First Year Survival of Hatchling Eastern Box Turtles (*Terrapene carolina carolina*) at Their Northern Range Limit in Michigan's Lower Peninsula

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Abstract.—As adult turtle mortality increases as a result of anthropogenic threats, understanding the survival of younger age classes may help mitigate population declines. We radiotracked hatchling Eastern Box Turtles (*Terrapene carolina carolina*) through the first year of life in a Michigan population, located on the northern edge of their range. We monitored 60 hatchlings for between 2 and 333 d and estimated annual survival using known-fate survival estimates. From 2013 to 2015, 14 hatchlings (23%) were depredated, 19 hatchlings (32%) died because of exposure, and 2 hatchlings (3%) were crushed by motor vehicles. Survival decreased through the first year of life with a drop in survival probability from nest emergence in the autumn, before it reached 50% during overwintering (day 50 = 0.503; SE = 0.067), then again decreased with spring emergence and ending with 0% survival (day 333 = 0.0). Hatchlings that emerged in September survived up to 107 d longer than hatchlings that emerged in October, and larger hatchlings had a significantly higher probability of survival over smaller individuals. No small hatchlings survived through overwintering, whereas large hatchlings had a 0.82 (±0.095 SE) survival probability 228 d posthatching. Threats to a species survival at the limits of its range are often different from those faced by populations centrally located within the range. Thus, studies should be conducted across the Eastern Box Turtle's range to determine how survival probabilities vary in populations experiencing different environmental conditions.

Turtles are one of the most globally threatened group of vertebrates, with 61% being threatened or extinct as a result of anthropogenic influences such as habitat fragmentation, over-exploitation for food and the pet trade, and the increased threat of global climate change (Gibbons et al., 2000; Nazdrowicz et al., 2008; Refsnider and Janzen, 2012; Lovich et al., 2018; Stanford et al., 2020). Life-history traits shared by most turtles exacerbate the effects of these stressors (Keevil et al., 2018). The majority of turtle species are long-lived, and it can take ≥10 yr for juvenile turtles to reach sexual maturity. Once sexually mature, individuals may only produce one or two clutches of eggs per year, and recruitment rates tend to be low (Galbraith et al., 1989; Congdon and Gibbons, 1990; Dodd, 2001).

Turtles typically experience the highest mortality rates during the embryonic, hatchling, and early life stages (Gibbons, 1987; Heppell et al., 1996; Perez-Heydrich et al., 2012). In a 3-d study of hatchling emergence conducted in northwestern Illinois, 41% of hatchling Snapping Turtles (*Chelydra serpentina*) were presumed dead by the end of a 3-d observation period (Janzen, 1993). Similarly, Paterson et al. (2012) found 58% of Wood Turtle (*Glyptemys insculpta*) and 89% of Blanding's Turtle (*Emydoidea blandingii*) hatchlings died before their first overwintering. In a multiyear study conducted by Hammer (1969), only 3% of hatchling Common Snapping Turtles survived the first year and of those yearlings, only 17% survived to 2 yr of age. However, survival rate increases rapidly as turtles grow and age, with Common Snapping Turtles achieving a survival probability of >0.65 by age 2 (Brooks et al., 1988; Congdon et al., 1994). Thus, like many other iteroparous species, the persistence of most turtle species relies on the adult age-classes' high survival rates to reproduce multiple times throughout their lives, compensating for the low survivorship of younger age-classes (Iverson 1991a; Congdon et al., 1993, 1994).

Much of the previous research concerning annual survival of North American turtles has focused on the adult age-class (Metcalf and Metcalf, 1979; Iverson, 1991b; Hall et al., 1999; Fredericksen, 2014; Agha et al., 2017). However, recent anthropogenic impacts (e.g., habitat loss, habitat fragmentation, overharvest) have increased adult mortality, straining populations that rely on high adult survivorship rates (Gibbons et al., 2000; Lovich et al., 2018). Mitigation is necessary to restore declining populations, which will require information on vital rates of all age classes. Thus, there is a need to fill existing information gaps regarding the survival of the early life stages of North American turtle populations to accurately assess population viability and determine how best to restore populations (Gibbons et al., 2000; Lovich et al., 2018).

Survival studies focusing on hatchling turtles have their own unique challenges. First, hatchling turtles are small and highly cryptic, making traditional capture and tracking techniques difficult. However, advances in radiotelemetry technology, chiefly decreased transmitter size, have allowed researchers greater opportunities to collect information on movement and survival of hatchling turtles over a biologically relevant period of time (Forsythe et al., 2004; Paterson et al., 2012; Michell, 2015). Information on hatchling survivorship will be important for accurately assessing population health and making informed management decisions.

Our study focused on understanding hatchling survival in Eastern Box Turtles (*Terrapene carolina carolina*; Fig. 1a), one of the most widespread terrestrial turtle species in the United States, with a large geographic range that covers much of the northeastern and midwestern United States (Dodd, 2001; Wilson and Ernst, 2008). Despite the species' broad geographic range, Eastern Box Turtles are protected in many states because of their continued population declines due to habitat loss, road mortality, and poaching (Harding, 1997; Hyde, 1999; Wilson and Ernst, 2008). Eastern Box Turtle embryos exhibit both temperature-dependent sex determination and temperature-dependent developmental rates (Burger, 1976; Head et al., 1987; Ewert and Nelson, 1991; Janzen and Paukstis, 1991; Charnov and Bull, 1997; Dodd, 2001). Like many turtle species, to maintain optimal

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Study Area.—Our study area was located within Manistee National Forest (MNF) in Michigan's Lower Peninsula. The MNF lies at the northern limit of the Eastern Box Turtle's range and primarily comprises National Forest System Land (United States Department of Agriculture Forest Service [USFS]) interspersed with private inholdings. MNF is managed for multiple uses including recreation, wildlife habitat, timber production, watershed quality improvement, and fuel management (USDA Forest Service, 2006). MNF has four distinct seasons with a generally wet, temperate climate. Yearly rainfall averages 99.6 cm while yearly snowfall averages 322.4 cm. Temperatures within MNF range from 1.7°C to 13.8°C (Midwestern Regional Climate Center, 2016).

Our study area in MNF is primarily dry-mesic northern forest consisting of Jack Pine (*Pinus banksiana*), Red Pine (*Pinus resinosa*), Red Maple (*Acer rubrum*), and various oak species (*Quercus* spp.) with small (0.5–50 ha) forest openings located throughout. Forest openings within MNF are typically natural oak savanna or pine barrens, managed through prescribed fire, mechanical brushing, mowing, and nonnative invasive species treatments. Openings consist of sandy soils covered with lichens (*Cladonia* spp.), grasses (*Andropogon* spp.), sedges (*Carex* spp.), bracken fern (*Pteridium* spp.), low bush blueberry (*Vaccinium angustifolium*), and sparse shrubs (e.g., *Hamamelis* and *Prunus* spp.).

We selected four natural forest openings within MNF historically used by Eastern Box Turtles as nesting areas, referred to as Turtle Bowl (TB), Savanna (SV), East–West (EW), and Gravel Pit (GP). Although the forest openings had previously been managed through controlled burns by the USFS, no management treatments were implemented during the duration of our study (2013–2015). The TB is a 1.9-ha, oval-shaped geological depression dominated by grasses (*Andropogon* spp.) mixed with large stretches of bare ground colonized by lichens. The TB has low canopy cover with few trees (*Quercus alba, Pinus banksiana,* and *Pinus strobus*) and a small number of shrubs (*Prunus virginiana* and *Vaccinium angustifolium*). The SV is the largest of the study forest openings (5.6 ha) and has relatively flat topography. The transition between forest opening and closed canopy forest was the least abrupt in SV, which held the largest density of trees (*Q. alba, P. banksiana,* and *P. strobus*) and the thickest shrub coverage (*P. virginiana, V. angustifolium, Andropogon* spp., and *Carex pensylvanica*) of the four forest openings. EW is a 0.9-ha rectangular-shaped opening with an approximately 60% to 80% slope running its entire length. Trees are sporadic around the margins of EW (*Q. alba, Quercus velutina,* and *P. banksiana*), and the center of the opening was a mosaic of open ground colonized by lichens and patches of *Andropogon* spp. GP is a 0.7-ha oval-shaped opening with topography similar to TB. Vegetation in GP is sparse, mainly consisting of invasive species like spotted knapweed (*Centaurea stoebe micranthos*), St. John's wort (*Hypericum perforatum*), and great mullein (*Verbascum thapus*). Although originally a natural forest opening, GP is the most heavily disturbed of the study openings as a result of frequent public use of recreational off-road vehicles. All nesting areas are located within a 3–4-km² area and are inhabited by a single Eastern Box Turtle population whose females show high rates of nest-site fidelity (Moore et al., 2020).

Nest Location and Radiotelemetry.—During the first 2 wk of June from 2013–2015, we monitored the four forest openings for nesting female Eastern Box Turtles. Visual surveys for nesting

FIG. 1. (A) A hatchling Eastern Box Turtle shortly after emerging from the nest in Manistee National Forest. (B) A hatchling Eastern Box Turtle fitted with a 0.5-g radiotransmitter on the posterior of the carapace using two-part epoxy.

thermal and hydrological conditions for embryonic development, female Eastern Box Turtles preferentially select forest openings or other open-canopy sites to lay their eggs (Williams and Parker, 1987; Janzen, 1994; Janzen and Morjan 2001; Flitz and Mullin, 2006; Hughes and Brooks, 2006; Burke and Capitano, 2011; Willey and Sievert, 2012, Altobelli, 2017). Eastern Box Turtle nests experience high predation rates from a variety of mammalian and insect predators (Dodd, 2001; Forsythe et al., 2004; Laarman et al., 2018). Following emergence from the nest, hatchling Eastern Box Turtles often do not disperse from forest openings, potentially leaving them exposed to overheating and desiccation (Madden, 1975; Laarman et al., 2018). Although turtle hatchlings are generally recognized as having high mortality rates and being vulnerable to predation (Butler and Sowell, 1996; Janzen et al., 2000; Nagy et al., 2015), few robust studies of Eastern Box Turtle hatchlings exist (but see: Madden 1975; Stickel and Bunck, 1989; Felix et al., 2008; Burke and Capitano, 2011; Laarman et al., 2018).

The objective of our study was to monitor hatchling Eastern Box Turtles throughout the first year of life at the species' northern range limit. Using data collected through radiotelemetry, we estimated annual survival with Kaplan–Meier models, creating known-fate survival estimates. Our goal was to provide novel insight into the survival of the Eastern Box Turtle yearling age class to inform future population viability analyses.

TABLE 1. The numbers of Eastern Box Turtle nests in each nesting area with hatchling emergence from 2013 to 2015, in northern Michigan.

	No. of nests per study opening			
Year	East–West	Gravel Pit	Savannah	Turtle Bowl
2013	4	4	3	6
2014	1	0	1	6
2015	3	4	3	3

females began at approximately 1900 h and continued throughout the night until eggs were deposited and covered with soil by the female turtle. Within 24 h of egg deposition, we installed predator-resistant exclosure boxes around each nest. Exclosure boxes were constructed using a wood frame with 6.35-mm-mesh steel hardware cloth fixed to the sides and top. Boxes were buried 20 cm into the ground and remained until hatchlings emerged. We began monitoring the nests daily for emergence events after 55 d of incubation. Once a hatchling was found at the surface of the nest, we collected morphometric data including midline carapace length (mm), maximum carapace width (mm), maximum carapace height (mm), midline plastron length (mm), and maximum plastron width (mm), using calipers. Each hatchling was fitted with a 0.35-g or 0.5-g radiotransmitter (model R1614, Advanced Telemetry Systems, Inc., Minnesota, USA) to the right posterior side of the carapace (Fig. 1b) using an animal-safe, clear, two-part epoxy adhesive (Gorilla Glue Company, Ohio, USA) to monitor first-year survival (Forsythe et al., 2004; Michell, 2015; Daly et al., 2018; Laarman et al., 2018). Combined weight of the radiotransmitter and epoxy did not exceed 8% of the hatchling's total body mass and did not appear to impede movement (Beaupre et al., 2004; Laarman et al., 2018). Following data collection and transmitter attachment, we released all hatchlings within 2 h after capture at the nest site.

We located each hatchling between 1–2 times/wk using radiotelemetry during the autumn activity season (from nest emergence to overwintering). If a hatchling's signal could not be detected, we would visually inspect the last recorded location for signs of activity or depredation. If no signal could be detected and the fate of the hatchling could not be determined, the individual was censored (i.e., lost) from the study.

Overwintering began when hatchlings were found burrowed into mineral soil or duff and movements ceased. During overwintering, predator-resistant exclosures were installed around each hatchling and monitored in the spring for reemergence. All hatchlings that survived overwintering were fitted with a new 0.35-g or 0.5-g R1614 radiotransmitter as described above. Hatchlings were located 1–3 times weekly until radio contact was lost or a mortality event occurred.

Statistical Analysis.—We used the survival data collected through radiotelemetry tracking of each hatchling to construct annual survival probabilities using nonparametric Kaplan–Meier survival estimators (Kaplan and Meier, 1958). The emergence time varied between and within nests, so we used a staggered-entry method (Pollock et al., 1989) that allowed for the right-censoring of individuals whose fates could not be determined as a result of signal loss (DeCesare et al., 2016). We considered all hatchlings at risk until death occurred and was confirmed by the retrieval of a carcass or radiotransmitter.

We constructed a cumulative survival curve for hatchlings within the MNF population to examine annual hatchling survival across the study period (2013–2015). Additional survival curve models included estimated annual survival by

nest, month of emergence (September or October), specific forest opening (TB, SV, EW, GP), and hatchling mass at emergence (small 5.5–7.0 g, medium 7.1–8.6 g, or large 8.7–10.2 g). We constructed mass classes using the first and third quartiles and the median of the range of hatchling masses measured from 2013 to 2015. We compared survival curves with two groups using log-rank tests. Survival curves with >2 groups were compared using pairwise log-rank tests with Holm's correction applied to control the family-wide error rate among comparisons (Holm, 1979). All analyses were conducted using the 'survival' package (Therneau, 2020) for Program R version 3.5.1 (R Core Team, 2020).

RESULTS

Hatchling Morphometric Data.—From 2013 to 2015, 38 Eastern Box Turtle nests across 4 study forest openings (EW $n = 8$, GP $n = 8$, SV $n = 7$, TB $n = 15$) were monitored for this study. The number of nests with hatchling emergence varied between years and between openings each year (Table 1), with a total of 18 nests having hatchlings emerge (EW $n = 4$, GP $n = 1$, SV $n = 4$, TB $n = 9$). The remaining 19 nests failed to produce hatchlings. Hatchling emergence began in late August and ended in late October. Only one hatchling emerged in the month of August across our study period (22 August 2013, TB opening) and represented the earliest hatchling emergence in this study. This hatchling could not be located 3 d after emergence and was thus not included in survival curves grouped by month of emergence. Over the course of the study period, we recorded the largest number of emergences during September ($n = 48$ individuals across all nests). Only 12 emergences were recorded in October, with the latest occurring on 25 October 2015.

Not including the August hatchling, we fitted 60 hatchling Eastern Box Turtles with radiotransmitters over the course of the study period (2013 $n = 26$, 2014 $n = 18$, 2015 $n = 16$), which were tracked for an average of 135.7 d (range = 2–333 d). From 2013 to 2015 we tracked 11 hatchlings in EW, 11 in SV, 4 in GP, and 36 in TB. The mean carapace length for marked hatchlings at hatch was 31.9 mm (SD = 1.98, range = 28.1–37.9), mean carapace width was 28.8 mm (SD = 1.91, range = 24.3–33.0), mean carapace height was 16.1 mm (SD = 1.60, range = 11.0–18.3), mean plastron length was 28.8 mm (SD = 2.34, range = 18.3–34.0), average plastron width was 23.1 mm (SD = 1.80, range = 19.3–28.5), and average mass at emergence was 7.97 g (SD = 1.00, range = 5.73–10.1).

Nest Emergence and Hatchling Survival.—We were unable to track any hatchling for a full year after emergence. However, we tracked a single, large individual from nest emergence on 18 September 2013 to 18 August 2014, a total of 333 d. This individual was presumed depredated because the carcass was never recovered and the transmitter was found covered in visible bite marks. Our cumulative Kaplan–Meier annual survival estimate for hatchlings predicted that the probability of hatchling survival decreased throughout the first year of life (Fig. 2). The probability of hatchling survival declined in the autumn, stayed constant during overwintering (day 50 = 0.503; SE = 0.067), and then decreased again throughout the spring season until reaching 0% survival (day 333 = 0.0; Table 2). From 2013 to 2015, 14 hatchlings (23.3%) were depredated, 19 hatchlings (30.6%) died because of exposure, and two hatchlings (3.2%) were found on the side of a dirt road adjacent to TB crushed by motor vehicles. Twenty-seven hatchlings (45%) were censored from our study because of transmitter signal loss or the absence of evidence to
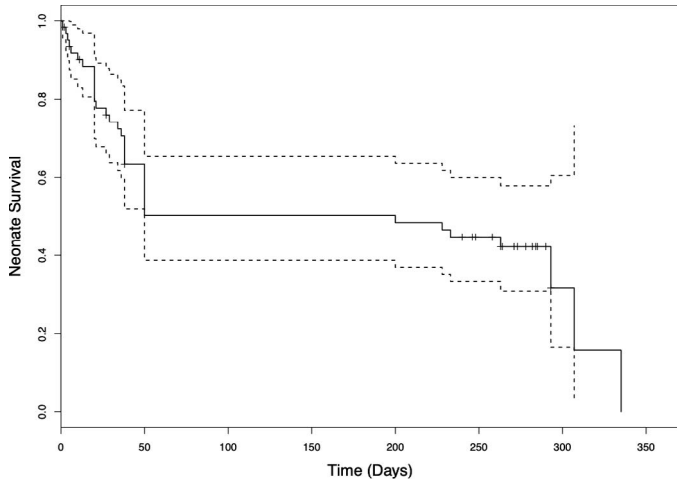
FIG. 2. Kaplan–Meier estimation of annual survival for Eastern Box Turtle hatchlings in Manistee National Forest for the 2013–2015 cohorts. Dashed lines indicate 95% confidence intervals with addition signs (+) representing dates when hatchlings were censored from study. Day 1 represents earliest hatchling emergence for the study period (22 August).

determine whether the hatchling had been depredated; however, it is possible that many of these individuals could have survived. The small sample size at our last survival estimate (day 307 = 0.151; SE = 0.124) meant that there is uncertainty surrounding the 0% survival estimate recorded on day 333 (Table 2).

Kaplan–Meier Survival Among Years.—Probability of hatchling survival did not differ significantly by nest or nesting area but did differ between years (Fig. 3). Our 2014 survival estimate was significantly lower than 2013 ($P = 0.005$) and 2015 ($P < 0.001$) because in 2014 no hatchlings ($n = 15$) across our four study openings survived through overwintering. Thus, our survival estimate only accounts for the estimated survival during the

TABLE 2. Kaplan–Meier survival estimates, standard error, and 95% confidence intervals for Eastern Box Turtle hatchling annual survival in Manistee National Forest in Michigan's Lower Peninsula for all individuals radiotracked from the 2013–2015 cohorts. Day 1 represents earliest hatchling emergence for the study period (22 August).

| Day	No. at risk	No. deaths	No. censored	Survival	SE	95% CI
1	62	1	1	0.984	0.016	0.953–1.000
3	60	1	0	0.967	0.023	0.924–1.000
4	59	1	0	0.951	0.028	0.899–1.000
5	58	1	0	0.935	0.032	0.875–0.999
6	56	1	1	0.918	0.035	0.852–0.990
10	55	1	0	0.901	0.038	0.829–0.980
13	51	1	0	0.884	0.041	0.806–0.969
20	50	5	0	0.795	0.053	0.698–0.906
21	45	1	0	0.778	0.055	0.678–0.892
27	44	1	1	0.760	0.056	0.658–0.878
29	42	1	0	0.742	0.058	0.637–0.864
34	41	1	0	0.724	0.059	0.617–0.849
36	40	1	0	0.706	0.061	0.597–0.834
38	39	4	1	0.633	0.064	0.520–0.772
50	34	7	0	0.503	0.067	0.387–0.653
200	27	1	0	0.484	0.067	0.369–0.636
228	26	1	0	0.466	0.067	0.351–0.618
233	25	1	6	0.447	0.067	0.333–0.600
263	18	1	13	0.422	0.068	0.308–0.578
293	4	1	1	0.317	0.104	0.166–0.605
307	2	1	0	0.158	0.124	0.034–0.731
333	1	1	0	0.000	——	——
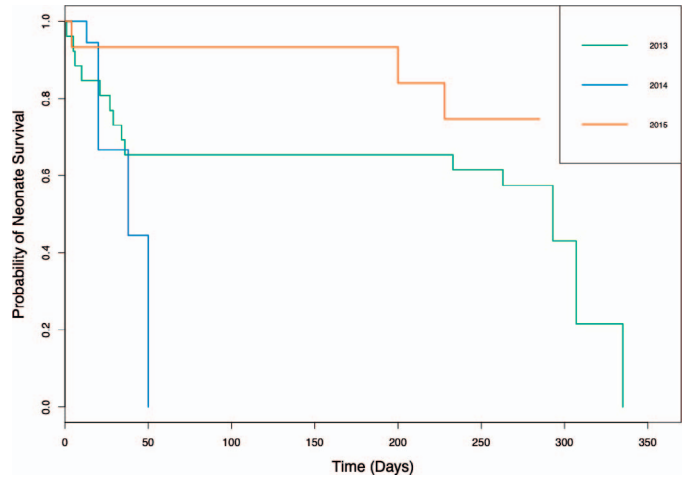
FIG. 3. Kaplan–Meier estimations of annual survival for Eastern Box Turtle hatchlings in Manistee National Forest separated by cohort year. Day 1 represents the first date of hatchling emergence per study year.

autumn activity period, ending on day 49 with a survival estimate of 0.444 (SE = 0.117). The 2014 survival estimate was similar to that in 2013 autumn (0.630; SE = 0.093), but lower than in 2015 (0.938; SE = 0.061; Fig. 4). However, Kaplan–Meier models for the 2013 and 2015 cohorts did not differ significantly ($P = 0.322$).

Kaplan–Meier Survival Between Months of Emergence.—Survival estimates predicted a significantly greater survival of hatchlings that emerge during September ($P < 0.001$; Fig. 3). Hatchlings that emerged from nests in the month of September had a higher rate of survival across the first 333 d outside of the nest than did those that hatched in October. Further, hatchlings that emerged in September survived an additional 107 d over hatchlings that emerged during the month of October (Fig. 5).

Kaplan–Meier Survival Among Mass Classes.—Of the 60 hatchling turtles fitted with radiotransmitters, 14 (23.3%) were categorized into the small mass class (5.5–7.0 g), 29 (48.3%) in the medium mass class (7.1–8.5 g), and 17 (28.3%) in the large mass class (8.7–10.2 g). We detected a significant survival advantage for hatchlings in the largest mass class when compared with those in both the small ($P = 0.0006$) and medium
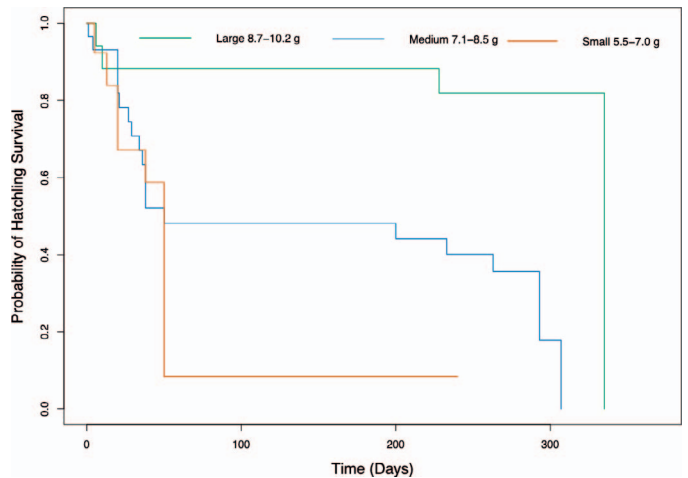

FIG. 4. Kaplan–Meier estimations of annual survival for Eastern Box Turtle hatchlings in Manistee National Forest for the 2013–2015 cohorts separated by month of emergence. Day 1 represents the date of first hatchling emergence in each month.
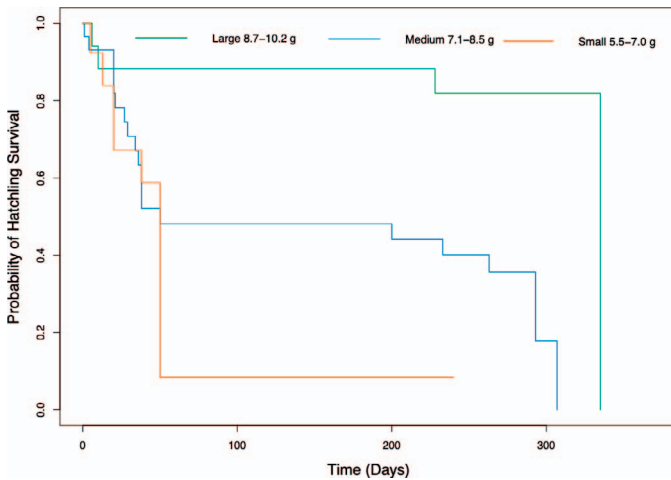
FIG. 5. Kaplan–Meier estimations of annual survival of Eastern Box Turtle hatchlings in Manistee National Forest for the 2013—2015 cohorts separated by mass class (small 5.5–7.0 g, medium 7.1–8.6 g, and large 8.7–10.2 g). Day 1 represents the first date of hatchling emergence for each mass class.

($P = 0.007$) mass classes (Fig. 5). Large hatchlings had the highest probability of survival before dropping to 0% by day 333 (autumn $= 0.941 \pm 0.057$; overwinter $= 0.882 \pm 0.078$; spring $= 0.819 \pm 0.095$; Fig. 5). However, there was no significant difference in the probability of survival between the small and medium mass classes ($P = 0.174$).

DISCUSSION

Hatchling Survival Estimates.—Our survival model estimated that hatchling Eastern Box Turtles within our observed population experience the largest drop in survival during the autumn activity season. Hatchling survival continued to decrease through the spring activity season. However, the interpretation of survival estimates during the spring activity season is complicated by the large increase in censored hatchlings from our study because their fates could not be determined because of radio failures, undetected predation, or individuals moving out of the detectable signal range. Thus, survival estimates in the spring activity season could be overly conservative because we were only able to use the survival data from the seven individuals of which fates were known. It is possible that many of the censored hatchlings survived the spring activity season but experienced radiotransmitter failure. Hatchling survival within the MNF population ranges from 43.6%, if all censored individuals did in fact survive the first year, to the 0% survival reported by our estimates, which removed all hatchlings with unknown fates from the analysis. Hatchling movements and dispersal from the forest openings also dramatically increased during the spring activity season, which could have negatively influenced our ability to track and locate the hatchlings through the forest, while also potentially exposing them to predators (Laarman et al., 2018). There are potentially multiple forces leading to this drop in survivorship, but exposure to suboptimal environmental conditions and predation were the main sources of mortality for hatchlings with known fates during our study period.

Survival Between Years.—Overwintering mortality is considerable for Eastern Box Turtle hatchlings at northern latitudes, as evidenced by the deaths of our entire 2014 hatchling cohort during winter. Many species of hatchling turtles in North America are known to survive winter through super-cooling or freeze tolerance, but most species only possess a modest capacity for super-cooling in the first few weeks after hatching and do not tolerate freezing for long periods of time, thus relying on the insulating properties of soil and snowpack to maintain higher temperatures (Costanzo et al., 2001; Packard and Packard, 2001). During the autumn and winter of 2014, our study sites experienced unseasonably early freezing temperatures, causing the ground to freeze quickly in the absence of snow cover. Hatchling Eastern Box Turtles are unable to burrow into the soil to any appreciable depth, thus snow cover provides an important insulating layer and likely facilitates hatchling survival through the winter by preventing sudden drops in temperature or long periods of freezing, both of which lead to hatchling death (Breitenbach et al., 1984; Claussen et al., 1991). Although the complete loss of a cohort was initially startling, mortality due to extreme winter weather events may be one factor limiting any northward range expansion of Eastern Box Turtles (Root, 1988; Stevens, 1989).

Predation was the second largest cause of hatchling mortality in our study. Roughly 15% of hatchling Eastern Box Turtles were verified as depredated, but this estimate is likely low because many hatchlings were lost, and predation was likely. Hatchlings remained within natal forest openings or took shelter along the edges of the forest opening, leaving them concentrated together and vulnerable to predators that frequently hunt in edge habitat (Laarman et al., 2018). Although not directly observed feeding on the radioed hatchlings, suspected predators include small mammals (e.g., Mice [*Mus musculus*] and Chipmunks [*Tamias striatus*]) and mesopredators (e.g., Raccoons [*Procyon lotor*] and Opossums [*Didelphis virginiana*]) on account of clear bite marks found on recovered radiotransmitters. Transmitters were often found with scute scales still attached and were left meters away from the last recorded hatchling location. Additionally, two transmitters were tracked to the canopy of trees that were located greater than double the longest recorded distance traveled by any hatchling during our study. Avian predation of hatchling turtles has been observed and is likely the explanation for both the large distance between the last observed location and how high in the tree the transmitter was located (Wilson, 1991; Janzen et al., 2000). Although hatchling survival declined throughout the activity season, survival rates during overwintering in 2013 and 2015 were stable. However, it should be noted that the chance of overwinter depredation of the hatchlings was removed through the use of exclosures.

Survival Between Seasons.—Earlier emergence from nests increases the probability of survival through the first year of life. Hatchlings that emerged from nests in September had a higher probability of survival across the first 333 d outside of the nest than did those that emerged in October, by an additional 107 d (Fig. 3). Further spatial analysis conducted on this population by Laarman et al. (2018) found that hatchlings that emerged earlier in the season also traveled further from the nest. By emerging from the nest earlier, it is possible that hatchlings have more time to search for suitable overwintering locations, thus increasing their probability of survival. This could explain the overwinter die-off of the 2014 cohort, many of which emerged during October, and may have been left exposed during the freeze (Costanzo et al., 1998).

Hatchling turtles often ingest soil and eggshell during the hatching process (Packard et al., 2001; Terebiznik et al., 2020), which could increase the likelihood of freezing to death.

Moisture within the soil can freeze at relatively high subfreezing temperatures, and as a result, ice can form in the gut of hatchling turtles (Costanzo et al., 2008). Ice could then propagate across the lining of the stomach, leading to the formation of ice in the extracellular fluids, ultimately causing death (Costanzo et al., 1998, 2000a, 2000b; Packard and Packard, 2001). The early freeze during the autumn of 2014 likely did not allow the hatchlings time to purge the contents of their gut, which is typically signaled by the gradual decrease in temperatures through autumn and into winter, in order to prevent the internal spread of ice (Packard et al., 2001). Although Eastern Box Turtle adults are known to be tolerant of freezing for short periods of time (Costanzo and Claussen, 1990), and hatchlings may be as well, this pattern of early, rapid, and prolonged freezing is likely lethal.

Survival between Mass Classes.—Larger hatchling Eastern Box Turtles have a higher probability of survival through the first year of life when compared with smaller individuals (Fig. 4). Our results align with the "Bigger is Better" hypothesis, where larger offspring of vertebrate species, including birds and nonavian reptiles, have a higher chance of survival when compared with smaller individuals within the same cohort (Ashton and Feldman, 2003; Krist, 2011). Though Congdon et al. (1999) did not find evidence for directional selection favoring large body size in hatchling Snapping Turtles, Janzen (1993) reported a positive relationship between hatchling size and survival in a population of Snapping Turtles in the midwestern United States. Paterson et al. (2014) found that smaller Wood and Blanding's Turtle hatchlings had higher survival rates from nesting to overwintering, which they attributed to differences in retreat-site selection, predator detection, or a performance advantage to being smaller. Discrepancies in results among studies illustrate the varied selection pressures experienced by different populations within a species across its range, and across different turtle species. Compared with smaller hatchlings, larger hatchling Eastern Box Turtles in MNF could have higher survival rates through increased locomotory capability (Miller et al., 1987; Jayne and Bennett, 1990; Janzen et al., 2007). If larger individuals have a locomotory advantage, they could be strongly selected for at the northern limit of a species range (Claussen et al., 1991). Michigan is the northern limit of the Eastern Box Turtle range, so there would be a strong survival advantage for larger hatchlings if they are better able to quickly disperse out of natal forest openings, seek improved refugia, and dig deeper into the substrate to escape potentially fatal early winter freezes.

Although we did not directly measure yolk mass at emergence, larger hatchlings typically had less yolk exposed at the time of emergence. Having fully absorbed their yolk could provide larger hatchlings with a survival advantage during early season cold snaps because ice crystals could form in exposed yolk and subsequently spread to the vital organs (Packard et al., 1999). We did not directly test whether fully internalized yolk confers a hatchling survival advantage, but all hatchlings in the 2014 cohort were in the small and medium mass classes and did not survive through overwintering. Our results contradict the findings of Costanzo et al. (2004), who postulated that smaller hatchling turtles could supercool more readily, providing an advantage to survival through hibernation over larger hatchlings. However, supercooling is only possible in the absence of ice nucleating agents (Packard and Packard, 2003). Thus, hatchling Eastern Box Turtles exposed to ice nucleating agents such as soil, ice, and other fine particulate during overwintering would be unable to supercool and is

likely the reason our findings contradict those of Costanzo et al. (2004). More recently, Mitchell et al. (2015) found a positive relationship between hatchling Painted Turtles body size and survival during overwintering. Thus, the overwinter die-off of the entire 2014 cohort could provide evidence that larger mass at emergence improves survival of Eastern Box Turtle hatchlings along their northern range limits.

Conclusions.—We identified the major sources of mortality (exposure, predation, vehicles) facing hatchling Eastern Box Turtles at the northern limit of their range within the midwestern United States. Depredation is a well-documented threat to turtle nest success, but we show that depredation is also a considerable source of hatchling mortality. We hypothesize that with the limited number of large forest openings available to nesting female Eastern Box Turtles in MNF, the openings we monitored could be concentrating the nesting activities of the local population of Eastern Box Turtles. As a result, the impact of predators surrounding nest sites could limit recruitment of Eastern Box Turtles in our study area. To mitigate the effects of depredation, managers are increasing the size and number of forest openings within MNF to provide more suitable nesting habitat for female Eastern Box Turtles, distributing nests and hatchlings across the landscape in an effort to reduce targeted depredation of future cohorts.

The challenges to a species' survival at the limits of its range are often different from those faced by the same species more centrally located within the species range (Parmesan et al., 2005). Our study found that exposure to freezing temperatures during the first activity season out of the nest negatively affected the probability of survival of smaller hatchlings and hatchlings that emerged late in the season, but studies similar to ours should be conducted across the geographic range of the Eastern Box Turtle because environmental conditions experienced by hatchlings (and consequently survival rates) are likely highly variable. As the likelihood of unseasonal extreme weather events increases with climate change (Stott, 2016), it is important that future studies focus on how our changing climate could influence the survival of the most vulnerable age class of many turtle species.

Huron–Manistee National Forest Biologists before sampling began.

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APPENDIX 1. Comparison of Kaplan–Meier endpoint survival estimates, standard error, and 95% confidence intervals for the 2013, 2014, and 2015 Eastern Box Turtle hatchling cohorts. Survival estimates are separated into the autumn activity period, overwintering period, and spring activity period for each year.

	2013 (n = 27)			2014 (n = 18)			2015 (n = 17)		
	Survival	SE	95% CI	Survival	SE	95% CI	Survival	SE	95% CI
Autumn	0.630	0.093	0.472–0.841	0.444	0.117	0.265–0.745	0.938	0.061	0.826–1.000
Overwinter	0.593	0.095	0.433–0.810	0.000	—	—	0.844	0.104	0.662–1.000
Spring	0.000	—	—	0.000	—	—	0.750	0.128	0.537–1.000

APPENDIX 2. Comparison of Kaplan–Meier survival estimates, standard error, and 95% confidence intervals for hatchling Eastern Box Turtles in Manistee National Forest in Michigan's Lower Peninsula for the 2013–2015 cohorts separated by month of emergence.

	September (n = 48)			October (n = 12)		
Day	Survival	SE	95% CI	Survival	SE	95% CI
1	0.979	0.021	0.940–1.000	1.000	———	1.000–1.000
3	0.979	0.021	0.940–1.000	1.000	———	1.000–1.000
50	0.576	0.065	0.619–0.877	0.208	0.130	0.061–0.710
200	0.576	0.065	0.619–0.877	0.104	0.098	0.016–0.663
228	0.576	0.065	0.619–0.877	0.000	———	———
263	0.522	0.077	0.391–0.696			
307	0.196	0.152	0.043–0.899			
333	0.000	———	———			

APPENDIX 3. Comparison of Kaplan–Meier survival estimates, standard error, and 95% confidence intervals for hatchling Eastern Box Turtles in Manistee National Forest in Michigan's Lower Peninsula for the 2013–2015 cohorts separated by mass class at emergence (small 5.5–7.0 g, medium 7.1–8.6 g, and large 8.7–10.2 g).

Day	Survival	SE	95% CI
Small mass class			
5	0.923	0.074	0.789–1.000
13	0.839	0.105	0.658–1.000
20	0.671	0.135	0.453–0.996
38	0.587	0.142	0.366–0.943
50	0.084	0.081	0.013–0.547
Medium mass class			
1	0.966	0.034	0.901–1.000
4	0.931	0.047	0.843–1.000
20	0.819	0.073	0.687–0.976
21	0.782	0.079	0.642–0.953
27	0.745	0.084	0.598–0.928
29	0.708	0.087	0.556–0.901
34	0.670	0.091	0.515–0.873
36	0.633	0.093	0.475–0.843
38	0.521	0.096	0.363–0.748
50	0.481	0.097	0.325–0.714
200	0.441	0.097	0.287–0.678
233	0.401	0.096	0.251–0.641
263	0.356	0.095	0.212–0.601
293	0.178	0.135	0.041–0.784
307	0.000	—	—
Large mass class			
6	0.941	0.057	0.836–1.000
10	0.882	0.078	0.742–1.000
228	0.819	0.095	0.653–1.000
333	0.000	—	—

APPENDIX 4. Table of *P*-values of pairwise log-rank tests with Holm's correction applied to control the family wide error rates for survival between nests.

	2014A	2014C	2015A	2015B	2015F	2015G	2015H	2015I	2015L	C393S14#1	C393S14#2	C393S14#3	C393S14#5	C393S43#2	C393S43#3
2014C	0.613	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2015A	0.533	1.000	-	-	-	-	-	-	-	-	-	-	-	-	-
2015B	0.310	1.000	1.000	-	-	-	-	-	-	-	-	-	-	-	-
2015F	1.000	1.000	1.000	1.000	-	-	-	-	-	-	-	-	-	-	-
2015G	0.533	1.000	1.000	1.000	1.000	-	-	-	-	-	-	-	-	-	-
2015H	0.897	1.000	1.000	1.000	1.000	1.000	-	-	-	-	-	-	-	-	-
2015I	1.000	1.000	1.000	1.000	1.000	1.000	1.000	-	-	-	-	-	-	-	-
2015L	0.533	1.000	1.000	1.000	1.000	1.000	1.000	1.000	-	-	-	-	-	-	-
C393S14#1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	-	-	-	-	-	-
C393S14#2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	-	-	-	-	-
C393S14#3	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	-	-	-	-
C393S14#5	0.108	1.000	1.000	1.000	1.000	0.897	1.000	1.000	1.000	1.000	1.000	1.000	-	-	-
C393S43#2	0.897	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	-	-
C393S43#3	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	-
2014E	0.076	0.276	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.276	1.000	0.276	1.000	1.000