



Population reinforcement accelerates subadult recruitment rates in an endangered freshwater turtle

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Keywords

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Abstract

Wildlife diversity and abundance are declining globally and population reinforcement with captive-reared animals is a common intervention used to prevent extinctions. Released captive-reared individuals may undergo an acclimation period before their behavior and success is comparable to wild-reared individuals because they lack experience with predators, complex habitats and variable environmental conditions. Quantifying post-release acclimation effects on fitness and behavior is important for maximizing the success of reintroduction programs and for predicting the number of captive-reared animals required for release. Endangered Blanding's turtles *Emydoidea blandingii* exhibit low recruitment and may benefit from population reinforcement with captive-reared, 'headstarted' individuals (headstarts). We used 6 years of data to compare survival, growth, habitat use and movement ecology between wild-hatched juvenile turtles and headstarts reared from eggs rescued from injured females. We found strong evidence of an acclimation effect in headstarts, with lower movement, growth, and survival during the first one to two years post-release. Following this acclimation period, headstarts had movement, growth and survival similar to wild-hatched juveniles. Habitat use did not differ between headstarts and wild-hatched juveniles. We hypothesize that the acclimation period occurred because headstarts were introduced directly into the wild (i.e. 'hard release') and that providing additional support before or after release may improve the success of headstarts. Headstarts had a monthly survival probability of 0.89 in the first year post-release, and 0.98 after the first year post-release. We estimated that headstarts at our sites have approximately three times higher probability of surviving to 10 years of age, compared to wild-hatched individuals at other sites. Our results highlight that headstarts should be released into habitat individually rather than in clusters, and highlight the need to investigate whether post-release mortality of captive-reared animals could be mitigated by increased acclimation to wild conditions, for example through prerelease periods in outdoor pens.

Introduction

Global wildlife diversity and abundance are declining due to habitat loss, overharvesting, road mortality and disease (Berger *et al.*, 1998; Gibbons *et al.*, 2000; Gibbs & Shriver, 2002; Schipper *et al.*, 2008; Frick *et al.*, 2015). Conservation interventions, such as population reintroductions, population reinforcements and captive assurance colonies can help stabilize threatened populations and prevent extinctions (Bowkett, 2009; Martin *et al.*, 2012; Batson *et al.*, 2015). However, tests of the effectiveness of conservation interventions are challenging because the specification of a baseline scenario or 'control' has a strong effect on evaluations of success (Tavecchia *et al.*, 2009). For example, a survival probability

of 50% for translocated individuals becomes most informative when compared to the survival probability of resident individuals in the same habitat, and translocations can reduce extinction risk in a target population even when survivorship is relatively low. Estimating appropriate reference values for comparison is key to the evaluation of conservation interventions and the adaptive management of endangered species.

Reinforcing or reintroducing endangered populations by releasing captive-reared animals is a common intervention for stabilizing declining populations in a wide variety of taxa, including birds (Jones *et al.*, 2008), fish (Rakes, Shute & Shute, 1999), frogs (Griffiths & Pavajeau, 2008), lizards (Alberts, 2007), mammals (Kleiman, 1989), snakes (Roe *et al.*, 2010) and turtles (Burke, 2015). In some cases,

species have been successfully reintroduced from captive stock after temporary extinction in the wild, including California condors (*Gymnogyps californianus*; Snyder & Snyder, 1989), Mauritius kestrels (*Falco punctatus*; Jones *et al.*, 2008) and black-footed ferrets (*Mustela nigripes*; Dobson & Lyles, 2000). These programs are sometimes criticized for the poor success rates of translocations involving captive-reared animals, high financial costs and challenges arising during captive husbandry (Snyder *et al.*, 1996).

Poor survival of captive-reared animals may occur because of inexperience in the release environment. Individuals may have lower survival and growth if they lack experience foraging, avoiding predators and seeking appropriate refuges from environmental conditions (Bacon, Robert & Hingrat, 2019). Individuals may also have lower survival rates if they disperse or migrate away from release sites, and this is a common reason for failures in translocations (Germano & Bishop, 2008). Testing for a behavioral acclimation period (hereafter 'acclimation period') in population reinforcement programs can identify opportunities to increase the number of captive-reared animals recruited into the breeding population through training or releasing animals into outdoor pens to expose them to local environmental conditions ('soft-releases') (White, Collazo & Vilella, 2005; Batson *et al.*, 2015). Furthermore, quantifying relative survivorship through any effects of an acclimation period is important for predicting the number of captive-reared animals required to establish new populations or increase recruitment in declining populations, and therefore essential for estimating the costs of such programs (Tavecchia *et al.*, 2009; Armstrong *et al.*, 2017).

Headstarting (captive hatching and rearing of oviparous reptiles before release into the wild) aims to increase recruitment to threatened populations (Heppell, Crowder & Crouse, 1996). In turtles, the merits and effectiveness of headstarting have been challenged compared to interventions that focus on increasing the survival of adults (Woody, 1990; Dodd & Seigel, 1991; Heppell *et al.*, 1996). Yet the effects of headstarting on population growth or persistence in turtles have not been empirically evaluated, partly because most species take a long time to reach maturity. A feasible short-term alternative is to compare indicators of success (e.g. survivorship and growth) between headstarts and wild-hatched individuals in a population. Rather than asking whether head-starting 'works' in general, such data could assess the conditions under which headstarting turtles would increase population growth.

We used an existing headstarting program at the Ontario Turtle Conservation Centre (OTCC, Selwyn, Ontario, Canada) to experimentally evaluate the effects of headstarting on the fitness of juvenile Blanding's turtle *Emydoidea blandingii*. Low recruitment in some areas may limit population growth (van Dijk & Rhodin, 2011); protection of adults may not be sufficient to slow long-term population declines. Headstarting has been used to reinforce population size in *E. blandingii* (Arsenault, 2011; Buhlmann *et al.*, 2015; Starking-Szymanski *et al.*, 2018) and understanding the fitness of headstarts relative to wild-hatched individuals is key to making cost-effective management decisions. We used 6 years of data to test

the hypothesis that headstarted, juvenile *E. blandingii* exhibit comparable fitness to wild-hatched juveniles by comparing the survival, movement patterns, growth and habitat use of headstarts ($n = 35$), wild-hatched juveniles ($n = 5$) and wild-hatched adults ($n = 13$). We also tested whether headstarts underwent an acclimation period after release.

Materials and methods

All use of animals in this study were approved by the Ontario Ministry of Natural Resources and Forestry Wildlife Animal Care Committee (protocols 325, 16-325, 17-325, 18-325) and authorized by permits from the Ontario Ministry of Natural Resources and Forestry (Wildlife Custodian Authorization 20025217, Wildlife Scientific Collectors Authorization 1073852, 1079730, 1082990, 1086260, and 1089569, Endangered Species Act permit SEZ-B-001-12).

Incubation, captive-rearing and release

We harvested eggs from gravid females injured on roads near the study site and delivered to the OTCC hospital for treatment (details on medical treatment and methods for egg harvesting available in the Data S1). We incubated eggs in vermiculite and raised hatchling turtles indoors in tubs or aquaria for 24 months (range 24–48 months) to a mean mass of 183 g (range 89–420 g) and mean carapace length of 99 mm (range 79–134 mm) until release. Prior to release, we attached VHF radio transmitters (Models R1680 and R1860, Advanced Telemetry Systems, Isanti, Minnesota, USA) to turtles' carapaces with epoxy (PC-7, LePage or JB WaterWeld). The transmitters weighed less than 5% of turtle mass.

Headstarts were directly released (i.e. 'hard-release') into a protected area in eastern Ontario with a resident population of *E. blandingii* (exact location omitted at the request of the responsible agency). The area is a mosaic of lakes, wetlands and forest. In 2012, we released headstarts in two groups of five. The first group was released adjacent to water on a small rocky island in fen habitat, and the second group was released adjacent to water on the opposite side of the same island. In 2013, 2016 and 2017 we released headstarts individually in fen habitat (Fig. S1).

We captured wild-hatched juvenile ($n = 5$, carapace length = 99 ± 44 mm, mass = 171 ± 76 g) and adult ($n = 13$, carapace length = 195 ± 52 mm, mass = 1124 ± 300 g) *E. blandingii* at the study site by hand and in sardine-baited hoop traps (30 cm, 50 cm, or 76 cm diameter; Memphis Net and Twine, Memphis, Tennessee, USA). Transmitters were attached as described above, and wild-hatched turtles were released at their capture location. We tracked wild-hatched juveniles from 2014 to 2017 and we tracked wild-hatched adults from 2013 to 2017.

We located turtles weekly to record the status (alive or dead) and locations (i.e. 'fixes', ± 5 m) during the active season (April–September), and tracked turtles to their overwintering sites. We took monthly measurements of mass and midline carapace length from April to September.

Survivorship

We investigated factors influencing headstart survival using known-fate mark–recapture models, using the *RMark* package (Laake, 2013) to access the program MARK (White & Burnham, 1999). We started with a general model including carapace length at release, year of release (cohort), season and experience. We included an effect of season, hypothesizing that headstarts' survival probability would differ between the active season (April to September) and overwintering season (October to March), because probabilities of predation, disease and environmental exposure vary seasonally. We also hypothesized that monthly survival of headstarts might be lower when they are first released. Therefore, we included a factor for experience where survival differed between the first year post-release and the remainder of the study. We assumed growth over the monitoring period had no effect on survival because the range of initial carapace lengths was large compared to the amount of growth we observed and because initial size had little effect on survival (within our limited range of release sizes; Data S1).

We constructed all subsets of this general model and ranked their relative support based on bias-corrected Akaike's Information Criterion (AIC_c ; Burnham & Anderson, 2002). To account for uncertainty in model selection, we model-averaged the predicted survival among relatively well-supported models ($\Delta AIC_c < 4$ compared to the most-supported model) to compare the relative effects of body size, cohort and experience (Burnham & Anderson, 2002; Cade, 2015).

We compared our model-averaged estimates of survival to estimated survival probabilities of wild-hatched turtles. We assumed the probability of an egg surviving until hatching was 0.2610 (based on 16 years of data; Congdon, Dunham & Van Loben Sels, 1993), the probability of surviving from hatching to the first year was 0.375 (based on 2 years of data; Paterson, Steinberg & Litzgus, 2014) and the annual survivorship from age 1–10 was 0.7826 (life table estimate based on 27 years of data; Congdon *et al.*, 1993).

Growth rates

We compared growth rates of headstarts and wild-hatched juveniles using linear mixed-effects broken-line regression models with the *lme4* package (Bates *et al.*, 2015). We used a linear model over von Bertalanffy or logistic growth models because growth in juveniles is often linear (Lester, Shuter & Abrams, 2004). We used carapace length as the response variable in the first model, and we used mass as the response variable in the second model. For both analyses, we included time since release (days), group (headstarts or wild-hatched juvenile) and the interaction between time since release and group as fixed effects. To test for a post-release acclimation period during which headstarts may exhibit slower growth, we estimated the slopes for headstarts and wild-hatched juveniles before and after a breakpoint. We identified meaningful breakpoints in the regressions by searching across the observed range in time since release to find the models with

the minimum deviance. In both models, we included a random effect of individual because individuals started at different sizes, and each was measured multiple times. For both growth analyses, we excluded turtles that were only measured within a single active season, and we only included wild-hatched turtles whose initial carapace length was within the range of headstarts' carapace length at release. We confirmed that linear models were appropriate for growth by examining the relationship between residuals and fitted values (Data S1).

Spatial analysis

To test whether headstarts exhibited similar movement patterns as wild-hatched turtles, we measured home-range sizes and the average daily distance traveled. We compared home ranges (100% minimum convex polygons) among headstarts in their first year post-release, headstarts after their first year post-release, juvenile wild-hatched turtles and adult wild-hatched turtles. We split headstart home ranges in two periods because their behavior may change after an initial period of adjustment to unfamiliar habitats. We split wild-hatched turtles into two groups because body size can influence home-range size (McRae, Landers & Garner, 1981; Lindstedt, Miller & Buskirk, 1986). Estimated home-range size typically increases with more locations, and the number of locations per turtle varied widely (6–85), so we also accounted for the number of locations. We used a mixed-effects linear model with log-transformed home-range size as the response variable, and group, carapace length and the number of locations as predictor variables. We included a random intercept term for turtle identity. We also used a linear model to test whether headstart home-range size (log-transformed) was affected by carapace length or cohort, with the number of locations as a covariate.

We divided the absolute distance between each relocation by the difference in time elapsed to estimate daily distance traveled, and then calculated the mean daily distance traveled per individual. We only used turtles with ≥ 10 locations for this analysis and locations separated by less than 14 days. We used a mixed-effects linear model with the mean daily distance travelled as the response, the group (headstarts in first year post-release, headstarts after the first year post-release, wild-hatched juveniles, wild-hatched adults) as the predictor variable, and turtle identity as a random effect. We also used a linear model to test whether headstarts' daily distance traveled was affected by carapace length and release cohort.

Habitat use

We classified the study site into five land cover categories using seven environmental variables derived from satellite imagery and a digital elevation model (DEM). We defined the study area as the minimum convex polygon around all turtle locations with a 2 km buffer. We used satellite imagery from Sentinel-2 (SERCO, 2017) taken on June 23, 2016 with four-band (blue, green, red, near infrared) spectral

regions at 10 m resolution. Multispectral bands were used to represent the study area topography and to derive the Normalized Difference Vegetation Index (NDVI; Rouse *et al.*, 1974), which is characterized along a scale from -1 to $+1$ where values around or below 0 typically indicate no vegetation present, and higher values indicate green vegetation (Chakraborty *et al.*, 2018). We rescaled a 2 m DEM from the Land Information Ontario database (Digital Raster Acquisition Project Eastern Ontario; Land Information Ontario, 2014) to 10 m to match the resolution of the multispectral bands. We used the DEM as a proxy for wetness and for characterizing low-lying wetlands, and to derive the slope gradient.

We classified each pixel in the study site into one of five land cover classes (adapted from Anderson, 1976; Table 1) using a Random Forest (RF) algorithm (Breiman, 2001) using the *randomForest* package (Liaw & Wiener, 2002). The four-band Sentinel-2 satellite image was combined with elevation estimated from the DEM, NDVI and slope gradient layers to create a seven-band composite used as the input for the RF land cover classification. We used a training set (924 points) and 500 trees for the classification with an out-of-bag error rate of 0.54% (Data S1). We compared the proportion of headstart and wild-hatched juvenile locations in each land-cover type with a Chi-square test.

Results

Tracking

We tracked five wild-hatched juveniles to 117 locations (26 ± 2 locations per turtle), and the 13 wild-hatched adults to 352 locations (26 ± 4 locations per turtle). We released and tracked 35 headstarts between 2012 and 2017 and 894 locations (27 ± 4 locations per turtle).

Survivorship

All tracked, wild-hatched turtles survived for the duration of the study. Of 35 headstarts, seven were lost (either the

transmitter failed, or the turtle moved out of range where it could be detected). Twelve survived to the end of the study and 16 died, with high mortality in some cohorts and low mortality in others (Fig. 1). Eleven mortalities were from predators, four occurred during overwintering, and one died of unknown causes. The turtle that died of unknown causes was lethargic and was brought into captivity on 31-07-2017 and died on 04-08-2017. Post mortem findings were inconclusive. The most-supported known-fate survival model for headstarts included effects of cohort and experience on monthly survival probability. Models including body size were also strongly supported (Table 2); turtles that survived the first year post-release had subsequent monthly survival probability of 0.98 (95% CI: 0.92–1.0; Fig. 1). The probability of a headstart surviving for 10 years post-release was 0.03 (95% CI: 0.000013–0.54). The probability of a wild-hatched turtle surviving from an egg to 10 years was 0.01 based on survival rates at other sites (Congdon *et al.*, 1993; Paterson *et al.*, 2014). Blanding's turtles reach maturity at 14–21 years, but survivorship is high once turtles reach 10 years (Congdon, Nagle & Kinney, 2018). Headstart survival probabilities were similar between the active season and the overwintering season (Data S1). Monthly survival of headstarts increased with carapace length at release, but the predicted difference in survival probability was low (total change in monthly survival = 0.07) across the range of carapace lengths (Data S1).

Growth rates

In the first 562 days post-release, wild-hatched juvenile carapace lengths grew faster (0.020 ± 0.002 mm day⁻¹) than headstarts (0.004 ± 0.002 mm day⁻¹; $F = 30.03$, $df = 1$, 234, $P < 0.001$; Fig. 2). After 562 days post-release, headstarts grew (0.015 ± 0.002 mm day⁻¹) at a similar rate to wild-hatched juveniles (0.012 ± 0.008 mm day⁻¹; $F = 0.12$, $d.f. = 234$, 1, $P = 0.73$). The carapace length model with a breakpoint in slope performed better than a model with no change in slope ($\chi^2 = 41.27$, $d.f. = 2$, $P < 0.001$).

In the first 445 days post-release, wild-hatched juvenile mass increased faster (0.019 ± 0.001 g day⁻¹) than headstarts (-0.003 ± 0.017 g day⁻¹; $F = 10.56$, $d.f. = 1$, 234, $P = 0.001$). After the first 445 days post-release, headstarts grew (0.068 ± 0.01 g day⁻¹) at a similar rate to wild-hatched juveniles (-0.001 ± 0.038 g day⁻¹; $F = 3.18$, $d.f. = 234$, 1, $P = 0.08$). The mass regression model with a breakpoint in slope performed better than a model with no change in slope ($\chi^2 = 15.78$, $d.f. = 2$, $P < 0.001$).

Spatial analysis

Home-angle size for turtles with \geq five locations varied from 0.003 to 28.0 ha. Home-range size (log-transformed) increased with the number of locations ($F = 8.79$, $d.f. = 1$, 56, $P < 0.005$) and differed among groups ($F = 12.00$, $d.f. = 3$, 54, $P < 0.0001$). Headstarts had smaller home ranges in their first year than headstarts after the first year, wild-hatched juveniles and wild-hatched adults ($P < 0.001$ for all three

Table 1. Land cover classes and descriptions based on the Canadian wetland classification system and Anderson (1976)

Land Cover Class	Description
Open Water	All areas that are persistently water-covered (e.g. lakes, reservoirs, streams, bays, estuaries)
Wetland	Bog, fen (or wet meadow), swamp, marsh, shallow open water
Shallow Water	Shallow water-covered area typically dominated by filamentous surface-bloom forming algae (e.g. <i>Hydrodictyon</i> spp., <i>Cladophora</i> spp)
Forested (Upland)	Closed canopy deciduous, coniferous, or mixed forests
Barren Land	Land of limited ability to support vegetation; less than one-third of the area has vegetation or other cover (e.g. sands, rocks, thin soil)

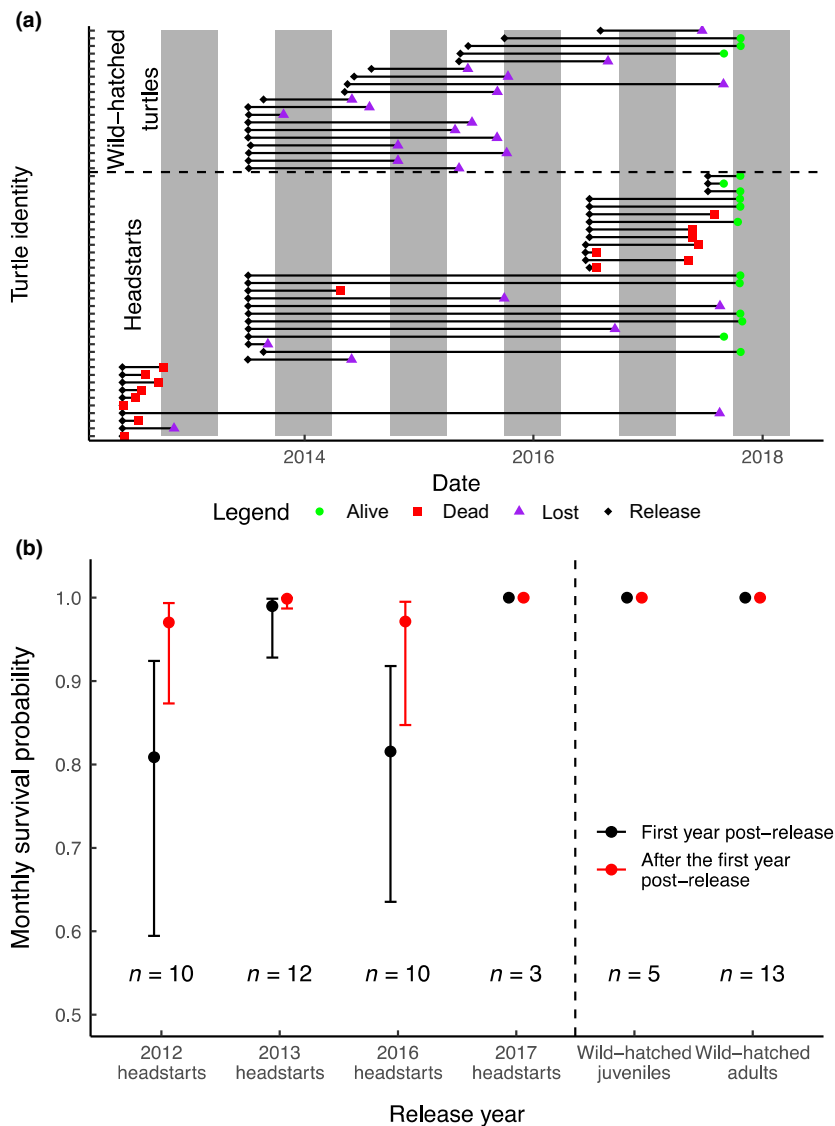


Figure 1 (a) Timeline of the headstarting study, showing 19 wild-hatched and 35 headstarted, released Blanding's turtles (*Emydoidea blandingii*; 2012–2017). Gray bars represent winters (October–March). (b) Predicted monthly survival probability (\pm 95% CI) of headstarts and wild-hatched turtles during the active season (April–September), derived from model-averaging known-fate models within four AIC_c of the most-supported model.

comparisons). Home-range size was similar for headstarts after the first year post-release, wild-hatched juveniles and wild-hatched adults ($P > 0.05$ for all pair-wise comparisons; Fig. 3). The model explained more than half of the variation in home-range size (approximate multiple $R^2 = 0.62$). Headstart home-range size was similar among release cohorts ($F = 0.18$, d.f. = 2, 10, $P = 0.83$) and was unaffected by starting carapace length ($F = 3.13$, d.f. = 1, 10, $P = 0.11$).

Mean daily distance traveled differed among groups ($F = 12.74$, d.f. = 3, 30, $P < 0.0001$). Headstarts moved less in the first year post-release (3 ± 1 m day⁻¹) than all other groups ($P < 0.05$ for all pairwise comparisons). Mean daily distances traveled were similar for headstarts after their first year (11 ± 1 m day⁻¹), juvenile wild-hatched turtles

(14 ± 2 m day⁻¹) and wild-hatched adults (14 ± 2 m day⁻¹; Fig. 4). The mean daily distance traveled by headstarts did not differ among release cohorts ($F = 2.92$, d.f. = 2, 8, $P = 0.11$) and was unaffected by carapace length at release ($F = 0.02$, d.f. = 1, 8, $P = 0.90$).

Habitat use

Land cover classification had an overall accuracy of 80.8%. Turtles were usually tracked to wetlands (headstarts = 67.8% of locations; wild-hatched = 63.2% of locations) and forested upland (headstarts = 29.5%; wild-hatched = 35.0%). Limited locations occurred in (deeper) open water (headstarts = 2.2% of locations; wild-hatched = 0.9% of locations) or rock barrens

Table 2. Known-fate survival models of headstarted Blanding's turtles *Emydoidea blandingii*, ranked from most to least supported

Model ^a	k	AIC _c	ΔAIC _c	ω	Deviance
S(~cohort + experience)	5	106.18	0.00	0.45	27.66
S(~cohort + CL + experience)	6	107.44	1.26	0.24	95.19
S(~season + cohort + experience)	6	107.64	1.46	0.22	27.05
S(~season * cohort + experience)	8	110.77	4.59	0.05	26.00
S(~season * cohort + CL + experience)	9	112.27	6.09	0.02	93.73
S(~cohort + CL)	5	113.68	7.50	0.01	103.50
S(~cohort)	4	113.72	7.54	0.01	37.26
S(~season + cohort)	5	115.59	9.41	0.00	37.08
S(~season * cohort)	7	118.59	12.41	0.00	35.92
S(~season * cohort + CL)	8	118.79	12.61	0.00	102.35
S(~experience)	2	120.69	14.51	0.00	48.32
S(~CL + experience)	3	121.37	15.20	0.00	115.30
S(~season + experience)	3	122.71	16.53	0.00	48.31
S(~season + CL + experience)	4	123.39	17.21	0.00	115.27
S(~1)	1	135.20	29.02	0.00	64.86
S(~CL)	2	136.36	30.18	0.00	132.32
S(~season)	2	137.15	30.97	0.00	64.78
S(~season + CL)	3	138.30	32.12	0.00	132.23

k, number of parameters; AIC_c, Akaike's information criterion; ΔAIC_c, difference in AIC_c between a model and the top-ranked model; ω, Akaike weight; CL, Carapace Length.

^aS is the monthly survival probability,

~cohort denotes different S estimates for each year,

~CL denotes a change in S in response to carapace length,

~experience denotes different S estimates for the first year post-release,

~season denotes different S estimates for the active and winter seasons

(headstarts = 0.8%; wild-hatched = 0.9%), and none were found in shallow algae-dominated water. The proportion of locations per land cover type did not differ between headstarts and wild-hatched juveniles ($\chi^2 = 3.08$, $df = 3$, $P = 0.38$).

Discussion

At our release site, *E. blandingii* that were headstarted (i.e. captive-reared) for up to two winters prior to release exhibited similar habitat use to wild-hatched turtles. Headstarts had an acclimation period of about a year post-release, with a post-release reduction in growth, survivorship and movement compared to wild-hatched turtles. Following this acclimation period, headstarts that survived their first year had similar growth rates to wild-hatched juveniles, and increased their movements to match those of wild-hatched turtles. Our data support the hypothesis that headstarting can increase recruitment of *E. blandingii* to declining populations and highlights the need to investigate whether post-release mortality of captive-reared animals could be mitigated by providing additional support before or during the acclimation period.

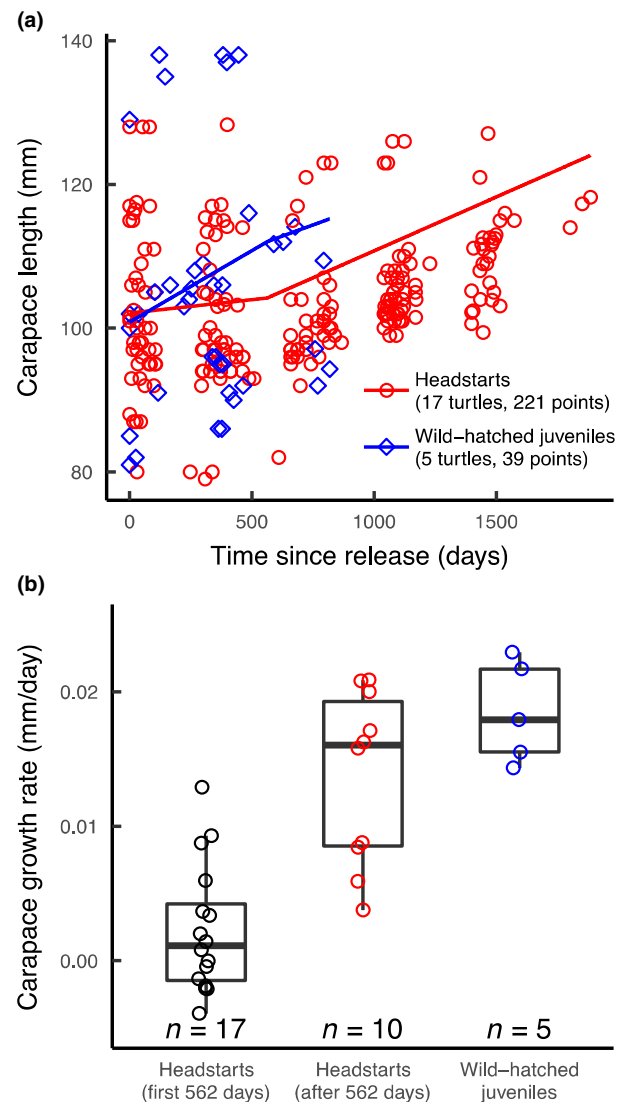


Figure 2 (a) Post-release size (carapace length; mm) of headstarted and wild-hatched Blanding's turtles *Emydoidea blandingii*. (b) Carapace length growth rate (mm/day) of headstarts and wild-hatched juveniles (Δ carapace length/day). Thick horizontal lines: medians; box outlines: 25th and 75th percentiles.

Once headstarts survive their first year, monthly survival (0.98) becomes comparable to survival estimates for wild-hatched juveniles (0.98/month, 0.7826/year) from a well-studied population in Michigan (Congdon *et al.*, 1993). Extrapolating our monthly survival (0.89/month in the first year, 0.98/month subsequently) to 10 years (the approximate time before survival is very high), we estimate that we would have to release approximately 36 headstarts to recruit one adult to the population. Extrapolating our survival estimate of wild-hatched turtles to 10 years, we estimate that 93 eggs must be laid to recruit one adult to the population. This difference is largely driven by the first year of survival (0.10 for wild-hatched turtles, 0.25 for headstarts after release), including mortality after hatchlings emerge. Therefore,

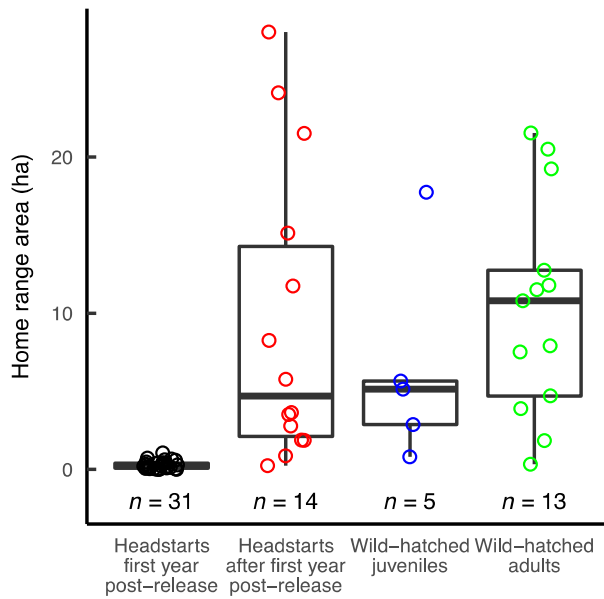


Figure 3 Home-range size of headstarted, wild-hatched juvenile, and wild-hatched adult Blanding's turtles *Emydoidea blandingii*. Thick horizontal lines: medians; box outlines: 25th and 75th percentiles.

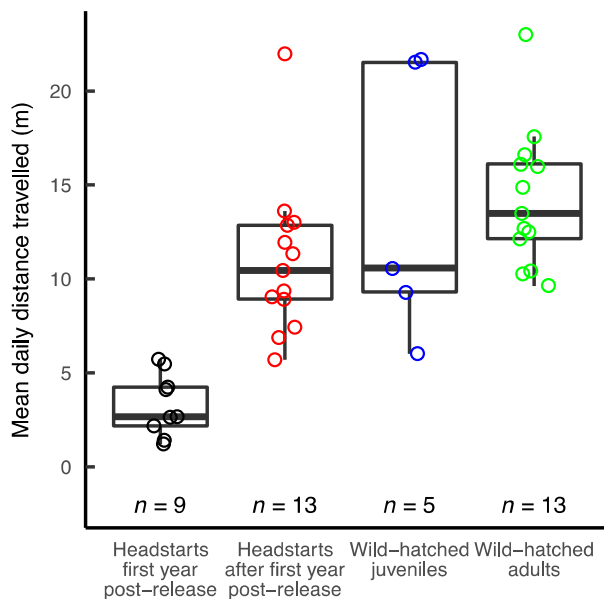


Figure 4 The mean distance traveled per day by headstarts, wild-hatched juveniles and wild-hatched adult Blanding's turtles *Emydoidea blandingii*. Thick horizontal lines: medians; box outlines: 25th and 75th percentiles.

survival rates of turtle hatchlings from in situ conservation strategies such as nest protection (Enneson & Litzgus, 2008; Riley & Litzgus, 2013) are still lower than our headstarts' survival rates. A full cost-benefit analysis of the tools available for turtle conservation is outside the scope of this study, but our results support headstarting as a viable tool for

population reinforcement if the necessary resources are available. Since we found little effect of body size on survival rates of headstarts (up to 130 mm carapace length), releasing a higher number of smaller headstarts may be more cost-effective.

Our largest source of headstart mortality was predation, which was highest in the first cohort during their first active season post-release (eight mortalities). We did not directly observe predation events but likely predators at the study site include raccoons *Procyon lotor*, coyotes and wolves *Canis sp.*, and otters *Lontra canadensis*. Release location may have played a role, since this cohort was released on land and in groups. Predation was infrequent in subsequent years when turtles were released separately into water beside suitable cover, and we did not experience another cluster of mortality events.

Changing our release methods to better prepare headstarts prior to release or to provide more support in the wild might further increase survival in the first year post-release. For example, headstarts could be kept briefly in outdoor prerelease enclosures to allow acclimation to weather patterns and noises. Releasing animals into outdoor enclosures increased survival, site fidelity and reproductive success in reintroduced burrowing owls (*Athene cunicularia*; Mitchell *et al.*, 2011). In contrast, releasing animals into outdoor enclosures ('soft-releases') did not increase survival in headstarted desert tortoises (*Gopherus agassizii*; Nagy *et al.*, 2015) or smooth green snakes (*Ophedryx vernalis*; Sacerdote-Velat *et al.*, 2014), and did not increase site fidelity of hare wallabies (*Lagostrophus fasciatus*; Hardman & Moro, 2006). Future work should test the effects of acclimation in outdoor enclosures on survival and behavior in Blanding's turtles. Survival of headstarts might increase if initial release into enclosures shortened the observed acclimation period. Alternatively, turtles in such enclosures could inadvertently become habituated to potential predators (e.g., birds of prey that might come to investigate the enclosures).

Our results are especially encouraging because of the relative ages and experience of the headstarts and wild-hatched individuals we studied. Growth rates of wild hatchlings are lower than growth rates of hatchlings in captivity, which consume a consistent, nutritious diet and do not brumate during the winter. Our 'controls' are likely approximately twice the age of the headstarts, with experience commensurate with their age. Direct comparisons of headstarts and wild-hatched juveniles in our study must consider that wild-hatched juveniles have already undergone a process of selection under the conditions specific to our study site. Wild, hatchling turtles typically experience higher mortality in the first few years of life (Congdon *et al.*, 1993). Our 'control' group is made up of individuals that survived this selective filter and are thus more likely to survive than the average hatchling. In contrast, we provided the minimum possible support to our headstarts, and the direct release methods we used in this study may represent a worst-case scenario (Bright & Morris, 1994). Even under these conditions, headstarts used similar habitat to wild-hatched turtles, and had survivorship, growth rates and behavior similar to those of

wild-hatched, well-adapted individuals after a brief acclimation period.

The post-release acclimation period we observed cannot be attributed solely to the effects of headstarting, *per se*. Captive-reared individuals face two distinct challenges on release (Bright & Morris, 1994). First, depending on the resources available in captivity, captive-reared individuals may have no experience with 'natural' conditions, and ours did not (*i.e.* cost of captivity). Second, they have no experience with the specific conditions of the release site (*i.e.* cost of release). This second challenge is equally relevant to translocations of wild-hatched individuals from one site to another (Dodd & Seigel, 1991; Nagy *et al.*, 2015), and a similar acclimation period occurs in some reptile translocations. Translocated, wild-hatched, subadult gopher tortoises *Gopherus polyphemus* and adult eastern box turtles *Terrapene carolina carolina* exhibited decreased survivorship in the first year at their new site, but subsequently survived as well as established individuals (Cook, 2004; Tuberville *et al.*, 2008). Translocated eastern hog-nosed snakes *Heterodon platyrhinos* and headstarted northern water snakes *Nerodia sipedon* exhibited different behaviors and lower survivorship than their resident or wild-raised counterparts (Plummer & Mills, 2000; Roe *et al.*, 2010). In contrast, no decline in survivorship was associated with translocations of adult *G. polyphemus* or eastern musk turtles (*Sternotherus odoratus*, Tuberville *et al.*, 2008; Attum *et al.*, 2013). It would require a meta-analysis to clarify the overall role of captivity versus site-specific factors in these datasets, and might still not provide information relevant to our site (Bennett *et al.*, 2017). At our study site, the effects of head-starting and translocation could be disentangled by introducing translocated wild-hatched individuals and comparing their fitness to headstarts and wild-hatched residents.

Evaluating the effects of perturbations on populations of long-lived species requires long-term monitoring (Franklin, 1989; Magurran *et al.*, 2010; King, Chamberlan & Courage, 2012; Canessa *et al.*, 2016); our current data capture only a 6-year snapshot. We can most accurately estimate recruitment of our headstarts to the breeding population by tracking them to maturity and comparing their reproductive success to their wild-hatched counterparts. Similar studies on other taxa show varied, long-term effects of translocations and captive-rearing. Captive-reared and wild-born, translocated western lowland gorillas *Gorilla gorilla gorilla* that survived their first 2 years post-release achieved the same reproductive success as wild-raised gorillas (King *et al.*, 2012). Reintroduced, translocated Mediterranean pond turtles *Mauremys leprosa* showed high survivorship but no measurable reproductive output following reintroduction (Bertolero & Oro, 2009), while captive-reared, released female pheasants *Phasianus colchicus* were less likely to survive to breeding, and exhibited reduced reproductive output compared to wild counterparts (Musil *et al.*, 2009).

Evaluating conservation interventions is critical to inform management decisions and allocate limited funds (Enneson & Litzgus, 2008; Martin *et al.*, 2018). Here, we applied a site-specific experimental approach to compare fitness

between captive-reared and wild-hatched individuals, as has been done elsewhere (Musil *et al.*, 2009; Nussear *et al.*, 2012; Attum *et al.*, 2013; Nagy *et al.*, 2015). Our approach provided a proxy of short-term success for headstarting in *E. blandingii*, and we identified a critical post-release acclimation period during which additional support might increase headstart fitness. Our estimated headstart survival rates indicate that this population reinforcement program has the potential to increase recruitment in *E. blandingii*, but we need to monitor headstarts as they reach maturity to measure the effects headstarting has on population viability.

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Data Accessibility

If accepted, data from our manuscript will be archived in the Figshare repository.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Data S1: Rearing facility and methods (Appendix S1), release information (Appendix S2), the effect of season and body size on survival (Appendix S3), linear growth models (Appendix S4), and land cover classification (Appendix S5) are available online.