1:1 sex ratio (χ^2 = 0.28, P = 0.600), but the 2014 sex ratio did (χ^2 = 4.69, P = 0.030).

Body mass did not differ between the sexes (P = 0.747), but males had a significantly longer SLCL than females (P = 0.005; Table 1). There were no significant sex differences in carapace width, carapace height, length of hinge, LAH, or LPH (Table 1). However, both LAH and LPH failed to meet the assumption of normality ($P < 0.001$ for both).

Discussion

***Population density*.**—The population density found at Nickajack of 14.0–15.5 turtles per ha is within the range of what has been reported. Stickel (1950) estimated a population density of approximately 11 *T. c. carolina* per ha in an 11.8 ha site in Maryland, and Williams (1961) estimated a population density of approximately 10 *T. c. carolina* per ha on a 34.4 ha study area in Indiana. However, Dolbeer (1969) found a high population density in Tennessee of approximately 20 *T. c. carolina*/ha. In addition, a study of a 36.4 ha island in Florida estimated a density of approximately 15 *T. c. bauri* (Florida Box Turtle) per ha (Langtimm et al. 1996). Our field site is not an island but a small pocket of habitat surrounded by an encroaching suburban housing community. The turtles at our field site are free to wander out of the wetland and onto the road or into the surrounding housing community or into adjacent forest corridors. Nevertheless, no road mortalities were witnessed adjacent to the site, and there were very few instances (three) when turtles were found on or near the road. Supplemental telemetry data on several turtles showed no sign of turtles ever leaving the field site to cross the road. Turtles were occasionally found on the edge of the site and could potentially wander into adjacent backyards of the surrounding homes. However, this was seldom witnessed and may indicate that turtles do not venture past the edge habitat very often. Indeed, box turtles are known to have small (1.13–1.20 ha) home ranges (Stickel 1989) and often exhibit fidelity to those ranges (Stickel 1950), their nesting sites (Kipp 2003), and their hibernacula (Vannatta and Klukowski 2015) and may have no need to travel out of the site. If these statements hold true, it is possible that Nickajack may be acting as an island for these turtles with little to no emigration or immigration. This is something that should be investigated further, as home range size was not measured in this study and the adjacent forest was not explored. This also poses an interesting question as to whether or not gene flow is occurring between the two areas separated by the road.

***Age class*.**—Age class structure had a non-normal distribution, although most individuals were in the middle age class and few turtles were in the 0–4 y age class or the 20+ y age class. However, some studies have found that many box turtles are in the 20+ y age class (Budischak et al. 2006; Weiss 2009). Dodd (2001) suggested that it is typical for a box turtle population to have few old and few young individuals, and this supports our findings of the age class structure. Additionally, finding few individuals within the 0–4 age class is not unusual, especially because juvenile box turtles are often reclusive and hard to find (Pilgrim et al. 1997; Dodd 2001; Budischak et al. 2006; Weiss 2009; Germano 2014).

Henry (2003) found few 20+ y individuals in a *T. c. carolina* population in Maryland, with most individuals in the 8–20 y age class, similar to our study. Henry (2003) suggested that the Maryland population may be a temporary population that is relatively new and passing

Table 1. Mean ± standard deviations of body mass (g), straight-line carapace length (SLCL), carapace height and width, length of shell hinge, length of shell anterior to hinge (LAH), and length of shell posterior to hinge (LPH) for male and female Eastern Box Turtles (*Terrapene carolina carolina*) at Nickajack Wetlands in Middle Tennessee, USA. All shell measurements are in millimeters. Sample sizes (n), t, and P values are provided for comparison of means by sex using the Welch t-test.

Variable	Male	n	Female	n	t value	P value
Body Mass	383.6 ± 72.1	77	388.3 ± 92.9	59	-0.32	0.747
SLCL	131.4 ± 8.8	74	126.4 ± 10.9	54	2.89	0.005
Carapace Width	99.2 ± 6.1	77	97.8 ± 7.6	59	1.16	0.250
Carapace Height	62.1 ± 3.9	77	63.6 ± 6.0	59	-1.65	0.102
Length of Hinge	69.0 ± 4.5	77	67.6 ± 5.8	58	1.55	0.125
LAH	52.0 ± 4.3	76	50.8 ± 5.9	59	1.25	0.215
LPH	72.3 ± 5.5	76	72.9 ± 7.5	59	0.57	0.572

through, leading to low numbers of 20+ y individuals. It is possible that the *T. c. carolina* population at Nickajack is relatively young, indicating that there has not been enough time for the population to accumulate many 20+ y individuals. However, older aerial photographs found on Google Earth Pro© for Nickajack suggest that the area was fully forested as early as 1997, and past land use data suggests that it has been protected since the early 1990s by the Black Fox Wetland League (now Stones River Watershed Association), the Tennessee Wildlife Resources Agency, and the city of Murfreesboro (Tennessee Department of Environment and Conservation 2003). It is unclear why there were so few turtles in the 20+ y age class found at Nickajack. Hall et al. (1999) suggested that females must travel and move around a great deal to find a proper nesting site, which makes them more vulnerable to predation and human-caused deaths, such as mowing or vehicular death. Although mowing does occur at this site, we have never observed a box turtle that was killed from mowing. While death due to mowing and vehicular collisions is thought to be rare at this site, it is possible that older females may have been killed during construction of the roads and housing communities in the area when they were travelling to appropriate nesting sites.

Another concern is the possible inaccuracy of aging by counting annular rings (Wilson et al. 2003). Wilson et al. (2003) found that most researchers do not determine if each ring is deposited on a yearly basis. False rings can be deposited as a result of varying weather patterns and activity (Ewing 1939; Legler 1960). However, many researchers have used this technique to obtain a general estimate of age (Ewing 1939; Legler 1960; Stickel and Bunck 1989; Budischak et al. 2006; Weiss 2009), and it is accurate for a large segment of a population when false rings are taken into account (Germano and Bury 1998).

In our study, only the major, prominent growth rings were counted. However, this, in turn, may have led to problems of age underestimation as well. Some turtles from 2013 showed deposition of a single new growth ring in 2014, while others showed no change in growth ring numbers and others showed a lower count than the previous year. Some of this variability can be attributed to researcher error, while some may be due to inconsistencies in annular deposition. This is why several pleural scutes were counted to determine the best estimation to allow for placement in the appropriate age class, with classes having a range of 5 y. This allowed for confidence in age class placement, but not for exact age. Because counts of scute annuli in young turtles are the only way to determine the age if a turtle is captured only once, this seems to be the best method to offset the inaccuracies of aging (Budischak et al. 2006; Weiss 2009). This is something that should be explored further by, for example, tracking several turtles over a long time period to analyze their growth and the deposition of growth rings (i.e., Stickel 1978; Stickel and Bunck 1989; Germano 2014).

Sex ratio.—The sex ratio recorded at Nickajack (1.26 male:1 female) was not significantly different from a 1:1 sex ratio. While significant male-skewed sex ratios have been found in some box turtle populations (Dolbeer 1969; Schwartz and Schwartz 1974; Stickel 1989; Dodd 1997; Hall et al. 1999), equal sex ratios have also been found (Stickel 1950; Williams and Parker 1987; Stickel 1989; Pilgrim et al. 1997; Weiss 2009). For example, Pilgrim et al. (1997) found a 1.12:1 sex ratio in *T. c. bauri* in Florida, and Stickel (1950, 1989) found a 1:1 sex ratio in *T. c. carolina* in Maryland in several years of sampling. It should be noted that a separate study conducted by other researchers took place at our field site during the 2014 active season and involved the capture of females for a short time period to test for gravidity. This could have led to a lower capture rate of females during both the summer and fall sampling periods and might have led to the male-skewed sex ratio observed in 2014. Dodd (2001) suggested that a sex ratio is really only indicative of the population at the time it was measured, because sex ratios are constantly fluctuating and changing in the population over time. It would be beneficial to continue monitoring the sex ratio at Nickajack over a long-term period to evaluate any fluctuations or patterns that may occur over time.

Body size.—Brisbin (1972) and Dodd (1997) found no sex related differences in body mass in *T. c. carolina* or *T. c. bauri*, respectively, which is consistent with our study, but sexual size dimorphism has been observed in box turtles (Dodd 1997; Clair 1998; Dodd 2001). In most populations, males are larger than females in terms of shell size, except for shell height, in which females are usually taller (Dodd 2001). In Maryland, Stickel and Bunck (1989) found that male *T. c. carolina* were larger in all shell measurements except height. Likewise, in West Virginia, Weiss (2009) found that males had a longer SLCL; whereas, females had a taller carapace height. Despite nearly all studies finding both a difference in SLCL and carapace height in *T. c. carolina*, our study only found a significant difference in SLCL, with males being longer than females. The most plausible reason for sexual size dimorphism is reproduction; larger males are better equipped to hold on to females and successfully reproduce (Dodd 2001). Overall, our results are consistent with other studies on body size in *T. c. carolina*.

Ultimately, the demographic data presented herein seem to indicate a stable population of turtles at Nickajack, which is similar to other box turtle populations. However, continual monitoring is necessary as many of these measures are known to fluctuate with time and will change if a population decline is occurring. While the Nickajack population is similar in demographic structure to other populations, this can change rapidly, as ranavirus has been detected in this box turtle population, albeit at a low prevalence (Vannatta et al. 2016). Because box turtles are a long-lived species, long-term monitoring will be the best course of action for this population. While this study only represents a two-year time period, these demographic measurements will be useful for monitoring the population and will aid in determining future conservation methods when necessary.

Acknowledgments.—We would like to thank Rachel Singer of Murfreesboro Parks and Recreation for allowing us to use Nickajack as our field site. We would very much like to thank the Chicago Herpetological Society and the Biology Department at Middle Tennessee State University for funding and support for this project. This study was completed with approval from Middle Tennessee State University IACUC (no. 13-014). Turtles were captured with permission from the Tennessee Wildlife Resources Agency (permit no. 3740).

Literature Cited

Allender, M.C., M.M. Fry, A.R. Irizarry, L. Craig, A.J. Johnson, and M. Jones. 2006. Intracytoplasmic inclusions in circulating leukocytes from an Eastern Box Turtle (*Terrapene carolina carolina*) with iridoviral infection. Journal of Wildlife Diseases 42:677–684.

Allender, M.C., M. Abd-Eldaim, J. Schumacher, D. McRuer, L.S. Christian, and M. Kennedy. 2011. PCR prevalence of ranavirus in free-ranging Eastern Box Turtles (*Terrapene carolina carolina*) at rehabilitation centers in three southeastern US states. Journal of Wildlife Diseases 47:759–764.

Brisbin, L. 1972. Seasonal variations in the live weights and major body components of captive box turtles. Herpetologica 28:70–75.

Budischak, S.A., J.M. Hester, S.J. Price, and M.E. Dorcas. 2006. Natural history of *Terrapene carolina* (box turtles) in an urbanized landscape. Southeastern Naturalist 5:191–204.

Cagle, F.R. 1939. A system of marking turtles for future identification. Copeia 1939:170–173.

Congello, K. 1978. Nesting and egg laying behavior in *Terrapene carolina*. Proceedings of the Pennsylvania Academy of Science 52:51–56.

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

Dolbeer, R.A. 1969. A study of population density, seasonal movements and weight changes, and winter behavior of the Eastern Box Turtle, *Terrapene c. carolina* Linnaeus, in eastern Tennessee. M.Sc. Thesis, University of Tennessee Knoxville, Knoxville, Tennessee, USA. 53 p.

Doroff, A.M. and L.B. Keith. 1990. Demography and ecology of an Ornate Box Turtle (*Terrapene ornata*) population in south-central Wisconsin. Copeia 1990:387–399.

Elghammer, R.W., R.O. Swan, R.E. Johnson, and D. Murphy. 1979. Physical characteristics of male and female Eastern Box Turtles (*Terrapene carolina carolina*) found in Illinois. Transactions of the Illinois State Academy of Science 72:1–8.

Ewert, M.A., and C.E. Nelson. 1991. Sex determination in turtles: diverse patterns and some possible adaptive values. Copeia 1991:50–69.

Ewing, H.E. 1939. Growth in the Eastern Box Turtle, with special reference to the dermal shields of the carapace. Copeia 1939:87–92.

Fisher, R.A. 1958. The Genetical Theory of Natural Selection. 2nd Edition. Dover Publications, Inc., New York, New York, USA.

Flitz, B.A., and S.J. Mullin. 2006. Nest-site selection in the Eastern Box Turtle, *Terrapene carolina carolina*, in Illinois. Chelonian Conservation and Biology 5:309–312.

Germano, D. J. 2014. Activity, growth, reproduction, and population structure of Desert Box Turtles (*Terrapene ornata luteola*) at the northern edge of the Chihuahua Desert. Chelonian Conservation and Biology 13:56–64.

Germano, D.J., and R.B. Bury. 1998. Age determination in turtles: evidence of annual deposition of scute rings. Chelonian Conservation and Biology 3:123–132.

Gibbons, J.W. 1987. Why do turtles live so long? BioScience 37:262–269.

Gibbs, J.P., and W.G. Shriver. 2002. Estimating the effects of road mortality on turtle populations. Conservation Biology 16:1647–1652.

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.

Kipp, B. 2003. Nesting ecology of the Eastern Box Turtle (*Terrapene carolina carolina*) in a fragmented landscape. M.Sc. Thesis, University of Deleware, Newark, Deleware, USA. 78 p.

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 Publications, Lawrence, Kansas, USA.

Litzgus, J.D., F. Bolton, and A.I. Schulte-Hostedde. 2008. Reproductive output depends on body condition in Spotted Turtles (*Clemmys guttata*). Copeia 2008:86–92.

McIntyre, S., and R. Hobbs. 1999. A framework for conceptualizing human effects on landscapes and its relevance to management and research models. Conservation Biology 13:1282–1292.

Pilgrim, M.A., T.M. Farrell, and P.G. May. 1997. Population structure, activity, and sexual dimorphism in a central Florida population of box turtles, *Terrapene carolina bauri*. Chelonian Conservation and Biology 2:483–488.

Pollock, K.H., J.D. Nichols, C. Brownie, and J.E. Hines. 1990. Statistical inference for capture-recapture experiments. Wildlife Monographs 107:3–97.

Rose, S., N. Spinks, and A.I. Canhoto. 2015. Management Research: Applying the Principles. Routledge, New York, New York, USA.

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 p.

Shapiro, S.S., and M.B. Wilk. 1965. An analysis of variance test for normality (complete samples). Biometrika 52:591–611.

Somers, A.B., and C.E. Matthews. 2006. The Box Turtle Connection: A Passageway into the Natural World. University of North Carolina, Greensboro, North Carolina, USA.

Stickel, L.F. 1950. Populations and home range relationships of the box turtle, *Terrapene c. carolina* (Linnaeus). Ecological Monographs 20:351–378.

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

Stickel, L.F. 1989. Home range behavior among box turtles (*Terrapene c. carolina*) of a bottomland forest in Maryland. Journal of Herpetology 23:40–44.

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

St. Clair, R.C. 1998. Patterns of growth and sexual size dimorphism in two species of box turtles with environmental sex determination. Oecologia 115:501–507.

Tennessee Department of Environment and Conservation. 2003. Stones River Watershed (05130203) of the Cumberland River Basin: Water Quality Management Plan. Tennessee Department of Environment and Conservation, Nashville, Tennessee, USA. 214 p.

Tennessee State Wildlife Action Plan Team. 2015. Tennessee State Wildlife Action Plan. Tennessee Wildlife Resources Agency, Nashville, Tennessee, USA. 193 p.

U.S. Army Corps of Engineers. 2000. Ecosystem Restoration Environmental Assessment: Black Fox, Murfree, and Oaklands Spring Wetlands Murfreesboro, Tennessee. U.S. Army Corps of Engineers, Nashville District, Murfreesboro, Tennessee, USA. 215 p.

Vannatta, J.M., and M. Klukowski. 2015. *Terrapene carolina carolina* (Eastern Box Turtle). hibernation site fidelity. Herpetological Review 46:622.

Vannatta, J.M., M. Klukowski, and S. Wright. 2016. Prevalence of ranavirus infection in the Eastern Box Turtle, *Terrapene carolina carolina*, in an isolated, suburban wetland habitat of middle Tennessee. Herpetological Review 47:55–56.

Wagner, N., J. Pellet, S. Lötters, B.R. Schmidt, and T. Schmitt. 2011. The superpopulation approach for estimating the population size of "prolonged" breeding amphibians: examples from Europe. Amphibia-Reptilia 32:323–332.

Weiss, J.A. 2009. Demographics, activity, and habitat selection of the Eastern Box Turtle (*Terrapene c. carolina*) in West Virginia. M.Sc. Thesis, Marshall University, Huntington, West Virginia, USA. 88 p.

Welch B.L. 1938. The significance of the difference between two means when the population variances are unequal. Biometrika 29:350–362.

Welch B.L. 1947. The generalization of 'Student's' problem when several different population variances are involved. Biometrika 34:28–35.

Williams, E.C. 1961. A study of the box turtle, *Terrapene carolina carolina* (L), population in Allee Memorial Woods. Proceedings of the Indiana Academy of Science 71:399–406.

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 growth rings: a critical evaluation of the technique. Herpetologica 59:178–194.

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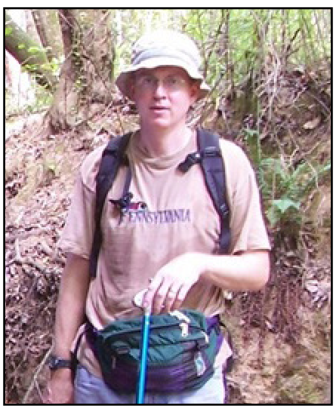

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