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Growth and Survival of Wild and Head-Started Blanding's Turtles (*Emydoidea blandingii*)

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Blanding's Turtles (International Union for Conservation of Nature [IUCN] Endangered) are long-lived reptiles with delayed sexual maturity. Anthropogenic landscape changes have increased threats to juvenile turtles, resulting in unnaturally low recruitment. Head-starting has become a popular conservation strategy that aims to increase juvenile recruitment by avoiding the increased predation of the vulnerable nest and hatchling age class. However, there is still debate about whether or not it is an effective management tool. Assessments of head-starting are becoming more prevalent, but long-term studies are needed to critically evaluate the success of such interventions. In particular, information is needed on how head-starts fare compared to wild-hatched turtles. The Lake County Forest Preserve District (LCFPD) in northeastern Illinois initiated a long-term capture–mark–recapture project in 2004. As of 2018, 127 wild-hatched juvenile turtles had been captured (59 of which had been captured in multiple years) and 148 adult turtles had been captured (116 of which had been recaptured in multiple years). Since 2010, LCFPD has released 491 head-started turtles during the year following hatching, 138 of which have been recaptured during successive years. We used von Bertalanffy growth analysis to compare growth trajectories and Cormack-Jolly-Seber modeling techniques to compare survival rates of wild-hatched and head-started turtles. At release, head-started turtles were about the size of two-year-old wild-hatched turtles and grew in parallel to their wild-hatched counterparts. The top-ranked survival models demonstrated that survival increased with age for both wild-hatched (71–98%) and head-started turtles (63–90%), with overlapping confidence intervals. These results suggest that head-started juveniles perform similarly to like-aged wild-hatched juveniles despite head-starts having attained greater body size. We estimated adult survival to be 95% with an environmental variance of 0.0011 and stable or positive population growth (λ). Although the success of head-starting cannot be fully assessed until turtles are recruited into the adult population and successfully reproduce, patterns of head-start growth and survival provide positive intermediate measures of success. Our estimation of juvenile and adult survival, along with other demographic information from this population, will provide for more accurate population projections that will aid in evaluating conservation strategies for this population and potentially for Blanding's Turtles elsewhere.

MANY wildlife populations are in decline and in need of conservation interventions, but management strategies must be evaluated to ensure they are effective (Martin et al., 2018). The life history strategy of long-lived species with delayed sexual maturity, as found in many chelonians, presents unique challenges which require unconventional strategies for conservation (Canessa et al., 2016). Anthropogenic land cover changes have increased threats, especially to juvenile turtles (e.g., lack of suitable habitat, subsidized predators), resulting in unsustainably low juvenile recruitment (Gibbons et al., 2000). This has led many managers to focus on mitigating threats to this age class (Seigel and Dodd, 2000) in addition to adult survival, which has long been recognized for its importance to turtle population dynamics (Heppell, 1998).

Head-starting has become a popular conservation strategy for turtle management (Burke, 2015). The goal is to increase juvenile recruitment by incubating eggs and rearing hatchling turtles in captivity, thus avoiding predation during the vulnerable nest and hatchling stage. It is hoped that this will boost the number of young turtles entering the population and halt population decline. While evidence is accumulating that head-starting can be an effective management strategy (Burke, 2015; Thompson et al., 2020), direct comparisons of head-started and wild-hatched turtles are rare.

The Blanding's Turtle (*Emydoidea blandingii*) is a long-lived species of freshwater turtle for which head-starting has been used (Buhlmann et al., 2015; Green, 2015; Thompson et al., 2020). Populations of Blanding's Turtles face imminent threats including habitat loss and degradation, road mortality, and meso-predator release. This causes reduced adult survival and reduced recruitment of young turtles. This has resulted in their designation as Endangered by the IUCN (International Union for Conservation of Nature), under review in 2023 by the US Endangered Species Act, and endangered in Illinois (ESA, 1973, as amended; Congdon et al., 2008; IUCN, 2012; USFWS, 2015). Long-term data are required to properly evaluate the efficacy of head-starting as a management strategy. Although assessments of head-starting are becoming more prevalent (Carstairs et al., 2019; Thompson et al., 2020), analyses of growth and survival in comparison to wild-hatched turtles are generally lacking.

The LCFPD (Lake County Forest Preserve District) in northeastern Illinois initiated long-term capture–mark–recapture of Blanding's Turtles in 2004. In 2010, an analysis reported a low number of juveniles, an unsustainably high rate of nest predation, and low rates of adult survival (AR Kuhns, pers. comm.). An initial population viability analysis predicted that habitat management and predator removal alone were not sufficient to ensure population viability.

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Consequently, in 2011, LCFPD initiated a head-starting program to increase juvenile recruitment in tandem with other management strategies (e.g., habitat restoration, predator control) aimed at addressing threats to the population. These 14 years of intensive monitoring provide a unique dataset from which we can quantitatively analyze the success of head-starting (Thompson et al., 2020).

The overall goal of this study is to assess head-start growth and survival compared to wild-hatched juveniles to better guide the use of head-starting in Blanding's Turtle management. Growth and survival over the ca. 14-year juvenile stage is less well known than other demographic parameters for both wild-hatched and head-started Blanding's Turtles. Even in longer term studies, these younger age classes are infrequently encountered, aged, and then recaptured, making it difficult to accurately estimate their growth and survival. We first characterize growth of wild-hatched turtles through the attainment of reproductive maturity (Objective 1). The relationship between size and age of wild-hatched Blanding's Turtles has been characterized qualitatively in several populations, demonstrating a steady increase in size until sexual maturity (Germano et al., 2000; Pappas et al., 2000; Congdon et al., 2001; Lefebvre et al., 2011; Reid et al., 2016). By providing a statistical analysis of wild-hatched Blanding's Turtle growth, we establish a baseline for comparison among populations and with head-starts. We then compare growth of head-starts to that of like-aged juvenile wild-hatched turtles (Objective 2). Existing studies that have compared growth of wild-hatched juveniles and head-starts have been over short time frames and included only modest sample sizes (Arsenault, 2011; D'Entremont, 2014). Next, we compare survival of head-starts to that of like-aged juvenile wild-hatched turtles (Objective 3). In general, survival increases as turtles age (Enneson and Litzgus, 2008; Bulté et al., 2009; Spencer et al., 2017; Arsovski et al., 2018; Crawford et al., 2018; Feng et al., 2019). While estimates of juvenile survival are accumulating (e.g., Enneson and Lizgus, 2008; Arsovski et al., 2018; Hanscom et al., 2020), direct comparisons of the survival of head-starts and wild-hatched juveniles are rare. As with juvenile growth, comparisons of wild-hatched juvenile and head-start survival are often of limited duration and sample size (Arsenault, 2011; D'Entremont, 2014; Starking-Szymanski et al., 2018). Finally, we assess local adult survival, process variance in adult survival, and realized adult population growth (Objective 4). Adult survival in Blanding's Turtles is known with high precision from several studies (Congdon et al., 1993, 2001; Rubin et al., 2004; Ruane et al., 2008; Reid et al., 2016), but estimates of the environmental (process) variance in survival and realized population growth are lacking. Environmental variance describes how much of the temporal variance in survival can be attributed to environmental fluctuation (vs. sampling error), giving a more accurate estimate of year-to-year variation in survival, e.g., for population viability analysis (Beissinger and McCullough, 2002; Morris and Doak, 2002). Realized population growth, λ, provides a characterization of population dynamics that may not be evident from a time series of population estimates and is thus useful in detecting population increases or declines (Burnham and Anderson, 2002; Anderson, 2008). Estimation of process variance and realized population growth both require long-term data (Burnham and Anderson, 2002; Anderson, 2008), as is provided by LCFPD monitoring efforts.

Table 1. Yearly sampling effort, adult capture success, and head-start releases of Blanding's Turtles at SBCP. Little or no sampling occurred in 2011 and 2012. Releases of head-starts began in 2012 with the release of 83 head-starts, 12 of which were recaptured 19 times in subsequent years.

Year	Sampling effort (trap nights)	Adults captured (females, males)	Head-starts released (individuals recaptured, total number recaptured)
2004	473	9 (2, 7)	–
2005	2488	61 (18, 43)	–
2006	3438	69 (27, 42)	–
2007	2711	56 (21, 35)	–
2008	1638	37 (13, 24)	–
2009	3696	38 (17, 21)	–
2010	1636	24 (11, 13)	–
2011	0	–	–
2012	32	–	83 (12, 19)
2013	490	34 (15, 19)	102 (33, 51)
2014	741	26 (13, 13)	70 (28, 35)
2015	855	45 (22, 23)	66 (4, 5)
2016	1081	42 (24, 18)	52 (25, 32)
2017	1305	45 (24, 21)	118 (36, 36)
2018	1086	53 (23, 30)	74 (NA)
Totals	21,576	540 (230, 310)	565 (138, 178)

MATERIALS AND METHODS

Field methods.—Blanding's Turtle monitoring was initiated in 2004 within the Spring Bluff-Chiwaukee Prairie (SBCP) complex in Lake County, Illinois and Kenosha County, Wisconsin. SBCP is a protected natural area consisting of 215 ha of high-quality coastal wetland habitat (Ramsar, 2016) located along the coast of Lake Michigan. This land is managed by LCFPD, Wisconsin Department of Natural Resources, and The Nature Conservancy. Habitat management aimed at improving the site for Blanding's Turtles includes prescribed fire (ca. 37% burned each year from 2000–2018), chemical and mechanical removal of invasive plants (ca. 42% treated each year from 2007–2018), and predator (raccoon) removal (18–45 animals per year from 2013–2018; Urbanek et al., 2016).

From 2004 to 2018, turtles were captured using baited collapsible minnow traps (Promar, 30 × 30 × 60 cm, 0.6 cm mesh or similar) and by hand during the active season (April–August). Little or no trapping occurred during 2011 and 2012 (Table 1). Turtles were marked for future identification with Passive Integrated Transponder tags and notching of marginal scutes and a plastron photo was taken (Cagle, 1939; Buhlmann and Tuberville, 1998). Younger turtles (typically weighing less than 750 g) were assigned ages by counting growth rings from photos or from known hatch dates of turtles that were nest-caged (Castanet, 1988). Photos that could not be scored consistently by two independent observers were excluded (n = 40 older juveniles with indistinct growth rings). In Blanding's Turtles at other sites, it was found that growth rings can be used as a reliable proxy for age until the attainment of sexual maturity (Congdon and van Loben Sels, 1993; Germano and Bury, 1998; Germano et al., 2000). Within our study site, there are a few examples that support that growth rings are deposited annually in younger turtles (one individual recaptured after nine years with nine additional growth rings, four recaptured after two years with two additional growth rings, and one recaptured after one year with one additional growth ring). However, in other turtle species, especially in older individuals, it has been found that growth rings are not deposited annually (Wilson et al., 2003; Howell and Seigel, 2018). Sex of adults was determined by observing the concavity of the plastron (Graham and Doyle, 1979).

Head-starting.—LCFPD began a head-starting program at SBCP in 2011 with the goal of increasing juvenile recruitment by mitigating threats to the vulnerable nest and hatchling life stages. Generally, head-starting involves collecting eggs from wild telemetered adult females encountered during nesting forays, incubating the eggs in captivity, and then rearing the young turtles in captivity (Thompson et al., 2020). In 2012, LCFPD began releasing individually marked young turtles. Head-starts were individually marked by notching marginal scutes when the young turtles were released and either Passive Integrated Transponder tagging prior to release or upon subsequent recapture (detailed in Thompson et al., 2020). Releases have continued annually, numbering 52–118 first-year head-starts and 0–46 older head-starts per year (Table 1). We include only first-year head-starts in analyses presented here because of their larger sample size and more homogeneous initial size distribution.

Growth analysis of wild and head-started turtles.—Turtles are typically measured by carapace length (CL), the longitudinal distance between the front and back of the carapace (Bjorndal and Bolten, 1989). We used non-linear regression in SPSS to model growth in CL for known-aged animals (Germano et al., 2000; Arsenault, 2011). We measured age on the date of capture in fractional years, computed from 1 January of the hatch year, given that we do not know the actual hatch date of wild turtles (Andrews, 1982). We fit the data to a three-parameter von Bertalanffy growth equation: $CL_t = CL_A - (CL_A - CL_0)e^{-kt}$, where CL_t is carapace length at age t, CL_A is asymptotic carapace length, CL_0 is carapace length at time zero, k is the growth constant, and t is age in fractional years (Arsenault, 2011; Anthony et al., 2015; King et al., 2016). We first analyzed wild-hatched juveniles separately to characterize growth through adulthood (1–26 years of age). Although the oldest turtle we aged via growth rings was 13 years old, subsequent recaptures resulted in known-age turtles up to 26 yr. Then we compared growth of head-starts with that of like-aged wild-hatched juveniles (1–7 years of age). We used a dummy variable to distinguish wild-hatched turtles (0) from head-starts (1), thus allowing for inclusion of a fourth parameter, a, to adjust the age of head-starts relative to wild-hatched turtles: $CL_t = CL_A - (CL_A - CL_0)e^{-k(t+a)}$.

Survival analysis.—Capture–mark–recapture modeling techniques based on individual capture histories were used to estimate apparent survival rates (which is different from true survival because emigration is indistinguishable from mortality) for wild-hatched juveniles, head-started juveniles, and adult turtles in three separate analyses (Lebreton et al., 1992; McCallum, 2000; Cooch and White, 2019). Survival (φ) and recapture (p) rates were estimated using live recapture Cormack-Jolly-Seber models with the log link function (Cormack, 1964; Jolly, 1965; Seber, 1965; Cooch and White, 2019) in Program MARK (White and Burnham, 1999; White et al., 2001) and in R version 3.5.1 (R Core Team, 2017) through the *RMARK* package (Laake, 2013).

In all analyses, we created encounter histories for each individual animal by assigning a "1" if the animal was encountered that year and a "0" if they were not encountered. We performed goodness-of-fit tests on global models to assess if overdispersion was present in the data. If any lack of fit was detected, we adjusted for overdispersion with the largest estimate (furthest from 1) of the variance inflation factor ($\hat{c}$) following the recommendations of Cooch and White (2019). Candidate models were ranked by comparing Akaike's information criterion values adjusted for small sample size (AICc) or corrected quasi-Akaike information criterion (QAICc) if overdispersion was detected. We examined all top-ranked models within 2 ΔAICc or 2 ΔQAICc to determine whether model averaging should be employed to account for model uncertainty (Akaike, 1973; Burnham and Anderson, 2002).

Survival analysis of wild and head-started turtles.—Age-specific survival rates were estimated separately for wild-hatched juveniles and head-starts due to differences in time span (13 vs. 7 sampling occasions) and number of age groups (1–26 yr of age vs. 1–7 yr). To minimize overparameterization and data dredging, we employed a backward step-down model selection process (Burnham and Anderson, 2002; Brown et al., 2007; Cooch and White, 2019; Morin et al., 2020). We first optimized recapture (p) while using the most inclusive parameterization for survival (φ) from among candidate models. We then used the most parsimonious parameterization for recapture and evaluated alternative survival models. This step-down methodology provides more power to detect age effects and obtain precise estimates of survival (Lebreton et al., 1992; Brown et al., 2007; Briggs-Gonzalez et al., 2017; Arsovski et al., 2018; Morin et al., 2020).

We created annual encounter histories for wild-hatched juveniles from 2004–2018 with 2011 and 2012 omitted due to low trap effort, resulting in 13 sampling occasions and 12 intervals. Intervals were one year except for 2010–2013 (3 years). Turtles were grouped by age at initial capture and only wild-hatched turtles that were initially captured as juveniles (≤ 13 yr) were included. The global model for wild-hatched juveniles included the discrete effect of age class and the additive effect of time on recapture probability. We only included the additive effect of time because recaptures spanned 14 years with only a few recaptures of any given age classes during each year. To avoid overparameterization, we considered a maximum of six age classes (1, 2–3, 4–6, 7–10, 11–14, 15+ yr) selected to provide similar size increments and sample sizes. The global model included age as a linear covariate of survival. In evaluating candidate models nested within this global model, we first optimized recapture by considering models with fewer than six age classes with and without the additive effect of time. Using the top-ranked model for recapture, we then evaluated models in which survival reached a plateau at successively younger ages (following Arsovski et al., 2018). Finally, we compared the top-ranked model that included age as linear covariate of survival with models that included age as a logarithmic or quadratic covariate or that included age as a discrete grouping variable (Arsovski et al., 2018).

For the analysis of head-started juveniles, we created annual encounter histories from 2012–2018 (releases of head-starts began in 2012), resulting in seven sampling occasions and six intervals. Year of release was treated as the first capture for head-started turtles. The global model for head-started juveniles included the discrete effect of age class and the interactive effect of age class and time on recapture probability. We included the interactive effect of time to account for observed complexity in year- and age-specific recapture numbers that suggested possible cohort (= year* age) effects. We considered a maximum of four age classes (1, 2, 3, 4+ yr post-release), selected to provide similar sample sizes, as the number released each year varied. The global model included age as a linear covariate of survival (ages 1–6+). In evaluating candidate models nested within this global model, we first optimized recapture by considering models with fewer than four age classes with the additive or interactive effect of time. As in the analysis for wild-hatched turtles, we used the top-ranked model for recapture and evaluated models in which survival reached a plateau at successively younger ages and varied models that included age as a logarithmic or quadratic covariate or that included age as a discrete grouping variation (Arsovski et al., 2018).

Survival and realized population growth of adult turtles.—We created encounter histories for adult turtles in an identical fashion as for wild-caught juveniles. Although some adults were affixed with radio transmitters, only trap and hand captures were utilized in the survival analysis. Adult turtles were grouped by sex, and individuals that were initially captured as subadults were included only after they reached adulthood. To test whether the cumulative effects of habitat management affected survival, we treated management as a dichotomous variable by allowing survival to differentiate early vs. late in our study (prior to 2010 when prescribed fire was the predominant management strategy vs. 2010 and beyond when prescribed fire was used in conjunction with chemical and mechanical control of invasive plants and predator removal).

We considered four global candidate models and selected the higher ranked of these global models for goodness-of-fit testing. The first global model included a sex-by-time interaction for survival and a sex-by-time interaction for recapture. We chose to test for an effect of time on recapture probability because of the extent of year-to-year variation in effort (Table 1). The second global model included a sex-by-time interaction for survival and a sex-by-effort interaction for recapture to determine whether sampling effort could be used as an environmental covariate to replace time and reduce the total number of parameters. The third global model included a sex-by-management interaction for survival and a sex-by-time interaction for recapture. The fourth global model included a sex-by-management interaction for survival and a sex-by-effort interaction for recapture. Candidate models included all models nested within all global models. We estimated variance components for adult turtle survival in Program MARK using the highest ranked model that included time-dependence for survival to determine temporal (process) variance in annual survival (Cooch and White, 2019).

We estimated realized population growth, λ, for the adult population using Pradel survival and population growth rate model in Program MARK (Pradel, 1996). We created a global model that included the interactive effect of sex and time on λ with survival and recapture parameterized as in the highest ranked model identified in our survival analysis (Cooch and White, 2019). Candidate models included all models nested within the global model.

Table 2. Number of captures by age class of wild-hatched Blanding's Turtles first encountered as juveniles (e.g., nine turtles first captured as members of age class 2 were captured a total of ten times over the course of this study).

Age class	Initial captures	Total captures
1	9	9
2	9	10
3	9	12
4	22	24
5	12	17
6	13	17
7	11	15
8	11	16
9	12	23
10	6	14
11	8	17
12	2	14
13	3	10
14		12
15		9
16		4
17		3
18		6
19		5
20		7
21		4
22		5
23		5
24		4
25		2
26		1
Total	127	265

RESULTS

Growth analysis of wild and head-started turtles.—We analyzed growth from 265 encounters of 127 unique wild-hatched turtles that ranged from age 1 to 26 years old (Table 2) and 665 encounters (including the size at release) of 491 unique head-started turtles that ranged from 1 to 7 years old (Table 1). We found no difference in growth between wild-hatched males and females ($n = 78$ and 78 encounters, respectively; test for coincident regressions: $F = 1.020$, $P = 0.314$) and so pooled males, females, and animals of unknown sex for subsequent analyses. Similarly, we found no difference in growth between head-starts incubated at low (male) vs. high (female) temperatures ($n = 323$ and 310 encounters, respectively; test for coincident regressions: $F = 0.559$, $P = 0.455$) and so pooled groups for subsequent analyses. Among wild-hatched turtles, growth was most rapid early in life but decreased as turtles aged to a population mean asymptotic *CL* estimate of 234 mm ($CL = 234–(234–23.3)*e^{(-0.082*t)}$; $r^2 = 0.891$; Fig. 1A). Growth differed significantly between wild-hatched turtles less than eight years old and head-starts ($n = 101$ and 665 encounters, respectively; test for coincident regressions: $F = 57.588$, $P < 0.001$). The resulting growth

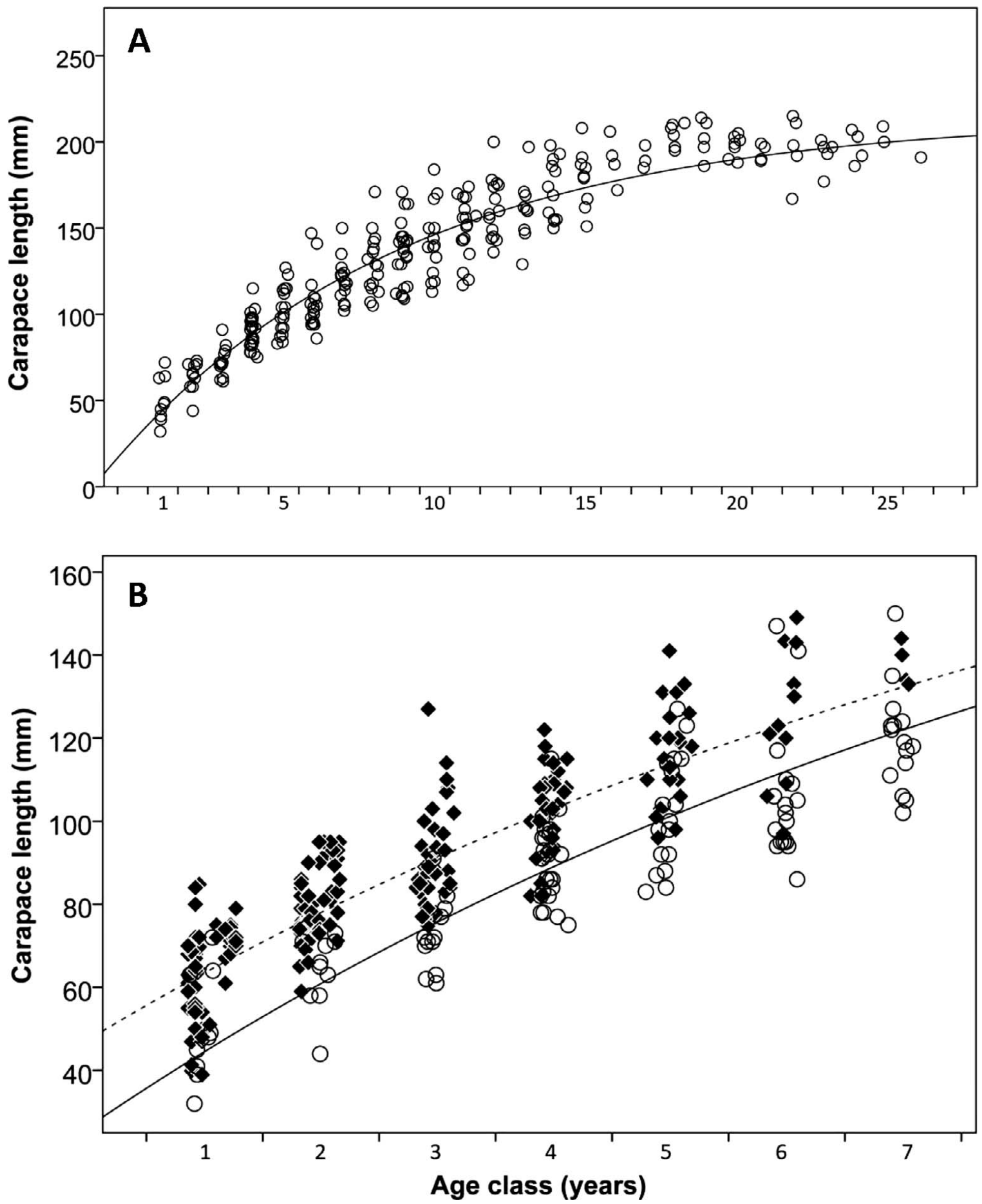

Fig. 1. Growth of Blanding's Turtles at SBCP. (A) Growth of wild-hatched turtles from age 1–26. $CL = 234.1 - (234.1 - 31.7)^{*}e^{(-0.082^{*}age)}$. (B) Growth of wild-hatched (open circles and solid line) and head-started (filled diamonds and dotted line) turtles from age class 1–7 (only a random subset of head-starts is shown for clarity). Wild-hatched: $CL = 234.1-(234.1-31.7)^{*}e^{(-0.082^{*}age)}$; head-starts: $CL = 211-(211-37.0)^{*}e^{(-0.109^{*}age)}$.

functions, $CL = 214.919–(214.919–16.652)^{*}e^{(-0.101^{*}t)}$ for wild-hatched juveniles and $CL = 214.919–(214.919–16.652)^{*}e^{(-0.101^{*}(t+1.167)}$ for head-starts, indicates that head-starts achieve a given *CL* 1.17 years sooner than wild-hatched turtles ($r^2 = 0.745$; Fig. 1B).

Survival analysis of wild and head-started turtles.—Recapture optimization of wild-hatched juveniles resulted in a top-ranked model ($\omega = 0.512$) that specified two discrete groups, age classes 1–6 and age classes seven and greater (Supplemental Table A; see Data Accessibility; Golba, 2019). The next three top-ranked models had increased numbers of age groups but no reduction in model deviance, suggesting that the inclusion of additional age classes was uninformative. Models that contained the additive effect of time on recapture were consistently ranked lower than models that lacked a time effect (ΔAICc > 10; Golba, 2019). Maintaining this best parameterization of recapture, the highest ranked model for survival of wild-hatched juveniles included age as a linear covariate and a plateau in survival at age 4 (Supplemental Table B; see Data Accessibility; Golba, 2019). Logarithmic and quadratic covariate models were within 2 ΔAICc but had similar deviances to the top-ranked model, suggesting little improvement. The discrete model was ranked the lowest with a ΔAICc of 5.97 (Supplemental Table A; see Data Accessibility). Based on the model-averaged results, survival increased from ages 1–6 (71–98%; Fig. 2, Supplemental Table C; see Data Accessibility). Recapture estimates varied by age from 0.26–0.37 (Golba, 2019).

Recapture optimization for head-starts resulted in a top-ranked model ($\omega = 0.71$) that specified three discrete age groups (1, 2, 3+) with an interactive effect of time. The other candidate models had ΔAICc > 2 (Supplemental Table B; see Data Accessibility; Golba, 2019). Maintaining this best parameterization of recapture, the highest ranked model for head-start survival included age as a linear covariate and specified a plateau in survival at age 3 (Supplemental Table B; see Data Accessibility; Golba, 2019). Logarithmic and quadratic covariate models were within 2 ΔAICc but had similar deviances to the top-ranked model, suggesting little

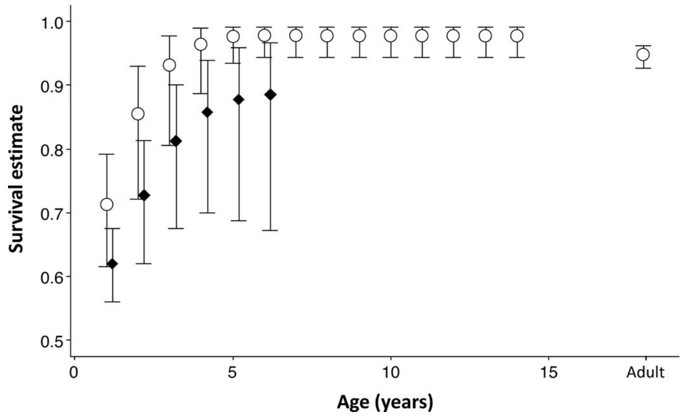

Fig. 2. Survival estimates generated from top-ranked models or model averaging of multiple top-ranked models for head-started juvenile (diamonds) and wild-hatched juvenile and adult (circles) Blanding's Turtles for the SBCP population.

improvement. The discrete model was ranked the lowest, with a ΔAICc of 3.60. The remaining four linear models have a cumulative weight of 0.78 and are within 2 ΔQAICc, so we employed model averaging to obtain model-averaged estimates of age-specific survival and recapture (Supplemental Table B; see Data Accessibility). Based on the model-averaged results, survival increased from ages 1–6 (63–90%; Fig. 2, Supplemental Table C; see Data Accessibility). Recapture estimates varied by age and year ranging from 0.02–0.72 (Golba, 2019).

Survival and realized population growth of adult turtles.—We analyzed adult survival using 540 encounters of 148 unique turtles (80 M, 68 F) from 2004 to 2018 (Table 1). Of the 64 candidate models we examined, the most parsimonious model ($\omega = 0.35$) was a 13-parameter model that held survival constant over time and between sexes and recapture rate dependent on time (Supplemental Table D; see Data Accessibility; Golba, 2019). The next four top-ranked models (cumulative $\omega = 0.48$) added an additional parameter of sex or management on survival or recapture. Model deviance was similar among these top five models, suggesting that sex and management are uninformative (Arnold, 2010). Models that included an effect of effort on recapture were consistently low ranking (Supplemental Table D; see Data Accessibility; Golba, 2019). The estimated survival of adult turtles was $\varphi = 0.95$ (95% CI = 0.93–0.96; Fig. 2, Supplemental Table C; see Data Accessibility). The process variance of adult survival was 0.0011 with 95% CI (0.0003 to 0.0059) or 3% of the total variance. Recapture estimates varied by year ranging from 0.30–0.89 (Golba, 2019).

When modeling realized adult population growth, we found that the global model that included the interactive effect of sex and time on λ, along with the most parsimonious parameterization for survival and recapture, was overparameterized and would not run. Consequently, we examined three simpler candidate models in which λ was constant, varied with time, or varied with sex. The most parsimonious model ($\omega = 0.70$) was a 16-parameter model where λ depended on sex. Based on this model, the adult population is stable (males: $\lambda \pm SE = 1.01 \pm 0.012$) or growing (females: $\lambda \pm SE = 1.04 \pm 0.016$).

DISCUSSION

Head-starting is a widely used conservation strategy in turtle species (Burke, 2015), but ways to make it more effective have been little investigated (Seigel and Dodd, 2000; Bennett et al., 2017). Our comparison of the growth and survival of wild-hatched and head-started juveniles within the same population provides quantitative data in support of head-starting as a management tool for Blanding's Turtles. We found that head-start growth follows a trajectory parallel to that of wild-hatched juveniles and that survival of head-starts was similar to like-aged wild-hatched Blanding's Turtles. Prior analyses at our study site and elsewhere have demonstrated that head-starting has shifted Blanding's Turtle population body size distributions to include a broader array of juvenile and adult-sized turtles, that head-starts are reproducing successfully, and that the spatial ecology of head-starts is similar to that of wild-hatched turtles (Starking-Symanski et al., 2018; Carstairs et al., 2019; Thompson et al., 2020). Although the success of head-starting cannot be fully assessed until turtles are recruited into the adult population and successfully reproduce, patterns of head-start growth and survival provide intermediate measures of success.

The growth function for wild-hatched Blanding's Turtles at SBCP conforms closely to that observed in Nova Scotia through about age 15 (Arsenault, 2011). In contrast, the growth function for a Nebraska population results in consistently greater carapace length over this age range (Germano et al., 2000). Although formal growth analyses are lacking for other sites, available data do allow qualitative comparison. Using the carapace length achieved in the fifth year as a benchmark, growth can be roughly categorized as slow (fifth year carapace length equals ca. 90 mm; southwestern Ontario; Petokas, 1986), intermediate (ca. 100 mm; Illinois, Michigan, Minnesota, Nova Scotia; Congdon and van Loben Sels, 1991; Pappas et al., 2000; Arsenault, 2011; this study), or rapid (110–120 mm; Wisconsin, Massachusetts, southeastern Ontario; Graham and Doyle, 1977; Petokas, 1986; Ross, 1989; Reid et al., 2016). Comparable variation in growth is also seen among populations of snapping turtles and pond turtles (Galbraith et al., 1989; Germano, 2016). Because juvenile growth is an important determinate of reproductive parameters (age at first reproduction, female size and consequently clutch size; Congdon et al., 2001; Ruane et al., 2008), future studies of its environmental determinants (e.g., Richard et al., 2014) would enhance understanding of turtle life history and aid in conservation planning.

Head-starts at SBCP released approximately one-year post-hatching were about the same size as two-year-old wild-hatched turtles. Importantly, growth of head-starts parallels that of wild-hatched turtles such that this difference in size persists for at least six years post-release. In Nova Scotia, head-starts were initially larger than their wild-hatched counterparts, but this size advantage decreased as they approached adulthood (Arsenault, 2011). Arsenault (2011) captured head-starts up to 15 years after release and so the convergence of head-start and wild-caught size may represent a cessation of growth with the onset of adulthood. Continued monitoring may reveal a similar pattern at SBCP. In contrast with our study, head-start growth rates in Ontario were initially lower than wild-hatched turtles, but after a one-year acclimation period, the growth rates became equivalent (Carstairs et al., 2019).

Our estimation of wild-hatched juvenile survival fills a data gap in Blanding's Turtle demography by providing age-specific survival rates through adulthood. The rates we estimated for wild-hatched juvenile survival are high, increasing from 71% at age 1 to 98% at age 6+. These values bracket the mean juvenile survival rate of 79% obtained by reverse modeling from estimates of age 0 survival, adult survival, and fecundity under the assumption of a stable population size by Congdon et al. (1993) and fall within the range of other direct estimates of Blanding's Turtle juvenile survival (from 33–100%; Arsenault, 2011; D'Entremont, 2014; A. R. Kuhns, pers. comm.). Reverse modeling is clearly useful when empirically based estimates are lacking (Pike et al., 2008; Rodríguez-Caro et al., 2019), but confirmation via analyses like ours are needed and have the added benefit of providing age-specific (vs. multi-year mean) values. Estimates of wild-hatched juvenile survival in other freshwater turtles, generated using Cormack-Jolly-Seber methods, conform with our estimates for Blanding's Turtles (58–92%; Blamires et al., 2005; Folt et al., 2016; Germano, 2016; Tutterow et al., 2017; Arsovski et al., 2018; Feng et al., 2019; Hanscom et al., 2020). As in Blanding's Turtles, survival increases with age to a plateau upon maturity in other freshwater turtles. Future studies should incorporate these age-specific survival rates to ensure accurate conservation management applications.

The results of our head-start survival analysis demonstrate that head-started Blanding's Turtles have annual survival of 63% during the first-year post-release and that survival increases in subsequent years, approaching 90% in their sixth-year post-release. Although point estimates of survival are lower than those for wild-hatched turtles of the same age, confidence intervals overlap, indicating that apparent differences are not statistically significant. Continued monitoring will allow future comparisons spanning additional years, with larger samples and the ability to determine whether there is a true difference in survival rates between groups, which could have important implications for management. This confirms several of the results from a similar study of Blanding's Turtles in Ontario but with a larger sample size (Carstairs et al., 2019). We did not observe the same lag in growth and survival for head-starts, suggesting that if a lag exists, it has little impact in the long term. Telemetry studies of head-started Blanding's Turtles have yielded survival estimates similar to ours: 63–96% (Starking-Szymanski et al., 2018), 70% (Arsenault, 2011; D'Entremont, 2014), 89–98% (Carstairs et al., 2019). In another mark–recapture study of head-started Blanding's Turtles, survival was estimated at 72% for the first-year post-release (Green, 2015). Post-release survival of head-started turtles is frequently lowest immediately post-release but then increases (e.g., Blanding's Turtles, Carstairs et al., 2019; Gopher Tortoise, Tuberville et al., 2015; Western Pond Turtle, Spinks et al., 2003; Vander Haegen, 2009). During three-years post-release, head-started European Pond Turtles had survival similar to that of wild-hatched turtles (Mitrus, 2005). Survival of head-started Wood Turtles at two sites increased from 37% and 53% during the first year following release to 100% by seven years post-release but survival rates of wild-hatched juveniles are unknown (Mullin et al., 2020).

Our survival estimates for adult Blanding's Turtles are comparable with other long-term studies, showing high (approaching or exceeding 90%) survival of this adult age class (Congdon et al., 1993, 2001; Rubin et al., 2004; Reid et al., 2016). The exception is found in a population in Nebraska where adult survival is estimated at 69% (Ruane et al., 2008), which is attributed to high female mortality from roads and rail lines adjacent to the site. Our estimate also falls toward the higher end of freshwater turtle species generally (45–99%; Rachmansah et al., 2020). Although survival of adults is well studied, establishing site-specific estimates of survival and its environmental (process) variance will be useful in ongoing population viability analyses (King et al., 2021). Our estimation of realized adult population growth equals (males) or exceeds (females) one, meaning our population is growing. This is useful for a planned start-from-scratch population because we can justify harvest within this population as a source without impacting its future.

Conservation implications.—Our results demonstrate that head-start growth and survival are comparable to that of wild-hatched turtles, which supports the use of head-starting as an effective tool for Blanding's Turtle conservation. In future studies, it would be useful to compare growth and survival of directly released hatchlings, first-year head-starts like those analyzed here, and second-year head-starts to refine head-starting methodology. Also needed are analyses of the reproductive competence of head-started turtles once they reach reproductive maturity. At another northeastern Illinois site, head-started females that attained reproductive maturity were captured and induced to oviposit in captivity (Thompson et al., 2020). Reproductive competency has been observed in head-started turtles of other species, such as in Wood Turtles (Vander Haegen et al., 2009; Mullin et al., 2020) and in Galápagos Tortoises (Tapia et al., 2015). The Galápagos Tortoise head-starting project stands out for successfully reestablishing an extirpated population to a self-sustaining level (Gibbs et al., 2014; Tapia et al., 2015).

Accurate site-specific demographic parameter estimates are essential for reliable projection of effects of management on populations (Morris and Doak, 2002). The demographic rates estimated in this study can be used to generate site-specific population viability analyses (King et al., 2021) and to more accurately model the use of head-starting for augmentation and reintroduction (cf. Buhlmann et al., 2015). Quantitative data on the effects of alternative management strategies (e.g., head-starting) on growth and survival (this study), and ultimately on reproduction and population growth, will further facilitate management decisions.

Although patterns of survival and growth of head-started Blanding's Turtles are promising, other factors must be considered before implementing a head-starting strategy. Not addressing the initial cause of decline is the leading cause of reintroduction failures (reviewed by Bubac et al., 2019). The SBCP Blanding's Turtle population has been the target of a number of management actions in addition to head-starting, including habitat management, meso-predator removal, and community outreach. These strategies have most likely increased the success of head-starting and also maintained high adult survivorship, a key demographic parameter in long-lived turtles (Heppell, 1998). Similarly, evaluations of head-starting in the Wood Turtle resulted in pessimistic population projections unless other interventions, such as predator removal, were implemented (Mullin et al., 2020), emphasizing that head-starting may only be successful in conjunction with other management strategies.

DATA ACCESSIBILITY

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