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Decline of Woodland Box Turtles (*Terrapene carolina carolina*) over 40 Years in Southeastern Pennsylvania, USA

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Abstract.—**Woodland Box Turtle (*Terrapene carolina carolina*) populations have declined over much of their range; however, conclusive quantitative data are rare due to the life-history traits of this species. Long-term data sets are required to quantify population decline. We present a comparison of box turtle population size spanning over 40 y at a site in southeastern Pennsylvania, USA. We individually marked box turtles or documented them photographically over this timeframe. We made comparative population size estimates of box turtles from data collected at the beginning to those from the most recent periods of the study (1978–1982; 2015–2020), derived from both open discrete and closed continuous-time, mark-recapture analysis methods. While population estimates from the different models varied, population trends estimated from both open Jolly-Seber/POPAN and closed, continuous time methods were strikingly similar. All models employed showed a population decline of between 71–74.1% over the 40+ y timespan. Speculative causes of box turtle decline in this population include vehicle strikes, subsidized predation, and removal for the pet trade. Timely steps are most likely needed to prevent extirpation of this population. Some potentially effective measures include public education, reduction of road mortality, and active habitat maintenance.**

Key Words.—Population decline; continuous-time; Jolly-Seber; long-term study; mark-recapture; photographic identification; POPAN model

Introduction

According to the International Union for Conservation of Nature and Natural Resources (IUCN), many Eastern Box Turtle (*Terrapene carolina*) populations have declined over 30% in the last 50–100 y. Causes of decline include habitat destruction, vehicle strikes, predation, pollution and pesticide effects, pet trade and personal pet removal, disease, fire suppression, and trends in ecological succession (Dodd 2001; van Dijk 2011; Kiester and Willey 2015). Because box turtles are long-lived as well as sensitive to environmental disturbance, a healthy population is a good indicator of overall ecosystem health (Lovich et al. 2018). Box turtles fill ecological roles as predators, prey, plant propagators, and ecosystem engineers (Dodd 2001). Loss of turtle populations therefore may lead to serious decline in ecosystem function (Braun and Brooks 1987; Fergus 2000; Lovich et al. 2018).

Long-term studies and data sets are rare, yet extremely important for understanding and quantifying population dynamics and trends of long-lived species (Tinkle 1979). Turtle life-history characteristics, including high adult survivorship, low juvenile survivorship, delayed maturation, and long reproductive lives all necessitate long term studies to determine population trends (e.g., Enneson and Litzgus 2009; Schneider et al. 2018; Keevil et al. 2018). These traits often cause turtle populations to undergo very slow dynamic trajectories that can take decades to detect. Population declines that occur over long-time scales can lead to distorted intergenerational perception of ecosystem productivity, which has been termed Shifting Baseline Syndrome (Pauly 1995; Papworth et al. 2009; Lovich et al. 2018). Because of the rarity of applicable studies, population trends are typically not quantified. Without such information, robust protection and restoration strategies appropriate to population status cannot be devised.

Using the results of a series of individual mark-recapture analyses on a Woodland Box Turtle (*T. c. carolina*) population in southeastern Pennsylvania, USA, from 1978 through 2020, we compare population size estimates from three mark-recapture models from periods at the beginning and end of the data set. The IUCN summarized population trends in Woodland Box Turtles as generally declining by about 30% over three turtle generations, or conservatively 50 y (vanDijk 2011). We hypothesized a decline in the population of box turtles at our site of at least this amount, as the 42-y timespan of our data set was comparable. This data set presents a rare opportunity to quantify long-term population trends in a Woodland Box Turtle population.

Materials and Methods

Site description.—Our study site was a moderately sized area of protected land located in southeastern Pennsylvania, USA. The land cover consisted of a patchwork of deciduous and evergreen forest in varying degrees of succession, and small ponds, creeks, and wetlands. The area was accessible to the public for a variety of uses.

Individual mark/recapture study.—In 1978 staff at the study site began collecting data on individual box turtles. Research staff did not perform deliberate surveys of box turtles but during the course of daily duties, they captured any encountered box turtles and marked them with notches upon their marginal scutes reflecting a unique individual code (Cagle 1939). Staff also recorded location, weight, length, sex, and age approximations of captures. Between 1982 and 2013, personnel collected data only intermittently with specific efforts to notch and document turtles in 1986 and from 1992 through 1994.

State-wide efforts to photograph and document reptiles and amphibians began in 2013 with programs such as the Pennsylvania Amphibian and Reptile Survey (PARS; https://paherpsurvey.org/). The purpose of the effort was to determine the distribution and status of all reptiles and amphibians in Pennsylvania. Current staff began deliberately taking digital photographs of all box turtles encountered during activities in 2015. In 2017, they realized that individual turtles were identifiable from scute pattern and coloration and that several box turtles had been photographed on multiple occasions. Scute color patterns have been shown to be identifiable over broad time scales and have been used in community science projects and other box turtle studies (e.g., Belzer and Seibert 2009; Cross et al. 2014; Sommers et al. 2017). Staff then established a database of box turtle individuals using digital photographs.

Photographic box turtle identification allowed for reinstituting box turtle individual identification at the site, where notching marginal scutes would not be required. The new method had the advantage of reducing the amount of time for organizing and training staff as well as physical contact with turtles. The Woodland Box Turtle is a Species of Special Concern in Pennsylvania and take is not permitted (Pennsylvania Fish and Boat Commission [PAFBC]. 2021. Fishing Summary Boating Handbook. PAFBC. Available from http://www.fishinpa.com/wp-content/uploads/2021/01/FINAL-2021-PA-Fishing-Summary_1-7-21_Web.pdf [Accessed 8 February 2021]). As the study progressed, staff and volunteers were trained to use personal cameras or cell phones to collect photographs of carapace, plastron, and side views of the turtles. Participants recorded data on shell anomalies and other traits to provide secondary identification information. As in the original study, staff did not implement intentional surveys for box turtles. Rather, staff and volunteers recorded turtle encounters during daily activity. The recent observational effort is therefore essentially comparable to the original effort implemented in 1978.

Population estimation: Jolly-Seber (POPAN).—An open population mark-recapture model estimate of population size was derived using the POPAN formulation (Schwarz and Arnason 1996) of the Jolly-Seber Mark-recapture Model (Jolly 1965; Seber 1965), using Program MARK, Ver. 9.0 (http://www.phidot.org/software/mark/). We focused on the first 5 y of the study (1978–1982) and the last 6 y (2015–2020) because of the comparable length of the time periods and because survey techniques and efforts were most consistent. Also, we were able to consult with the primary study investigators from the earlier time period (1978–1982).

An entire calendar year served as one sampling event. One justification for this abstraction of sampling period is that box turtles are a long-lived species with high site and territory fidelity, resulting in relatively low recruitment potential (e.g., Dodd 2001; Reinke et al. 2019). O'Brien et al. (2005) recommended that maximizing sample size during sampling occasion, as is accomplished by implementing one-year aggregate sampling events, results in the lowest level of population estimate bias in mark-recapture analyses. We are aware that several assumptions of population estimation are not met in this abstraction; however, the main goal of this analysis is comparison between population sizes over a 40-y interval, and not population density estimation *per se*. Because the data collection and analysis are very similar between time periods, we are confident that a valid comparison of adult population size may be made using this approach.

We rarely encountered hatchling or young box turtles, and therefore they were not included in the population analyses. Low occurrence of juveniles is typical in many box turtle studies (Dodd 2001). For example, in one 50-y study in Maryland, box turtles under 5 y of age, using scute growth rings (annuli) to determine age, were observed only three times out of 3,800 captures (Hall et al. 1999). Also, very young box turtles have dynamic shell pattern and coloration that does not allow for long term individual identification.

We used the Jolly-Seber/POPAN model under full parametrization, constant survivorship, constant survivorship and capture probability, and constant capture probability to compare population sizes between survey periods. We used the link function for survivorship (Phi), Sin function for capture probability (p), MLogit1 for probability of entry (pent), and Log for N (see Schwarz and Arnason 2009). We chose the model with the lowest Aikake's Information Criterion (AIC) score. Goodness of fit was assessed using the RELEASE program (V. 3.0), included with program MARK.

Population estimation: continuous time/closed population.—We also derived population estimates by using Closed Continuous-time (CT) Mark-recapture Analysis methods. We implemented these methods in R (Ver. 4.0.3) using the R package ctime (Schofield et al. 2018). The package contains assumption tests for equal catchability (hettest) and for behavioral impacts on catchability (behtest), as well as model-fitting routines appropriate for relaxing either of these assumptions, if necessary. Employment of the hettest procedure for data from both time periods revealed strong evidence of heterogeneity of capture for both periods ($P < 0.001$). The behtest procedure showed that the test was not significant for 1978–1982, though P-values were low (P = 0.080). It was significant for the 2015–2020 period ($P < 0.001$). We therefore derived population estimates for both heterogeneity (M_{th}) and behavioral (M_{tb}) models available in ctime. The M_{th} model required a vector summary of capture occasions (c) and the M_{tb} model used a vector of sequential capture history of individuals (y) for input. We employed default values for M_{th} for the theta parameter (ln[100] or 4.6) as suggested by Schofield et al. (2018), and chose theta for the M_{tb} model using a recommended lower informed prior value (ln[100]/ln[3] or 4.2). We fit both models using three Markov chains, each sampled 25,000 times. We determined population estimates as median values of N, and 95% confidence interval (two-tailed) of the overall distribution through rank and percentile analysis.

Results

During the first year that data was collected (1978), staff encountered box turtles 103 times. Staff identified 77 individual turtles that year, with 16 of the 77 seen more than once. This was the highest number of individual turtles encountered during any year of the study.

From May 1978 through July 1982, staff captured and notched 187 turtles (Table 1). They resumed identification and documentation of box turtles in 2015 and developed a digital photographic database. Box turtle captures were low in 2015 and 2016 but increased in subsequent years due to additional staff and volunteer training. As of 2020, there were 66 identifiable individual box turtles in the database (Table 1). Four box turtles in the photographic database are turtles that were notched on their marginal scutes in the earlier years of the study, two were notched in 1980, and two in 1994. Anecdotally, staff found all four turtles near to where they had been documented many years earlier.

The sex ratio of individual box turtles in the 1978–1982 period was 0.93 M: 1.00 F (48.3% male) and for

Table 1. The number of individual Woodland Box Turtles (*Terrapene c. carolina*) observed in southeastern Pennsylvania, USA, by year, including the portion of turtles previously observed, and newly documented individuals. An asterisk (*) indicates where turtle descriptions are missing or lost. Sex that was conclusively determined for newly identified individuals are also shown annually in the table.

Year	Total Encountered	Recaptured	Newly Documented	Males	Females	Undetermined Sex
1978	77	0	77	37	38	2
1979	31	9	22	13	15	3
1980	35	7	28	24	11	0
1981	41	14	27	16	25	0
1982	52	19	33	21	31	0
1986	15	9	3 (+3*)	10	5	0
1992	16	5	11	7	9	0
1993	17	6	11	12	5	0
1994	10	1	9	9	1	0
1999	20	6	(14*)	11	9	0
2015	3	0	3	1	1	1
2016	2	1	1	1	0	1
2017	19	1	18	6	3	10
2018	25	8	17	9	6	10
2019	19	12	7	6	6	7
2020	30	10	20	11	11	8

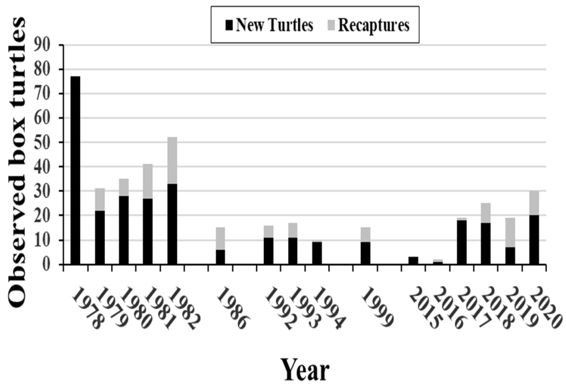

Figure 1. Number of Woodland Box Turtles (*Terrapene c. carolina*) captured each year of active study in southeastern Pennsylvania, USA.

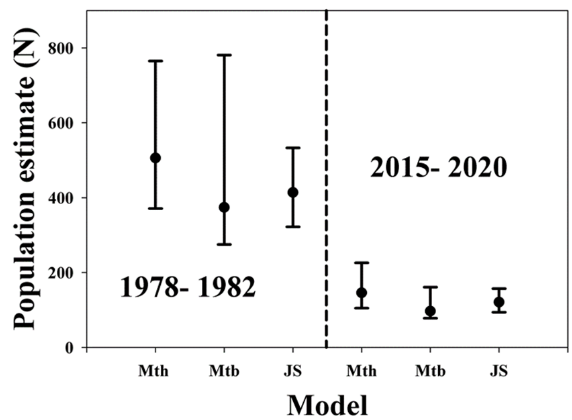

Figure 2. Population size estimates of Woodland Box Turtles (*Terrapene c. carolina*) at the study site in southeastern Pennsylvania, USA, from the early and most recent periods of individual mark-recapture study. JS indicates population estimates from the open Jolly-Seber/POPAN model, M_{th} indicates population estimates from the Continuous-time Heterogeneity Model, and M_{tb} indicates population estimates from the Continuous-time Behavioral Model. Error bars represent 95% confidence intervals of population estimates.

the 2015–2020 period was 1.26 M: 1.00F (55.7% male). The difference in sex ratios between time periods was not significant ($X^2 = 0.931$, df = 1, $P = 0.335$). In the first 5 y of the study (1978–1982), staff re-captured many turtles, but over half of turtles found each season were newly encountered (Fig. 1). Over the following decades, encounters with box turtles declined. The annual number of individual box turtle observations after 1982 never again reached levels seen in years prior. The mean number of box turtle individuals observed annually during 1978–1982 was 47.2 ± 8.25 (standard deviation). Excluding the years when turtle observations were very low (2015–2016), the mean number of box turtle individuals observed annually in subsequent years where data were collected intentionally was 18.4 ± 5.9. In the 2015–2020 period, we documented 66 individual box turtles. In 2020, staff, volunteers, and visitors photographed 30 different individuals. We documented 10 of those 30 individuals in recent years, and eight of those 10 were observed as recently as 2019.

Population estimates: Jolly-Seber (POPAN).—For 1978–1982, the Jolly- Seber/POPAN model with the lowest AIC value (333.38) was one with constant survivorship only. An initial parameter value for survivorship was applied in the model, using an average value (0.84) for 12 Piedmont box turtle populations found in the literature (Roe et al. 2021). The model passed a combined Goodness-of-Fit test (RELEASE: Test 2 + Test 3) for survivorship (Test 2) and catchability (Test 3) assumptions ($X^2 = 2.89$, df = 8, $P = 0.941$). Individual tests for Goodness-of-Fit for catchability (Test 2) and survivorship (Test 3) also passed (Test 2: $X^2 = 0.425$, df = 3, $P = 0.935$, Test 3: $X^2 = 2.47$, df = 5, $P = 0.781$). The number of estimated individuals in the superpopulation (N*) was 414 individuals (standard error [SE] = 53.34), with a 95% confidence interval between 322–533 individuals (Fig. 2).

For 2015–2020, the Jolly-Seber/POPAN model with the lowest AIC value (167.88) was one with constant survivorship and constant capture probability. As was done with the 1978–1982 estimate, an initial value of 0.84 was supplied for annual survivorship. The model passed a combined Goodness-of-Fit test (RELEASE: Test 2 + Test 3) for survivorship (Test 2) and catchability (Test 3) assumptions ($X^2 = 3.37$, df = 9, $P = 0.948$). The number of estimated individuals in the superpopulation (N*) was 121 individuals (SE = 15.88), with a 95% confidence interval of between 94–157 individuals (Fig. 2). According to these estimates, there has been a decline in the population of box turtles of approximately 71% between 1978–1982 and 2015–2020.

Population estimates: continuous time/closed population.—In the heterogeneity model (M_{th}), the CT median N for 1978–1982 was 506 individuals, with a 95% confidence interval between 371–765 (Fig. 2). For 2015–2020, the CT estimate of N using the M_{th} model was 146 individuals, with a 95% CI between 105–226 individuals. For the behavioral model (M_{tb}), the CT median N for 1978–1982 was 374 individuals, with a 95% CI between 275–781. The population estimate for 2015–2020 using M_{tb} was 97 individuals, having a 95% CI between 78–161. Comparing within models between 1978–1982 and 2015–2020, the M_{th} estimates indicate a population decline of about 71.2%, while those from the M_{tb} estimates suggest a decline of about 74.1%.

Discussion

Our estimates indicate a box turtle population decline of 70% or greater within the last 40 y at our site. While due caution should be exercised in using our estimates as exact population size or density measures, we are confident that the comparison between the population relative sizes of the two time periods is valid, and that a steep decline in box turtle population has occurred during the course of the study. This substantially exceeds the 30% decline over 50 y, or approximately three generations, suggested by the IUCN (van Dijk 2011). Several other long-term studies demonstrate similar declines in box turtle population size (e.g., Williams and Parker 1987; Hall et al. 1999; Dodd 2001), though this study represents a more recent assessment. In terms of timing, a substantial and lasting reduction in box turtle encounters by staff occurred during the early 1980s.

As CT-type data increases in importance and prevalence (sighting-type data, camera trap information), the need for determination of the utility of these methods has increased as well. Consensus on the usefulness of these methods does not yet exist in the literature, as how CT methods influence estimates is currently unclear (Borchers et al. 2014). While models from both discrete and continuous time mark-recapture models produced varying estimates of population size for box turtles at our site, the degree of decline estimated within models was remarkably similar. Population size estimates from the open Jolly-Seber/POPAN model were intermediate between the closed CT M_{th} and M_{tb} models. For both periods, estimates from the M_{th} model exceeded those of the M_{tb} model. Confidence intervals for the CT models were much larger than the Jolly-Seber/POPAN model. Actual numeric population estimates from the Jolly-Seber/POPAN open population model are bounded most narrowly by 95% confidence intervals. Strong evidence for violation of the equal catchability assumption was found in the hettest procedure for the CT method, for both time periods. Heterogeneity of capture of box turtles is plausible because the ranges of some turtles are heavily used by staff and volunteers, while the ranges of other observed turtles are not heavily used, or only to a low degree. Therefore, consideration of heterogeneity is warranted. Behavioral effects modeled in M_{tb} can be seen as a special case of the heterogeneity model M_{th} (Schofield et al. 2018), as heterogeneity of capture and behavioral impacts may be indistinguishable from mark-recapture data alone. As shown by Schofield et al. (2018), there is substantial sensitivity of the probability model outcome (N) to unknown input parameters, and caution should be exercised in interpreting estimates of N from the CT methods used. Nevertheless, it is important to note that regardless of the mark-recapture method used to estimate population size, the degree of decline observed in the box turtle population was consistent, ranging from 70.2% to 74.1%. As the primary goal of this paper was to assess population trends in the studied population of box turtles, this congruence of estimated trends lends confidence to our conclusion that there has been substantial decline across the two selected time periods at the study site.

Between sampling periods a non- significant trend was observed in M:F sex ratio, shifting from 0.925 to 1.259. Observed and theorized shifts in turtle sex ratios may be attributed to many potential causes, including unequal rates of road mortality between sexes (Gibbs and Steen 2005; Steen et al. 2006) and interactions between climate change and temperature sex determination (Janzen 1994). Should sex ratios continue to diverge in the direction suggested by the trend, the disproportionate loss of mature females from the population could limit future population resilience and reproductive output.

Habitat fragmentation, degradation and succession, more invasive plants, subsidized predators, fewer native food sources, vehicle strikes, disease, opportunistic removal, and poaching for the pet trade are all implicated as factors in the decline of Eastern Box Turtle populations (IUCN 2020). We believe many of the same factors may play a role in the decline observed at our site. Aerial photographs of the site are available beginning in 1939, and a transition from open and successional habitat to more mature forest occurred. Observations of habitat use suggest that habitat complexity and a mosaic of land cover types increase habitat suitability for Eastern Box Turtles (Dodd 2001; Kiester et al. 2015). Canopy-free areas required for nesting activities (Flitz and Mullin 2006; Fredericksen 2014; Moore et al. 2020) have declined but not disappeared at our site. One potential factor that may have also impacted box turtle populations is an increase in invasive species and exotic ground cover (e.g., Japanese Stilt Grass, *Microstegium vimineum*, Japanese Barberry, *Berberis thunbergii*, Wineberry, *Rubus phoenicolasius*, and Angelica Tree, *Aurelia elata*). Recent research examining forest plant cover has shown an ongoing dynamic shift to invasive species (especially *M. vimineum*) in plots over a range of disturbance. The degree of the observed shift was greater in disturbed plots, however (David Osgood and Stephen Mech, unpubl. data). Because of development in general, habitat for connected populations outside of the park may have experienced even greater changes; however, the box turtle population apparently survived through prior uses of the land, including clearing for charcoal production, agriculture, and timber operations. This suggests that factors other than habitat-related ones may be primary contributive causes of decline.

Increased contact with human populations has been implicated as a primary cause of decline in several other

Eastern Box Turtle populations (e.g., Williams and Parker 1987; Dodd 2001; Belzer 1997 as cited in Dodd 2001), as well as for other turtles (Garber and Burger 1995). Removal as pets, poaching for the pet trade, direct vehicle strikes, contact with off-leash dogs, and damage from other activities have all potentially increased at the site. Direct mortality of turtles from vehicle strikes occurs wherever roads and habitat intersect (Howell and Seigel 2019). We have observed dead turtles caused by vehicle strikes each year on roads around and within the site. In the 2020 season alone, we were aware of six fatal vehicle strikes of adult box turtles on roads in and adjacent to the site.

The term Shifting Baseline Syndrome is a general term referring to a loss of knowledge and expectation of the true productivity of an ecosystem due to a long decline in that productivity (Pauly 1995). A dimming perception exists that more box turtles were encountered 40 y ago and were found in more locations. The current study supports and quantifies this generally held assumption. In a world where box turtles are a rare and seemingly insignificant part of the ecosystem and have been for some time, it is understandable that people would conclude their importance to the ecosystem is low and have a low conservation priority. The apparent magnitude of decline (> 70%) in the population at our site, however, is staggering. Without proper implementation of management strategies to protect and support this population now, it may soon be lost. In publicly protected areas, coordinated and intentional strategies for box turtle preservation are possible but have been rarely implemented. Globally, conservation strategies and refuge designs have leaned towards preservation of mammal, amphibian, and bird populations (Roll et al. 2017). Extirpation of box turtle populations in protected areas represents a lost opportunity to actively manage and maintain core populations, which can act as a source to other surrounding areas.

Potential components of a more intentional approach to increase the chance of survival for this population may include several actions. While not an option for all highways and roads, roads would be made safer for turtles through the installation of barriers and culverts, which have been shown to reduce highway mortality in similar terrestrial and freshwater chelonian species (Ruby et al. 1994; Boarman and Sazaki 1996; Aresco 2005; Huijser et al. 2017; Heaven et al. 2019). Maintaining diverse, native landscapes and retaining areas of canopy-free nesting habitat is essential (Flitz and Mullin 2006; Fredericksen 2014; Moore et al. 2020). Informed mowing practices to protect turtles and other wildlife have been developed (e.g., Massachusetts Division of Fisheries and Wildlife [MDFW]. Natural Heritage and Endangered Species Program. 2009. Mowing Advisory Guidelines in Rare Turtle Habitat. MDFW. Available from https://www.mass.gov/doc/mowing-guidelines-in-rare-turtle-habitat/download [Accessed 8 February 2021]). Importantly, education of visitors and the general public regarding the status of this popular and charismatic (Dodd 2001; Lovich et al. 2018) species is an essential ingredient for mobilizing public support of preservation efforts and preventing harmful human contact. Such implementations could be a substantial part of a range-wide box turtle conservation plan that addresses the needs of this species directly, where such measures can be implemented. Box turtles represent an ancient lineage, which occupies a unique niche and set of roles, some of which are most likely unknown, in the forests of North America. If this is to be the case in the future, intentional management strategies for box turtle survival need to supplant passive management actions.

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