

1 **Population reinforcement accelerates subadult recruitment rates in an**
2 **endangered freshwater turtle**

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15 **Running Title:** Population reinforcement for turtles

16 **Abstract**

17 Wildlife diversity and abundance are declining globally and population
18 reinforcement with captive-reared animals is a common intervention used to prevent
19 extinctions. Released captive-reared individuals may undergo an acclimation period
20 before their behaviour and success is comparable to wild-reared individuals because
21 they lack experience with predators, complex habitats, and variable environmental
22 conditions. Quantifying post-release acclimation effects on fitness and behaviour is
23 important for maximizing the success of reintroduction programs and for predicting the
24 number of captive-reared animals required for release. Endangered Blanding's turtles
25 (*Emydoidea blandingii*) exhibit low recruitment and may benefit from population
26 reinforcement with captive-reared, "headstarted" individuals (headstarts). We used six
27 years of data to compare survival, growth, habitat use and movement ecology of
28 headstarts and wild-hatched juvenile turtles. We found strong evidence of an
29 acclimation effect in headstarts, with lower movement, growth, and survival during the
30 first one to two years post-release. Following this acclimation period, headstarts had
31 movement, growth, and survival similar to wild-hatched juveniles. Habitat use did not
32 differ between headstarts and wild-hatched juveniles. We hypothesize that the
33 acclimation period occurred because headstarts were introduced directly into the wild
34 (i.e. "hard release") and that providing additional support before or after release may
35 improve the success of headstarts. Headstarts had a monthly survival probability of 0.89
36 in the first year post-release, and 0.98 after the first year post-release. We estimated
37 that headstarts at our sites have approximately three times higher probability of
38 surviving to 10 years of age, compared to wild-hatched individuals at other sites. Our

39 results highlight that headstarts should be released into suitable habitat individually
40 rather than in clusters, and highlight the need to investigate whether post-release
41 mortality of captive-reared animals could be mitigated by increased acclimation to wild
42 conditions, for example through pre-release periods in outdoor pens.

43 **Keywords:** Blanding’s turtle, conservation intervention, *Emydoidea blandingii*,
44 headstarting, long-term monitoring, population augmentation, population reinforcement,
45 post-release effects

46 **Introduction**

47 Global wildlife diversity and abundance are declining due to habitat loss,
48 overharvesting, road mortality, and disease (Berger et al., 1998; Gibbons et al., 2000;
49 Gibbs & Shriver, 2002; Schipper et al., 2008; Frick et al., 2015). Conservation
50 interventions, such as population reintroductions, population reinforcements, and
51 captive assurance colonies can help stabilize threatened populations and prevent
52 extinctions (Bowkett, 2009; Martin et al., 2012; Batson et al., 2015). However, tests of
53 the effectiveness of conservation interventions are challenging because the
54 specification of a baseline scenario or “control” has a strong effect on evaluations of
55 success (Tavecchia et al., 2009). For example, a survival probability of 50% for
56 translocated individuals becomes most informative when compared to the survival
57 probability of resident individuals in the same habitat, and translocations can reduce
58 extinction risk in a target population even when survivorship is relatively low. Estimating
59 appropriate reference values for comparison is key to the evaluation of conservation
60 interventions and the adaptive management of endangered species.

61 Reinforcing or reintroducing endangered populations by releasing captive-reared
62 animals is a common intervention for stabilizing declining populations in a wide variety
63 of taxa, including birds (Jones et al., 2008), fish (Rakes, Shute, & Shute, 1999), frogs
64 (Griffiths & Pavajeau, 2008), lizards (Alberts, 2007), mammals (Kleiman, 1989), snakes
65 (Roe et al., 2010), and turtles (Burke, 2015). In some cases, species have been
66 successfully reintroduced from captive stock after temporary extinction in the wild,
67 including California condors (*Gymnogyps californianus*; Snyder & Snyder, 1989),
68 Mauritius kestrels (*Falco punctatus*; Jones et al., 2008), and black-footed ferrets
69 (*Mustela nigripes*; Dobson & Lyles, 2000). These programs are sometimes criticized for
70 the poor success rates of translocations involving captive-reared animals, high financial
71 costs, and challenges arising during captive husbandry (Snyder et al., 1996).

72 Poor survival of captive-reared animals may occur because of inexperience in
73 the release environment. Individuals may have lower survival and growth if they lack
74 experience foraging, avoiding predators, and seeking appropriate refuges from
75 environmental conditions (Bacon, Robert, & Hingrat, 2018). Individuals may also have
76 lower survival rates if they disperse or migrate away from release sites, and this is a
77 common reason for failures in translocations (Germano & Bishop, 2008). Testing for a
78 behavioural acclimation period (hereafter “acclimation period”) in population
79 reinforcement programs can identify opportunities to increase the number of captive-
80 reared animals recruited into the breeding population through training or releasing
81 animals into outdoor pens to expose them to local environmental conditions (“soft-
82 releases”) (White, Collazo, & Vilella, 2005; Batson et al., 2015). Furthermore,
83 quantifying relative survivorship through any effects of an acclimation periods is

84 important for predicting the number of captive-reared animals required to establish new
85 populations or increase recruitment in declining populations, and therefore essential for
86 estimating the costs of such programs (Tavecchia et al., 2009; Armstrong et al., 2017).

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

98 We used an existing headstarting program at the Ontario Turtle Conservation
99 Centre (OTCC, Selwyn, Ontario, Canada) to experimentally evaluate the effects of
100 headstarting on the fitness of juvenile Blanding’s turtle (*Emydoidea blandingii*). Low
101 recruitment in some areas may limit population growth (IUCN; van Dijk & Rhodin, 2011);
102 protection of adults may not be sufficient to slow long-term population declines.
103 Headstarting has been used to reinforce population size in *E. blandingii* (Arsenault,
104 2011; Buhlmann et al., 2015; Starking-Szymanski et al., 2018) and understanding the
105 fitness of headstarts relative to wild-hatched individuals is key to making cost-effective
106 management decisions. We used six years of data to test the hypothesis that

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

111 **Materials and Methods**

112 All use of animals in this study were approved by the Ontario Ministry of Natural
113 Resources and Forestry Wildlife Animal Care Committee (protocols 325, 16-325, 17-
114 325, 18-325) and authorized by permits from the Ontario Ministry of Natural Resources
115 and Forestry (Wildlife Custodian Authorization 20025217, Wildlife Scientific Collectors
116 Authorization 1073852, 1079730, 1082990, 1086260, and 1089569).

117 *Incubation, captive-rearing, and release*

118 We harvested eggs from gravid females injured on roads near the study site and
119 delivered to the OTCC hospital for treatment (details on medical treatment and methods
120 for egg harvesting available in the Supporting Information). We incubated eggs in
121 vermiculite and raised hatchling turtles indoors in tubs or aquaria for 24 months (range
122 24 – 48 months) to a mean mass of 183 g (range 89 – 420 g) and mean carapace
123 length of 99 mm (range 79 – 134 mm) until release. Prior to release, we attached VHF
124 radio transmitters (Models R1680 and R1860, Advanced Telemetry Systems, Isanti,
125 Minnesota, USA) to turtles' carapaces with epoxy (PC-7, LePage or JB WaterWeld).
126 The transmitters weighed less than 5% of turtle mass.

127 Headstarts were directly released (i.e. “hard-release”) into a protected area in
128 eastern Ontario with a resident population of *E. blandingii* (exact location omitted at the

129 request of the responsible agency). The area is a mosaic of lakes, wetlands, and forest.
130 In 2012, we released headstarts in two groups of 5. The first group was released
131 adjacent to water on a small rocky island in fen habitat, and the second group was
132 released adjacent to water on the opposite side of the same island. In 2013, 2016, and
133 2017 we released headstarts individually in fen habitat (Supporting Information; Fig. 1).

134 We captured wild-hatched juvenile ($n = 5$, carapace length = 99 ± 44 mm, mass =
135 171 ± 76 g) and adult ($n = 13$, carapace length = 195 ± 52 mm, mass = 1124 ± 300 g) *E.*
136 *blandingii* at the study site by hand and in sardine-baited hoop traps (30 cm, 50 cm, or
137 76 cm diameter; Memphis Net and Twine, Memphis, Tennessee, USA). Transmitters
138 were attached as described above, and wild-hatched turtles were released at their
139 capture location. We tracked wild-hatched juveniles from 2014 to 2017. We tracked
140 wild-hatched adults from 2013 to 2017.

141 We located turtles weekly to record the status (alive or dead) and locations (i.e.
142 “fixes”, ± 5 m) during the active season (April to September), and tracked turtles to their
143 over-wintering sites. We took monthly measurements of mass and mid-line carapace
144 length from April to September.

145 *Survivorship*

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

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

166 We compared our model-averaged estimates of survival to estimated survival
167 probabilities of wild-hatched turtles. We assumed the probability of an egg surviving

168 until hatching was 0.2610 (based on 16 years of data; Congdon, Dunham, & Van Loben
169 Sels, 1993), the probability of surviving from hatching to the first year was 0.375 (based
170 on 2 years of data; Paterson, Steinberg, & Litzgus, 2014), and the annual survivorship
171 from age 1 – 10 was 0.7826 (life table estimate based on 27 years of data; Congdon,
172 Dunham, & Van Loben Sels, 1993).

173 *Growth rates*

174 We compared growth rates of headstarts and wild-hatched juveniles using linear
175 mixed-effects broken-line regression models with the *lme4* package (Bates et al., 2015).
176 We used a linear model over von Bertalanffy or logistic growth models because growth
177 in juveniles is often linear (Lester, Shuter, & Abrams, 2004). We used carapace length
178 as the response variable in the first model, and we used mass as the response variable
179 in the second model. For both analyses, we included time since release (days), group
180 (headstarts or wild-hatched juvenile), and the interaction between time since release
181 and group as fixed effects. To test for a post-release acclimation period during which
182 headstarts may exhibit slower growth, we estimated the slopes for headstarts and wild-
183 hatched juveniles before and after a breakpoint. We identified meaningful breakpoints in
184 the regressions by searching across the observed range in time since release to find the
185 models with the minimum deviance. In both models, we included a random effect of
186 individual because individuals started at different sizes, and each was measured
187 multiple times. For both growth analyses, we excluded turtles that were only measured
188 within a single active season, and we only included wild-hatched turtles whose initial
189 carapace length was within the range of headstarts' carapace length at release. We

190 confirmed that linear models were appropriate for growth by examining the relationship
191 between residuals and fitted values (Supporting information).

192 *Spatial analysis*

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

209 We divided the absolute distance between each relocation by the difference in
210 time elapsed to estimate daily distance travelled, and then calculated the mean daily
211 distance travelled per individual. We only used turtles with ≥ 10 locations for this
212 analysis and locations separated by less than 14 days. We used a mixed-effects linear

213 model with the mean daily distance travelled as the response, the group (headstarts in
214 first year post-release, headstarts after the first year post-release, wild-hatched
215 juveniles, wild-hatched adults) as the predictor variable, and turtle identity as a random
216 effect. We also used a linear model to test whether headstarts' daily distance travelled
217 was affected by carapace length and release cohort.

218 *Habitat use*

219 We classified the study site into five land cover categories using seven
220 environmental variables derived from satellite imagery and a digital elevation model
221 (DEM). We defined the study area as the minimum convex polygon around all turtle
222 locations with a 2 km buffer. We used satellite imagery from Sentinel-2 (SERCO, 2017)
223 taken on June 23, 2016 with four-band (blue, green, red, near infrared) spectral regions
224 at 10 m resolution. Multispectral bands were used to represent the study area
225 topography and to derive the Normalized Difference Vegetation Index (NDVI; Rouse et
226 al., 1974), which is characterized along a scale from -1 to +1 where values around or
227 below 0 typically indicate no vegetation present, and higher values indicate green
228 vegetation (Chakraborty et al., 2018). We rescaled a 2 m DEM from the Land
229 Information Ontario database (Digital Raster Acquisition Project Eastern Ontario; Land
230 Information Ontario, 2014) to 10 m to match the resolution of the multispectral bands.
231 We used the DEM as a proxy for wetness and for characterizing low-lying wetlands, and
232 to derive the slope gradient.

233 We classified each pixel in the study site into one of five land cover classes
234 (adapted from Anderson 1976; Table 1) using a Random Forest (RF) algorithm
235 (Breiman, 2001) using the *randomForest* package (Liaw & Wiener, 2002). The four-

236 band Sentinel-2 satellite image was combined with elevation estimated from the DEM,
237 NDVI, and slope gradient layers to create a seven-band composite used as the input for
238 the RF landcover classification. We used a training set (924 points) and 500 trees for
239 the classification with an out-of-bag error rate of 0.54% (Supporting Information). We
240 compared the proportion of headstart and wild-hatched juvenile locations in each
241 landcover type with a Chi-square test.

242 **Results**

243 *Tracking*

244 We tracked 5 wild-hatched juveniles to 117 locations (26 ± 2 locations per turtle),
245 and the 13 wild-hatched adults to 352 locations (26 ± 4 locations per turtle). We
246 released and tracked 35 headstarts between 2012 and 2017 to 894 locations (27 ± 4
247 locations per turtle).

248 *Survivorship*

249 All tracked, wild-hatched turtles survived for the duration of the study. Of 35
250 headstarts, seven were lost (either the transmitter failed, or the turtle moved out of
251 range where it could be detected). Twelve survived to the end of the study and 16 died,
252 with high mortality in some cohorts and low mortality in others (Fig. 1). Eleven
253 mortalities were from predators, four occurred during overwintering, and one died of
254 unknown causes. The turtle that died of unknown causes was lethargic and was brought
255 into captivity on 31-07-2017 and died on 04-08-2017. Post mortem findings were
256 inconclusive. The most-supported known-fate survival model for headstarts included
257 effects of cohort and experience on monthly survival probability. Models including body

258 size were also strongly supported (Table 2); turtles that survived the first year post-
259 release had subsequent monthly survival probability of 0.98 (95% CI: 0.92 – 1.0; Fig. 1).
260 The probability of a headstart surviving for 10 years (the approximate time to reach
261 maturity) was 0.03 (95% CI: 0.000013 – 0.54). The probability of a wild-hatched turtle
262 surviving from an egg to 10 years was 0.01 based on survival rates at other sites
263 (Congdon, Dunham, & Van Loben Sels, 1993; Paterson, Steinberg, & Litzgus, 2014).
264 Headstart survival probabilities were similar between the active season and the
265 overwintering season (Supporting Information). Monthly survival of headstarts increased
266 with carapace length at release, but the predicted difference in survival probability was
267 low (total change in monthly survival = 0.07) across the range of carapace lengths
268 (Supporting Information).

269 *Growth rates*

270 In the first 562 days post-release, wild-hatched juvenile carapace lengths grew
271 faster (0.020 ± 0.002 mm/day) than headstarts (0.004 ± 0.002 mm/day; $F = 30.03$, $df =$
272 $1, 234$, $P < 0.001$; Fig. 2). After 562 days post-release, headstarts grew (0.015 ± 0.002
273 mm/day) at a similar rate to wild-hatched juveniles (0.012 ± 0.008 mm/day; $F = 0.12$, df
274 $= 234, 1$, $P = 0.73$). The carapace length model with a breakpoint in slope performed
275 better than a model with no change in slope ($\chi^2 = 41.27$, $df = 2$, $P < 0.001$).

276 In the first 445 days post-release, wild-hatched juvenile mass increased faster
277 (0.019 ± 0.001 g/day) than headstarts (-0.003 ± 0.017 g/day; $F = 10.56$, $df = 1, 234$, $P =$
278 0.001). After the first 445 days post-release, headstarts grew (0.068 ± 0.01 g/day) at a
279 similar rate to wild-hatched juveniles (-0.001 ± 0.038 g/day; $F = 3.18$, $df = 234, 1$, $P =$

280 0.08). The mass regression model with a breakpoint in slope performed better than a
281 model with no change in slope ($\chi^2 = 15.78$, $df = 2$, $P < 0.001$).

282 *Spatial analysis*

283 Home range size for turtles with ≥ 5 locations varied from 0.003 to 28.0 ha. Home
284 range size (log-transformed) increased with the number of locations ($F = 8.79$, $df = 1$,
285 56, $P < 0.005$) and differed among groups ($F = 12.00$, $df = 3$, 54, $P < 0.0001$).

286 Headstarts had smaller home ranges in their first year than headstarts after the first
287 year, wild-hatched juveniles, and wild-hatched adults ($P < 0.001$ for all three
288 comparisons). Home range size was similar for headstarts after the first year post-
289 release, wild-hatched juveniles, and wild-hatched adults ($P > 0.05$ for all pair-wise
290 comparisons; Fig. 3). The model explained more than half of the variation in home
291 range size (approximate multiple $R^2 = 0.62$). Headstart home range size was similar
292 among release cohorts ($F = 0.18$, $df = 2$, 10, $P = 0.83$) and was unaffected by starting
293 carapace length ($F = 3.13$, $df = 1$, 10, $P = 0.11$).

294 Mean daily distance travelled differed among groups ($F = 12.74$, $df = 3$, 30, $P <$
295 0.0001). Headstarts moved less in the first year post-release (3 ± 1 m/day) than all other
296 groups ($P < 0.05$ for all pairwise comparisons). Mean daily distances travelled were
297 similar for headstarts after their first year (11 ± 1 m/day), juvenile wild-hatched turtles
298 (14 ± 2 m/day), and wild-hatched adults (14 ± 2 m/day; Fig. 4). The mean daily distance
299 travelled by headstarts did not differ among release cohorts ($F = 2.92$, $df = 2$, 8, $P =$
300 0.11) and was unaffected by carapace length at release ($F = 0.02$, $df = 1$, 8, $P = 0.90$).

301 *Habitat use*

302 Landcover classification had an overall accuracy of 80.8%. Turtles were usually
303 tracked to wetlands (headstarts = 67.8% of locations; wild-hatched = 63.2% of
304 locations) and forested upland (headstarts = 29.5%; wild-hatched = 35.0%). Limited
305 locations occurred in (deeper) water (headstarts = 2.2% of locations; wild-hatched =
306 0.9% of locations) or rock barrens (headstarts = 0.8%; wild-hatched = 0.9%), and none
307 were found in shallow algae-dominated water. The proportion of locations per landcover
308 type did not differ between headstarts and wild-hatched juveniles ($\chi^2 = 3.08$, $df = 3$, $P =$
309 0.38).

310 Discussion

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

321 Once headstarts survive their first year, monthly survival (0.98) becomes
322 comparable to survival estimates for wild-hatched juveniles (0.98/month, 0.7826/year)
323 from a well-studied population in Michigan (Congdon, Dunham, & Van Loben Sels,

324 1993). Extrapolating our monthly survival (0.89/month in the first year, 0.98/month
325 subsequently) to 10 years (the approximate time for a released headstart to reach
326 maturity), we estimate that we would have to release approximately 36 headstarts to
327 recruit one adult to the population. Extrapolating our survival estimate of wild-hatched
328 turtles to 10 years, we estimate 93 eggs must be laid to recruit one adult to the
329 population. This difference is largely driven by the first year of survival (0.10 for wild-
330 hatched turtles, 0.25 for headstarts after release), including mortality after hatchlings
331 emerge. Therefore, survival rates of turtle hatchlings from *in situ* conservation strategies
332 such as nest protection (Enneson & Litzgus, 2008; Riley & Litzgus, 2013) are still lower
333 than our headstarts' survival rates. A full cost-benefit analysis of the tools available for
334 turtle conservation is outside the scope of this study, but our results support
335 headstarting as a viable tool for population reinforcement if the necessary resources are
336 available. Since we found little effect of body size on survival rates of headstarts (up to
337 130 mm carapace length), releasing a higher number of smaller headstarts may be
338 more cost-effective.

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

347 Changing our release methods to better prepare headstarts prior to release or to
348 provide more support in the wild might further increase survival in the first year post-
349 release. For example, headstarts could be kept briefly in outdoor pre-release enclosures
350 to allow acclimation to weather patterns and noises. Releasing animals into outdoor
351 enclosures increased survival, site fidelity, and reproductive success in reintroduced
352 burrowing owls (*Athene cunicularia*; Mitchell, Wellicome, Brodie, & Cheng, 2011). In
353 contrast, releasing animals into outdoor enclosures (“soft-releases”) did not increase
354 survival in headstarted desert tortoises (*Gopherus agassizii*; Nagy et al., 2015) or
355 smooth green snakes (*Opheodrys vernalis*; Sacerdote-Velat et al., 2014), and did not
356 increase site fidelity of hare wallabies (*Lagostrophus fasciatus*; Hardman & Moro, 2005).
357 Future work should test the effects of acclimation in outdoor enclosures on survival and
358 behaviour in Blanding’s turtles. Survival of headstarts might increase if initial release
359 into enclosures shortened the observed acclimation period. Alternately, turtles in such
360 enclosures could inadvertently become habituated to potential predators (for example,
361 birds of prey that might come investigate the enclosures).

362 Our results are especially encouraging because of the relative ages and
363 experience of the headstarts and wild-hatched individuals we studied. Growth rates of
364 wild hatchlings are lower than growth rates of hatchlings in captivity, which consume a
365 consistent, nutritious diet and do not brumate during the winter. Our “controls” are likely
366 approximately twice the age of the headstarts, with experience commensurate with their
367 age. Direct comparisons of headstarts and wild-hatched juveniles in our study must
368 consider that wild-hatched juveniles have already undergone a process of selection
369 under the conditions specific to our study site. Wild, hatchling turtles typically

370 experience higher mortality in the first few years of life (Congdon, Dunham, & Van
371 Loben Sels, 1993). Our “control” group is made up of individuals that survived this
372 selective filter and are thus more likely to survive than the average hatchling. In
373 contrast, we provided the minimum possible support to our headstarts, and the direct
374 release methods we used in this study may represent a worst-case scenario (Bright &
375 Morris, 1994). Even under these conditions, headstarts used similar habitat to wild-
376 hatched turtles, and had survivorship, growth rates and behaviour similar to those of
377 wild-hatched, well-adapted individuals after a brief acclimation period.

378 The post-release acclimation period we observed cannot be attributed solely to
379 the effects of headstarting, *per se*. Captive-reared individuals face two distinct
380 challenges on release (Bright & Morris, 1994). First, depending on the resources
381 available in captivity, captive-reared individuals may have no experience with “natural”
382 conditions, and ours did not (i.e. cost of captivity). Second, they have no experience
383 with the specific conditions of the release site (i.e. cost of release). This second
384 challenge is equally relevant to translocations of wild-hatched individuals from one site
385 to another (Dodd & Seigel, 1991; Nagy et al., 2015), and a similar acclimation period
386 occurs in some reptile translocations. Translocated, wild-hatched, subadult gopher
387 tortoises (*Gopherus polyphemus*) and adult eastern box turtles (*Terrapene carolina*
388 *carolina*) exhibited decreased survivorship in the first year at their new site, but
389 subsequently survived as well as established individuals (Cook, 2004; Tuberville et al.,
390 2008). Translocated eastern hog-nosed snakes (*Heterodon platyrhinos*) and
391 headstarted northern water snakes (*Nerodia sipedon*) exhibited different behaviours and
392 lower survivorship than their resident or wild-raised counterparts (Plummer & Mills,

393 2000; Roe et al., 2010). In contrast, no decline in survivorship was associated with
394 translocations of adult *G. polyphemus* or eastern musk turtles (*Sternotherus odoratus*,
395 Attum, Cutshall, Eberly, Day, & Tietjen, 2013; Tuberville, Norton, Todd, & Spratt, 2008).
396 It would require a meta-analysis to clarify the overall role of captivity versus site-specific
397 factors in these datasets, and might still not provide information relevant to our site
398 (Bennett et al., 2017). At our study site, the effects of head-starting and translocation
399 could be disentangled by introducing translocated wild-hatched individuals and
400 comparing their fitness to headstarts and wild-hatched residents.

401 Evaluating the effects of perturbations on populations of long-lived species
402 requires long-term monitoring (Franklin, 1989; Magurran et al., 2010; King, Chamberlan,
403 & Courage, 2012; Canessa et al., 2016); our current data capture only a six-year
404 snapshot. We can most accurately estimate recruitment of our headstarts to the
405 breeding population by tracking them to maturity and comparing their reproductive
406 success to their wild-hatched counterparts. Similar studies on other taxa show varied,
407 long-term effects of translocations and captive-rearing. Captive-reared and wild-born,
408 translocated Western lowland gorillas (*Gorilla gorilla gorilla*) that survived their first two
409 years post-release achieved the same reproductive success as wild-raised gorillas
410 (King, Chamberlan, & Courage, 2012). Reintroduced, translocated Mediterranean pond
411 turtles (*Mauremys leprosa*) showed high survivorship but no measureable reproductive
412 output following reintroduction (Bertolero & Oro, 2009), while captive-reared, released
413 female pheasants (*Phasianus colchicus*) were less likely to survive to breeding, and
414 exhibited reduced reproductive output compared to wild counterparts (Musil et al.,
415 2009).

416 Evaluating conservation interventions is critical to inform management decisions
417 and allocate limited funds (Enneson & Litzgus, 2008; Martin et al., 2018). Here, we
418 applied a site-specific experimental approach to compare fitness between captive-
419 reared and wild-hatched individuals, as has been done elsewhere (Musil et al., 2009;
420 Nussear et al., 2012; Attum et al., 2013; Nagy et al., 2015). Our approach provided a
421 proxy of short-term success for headstarting in *E. blandingii*, and we identified a critical
422 post-release acclimation period during which additional support might increase
423 headstart fitness. Our estimated headstart survival rates indicate that this population
424 reinforcement program has the potential to increase recruitment in *E. blandingii*, but we
425 need to monitor headstarts as they reach maturity to measure the effects headstarting
426 has on population viability.

427 **Data Accessibility**

428 If accepted, data from our manuscript will be archived in the Dryad Digital Repository.

429 **Supporting Information**

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

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440

441

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638

639 **Tables**

640 **Table 1.** Land cover classes and descriptions based on the Canadian wetland
641 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 Open 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)

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644

645 **Table 2.** Known-fate survival models of headstarted Blanding's Turtles (*Emydoidea*
646 *blandingii*), ranked from most to least supported. k = number of parameters; AIC_c =
647 Akaike's information criterion; ΔAIC_c = difference in AIC_c between a model and the top-
648 ranked model; ω = Akaike weight. CL = Carapace Length.

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

^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

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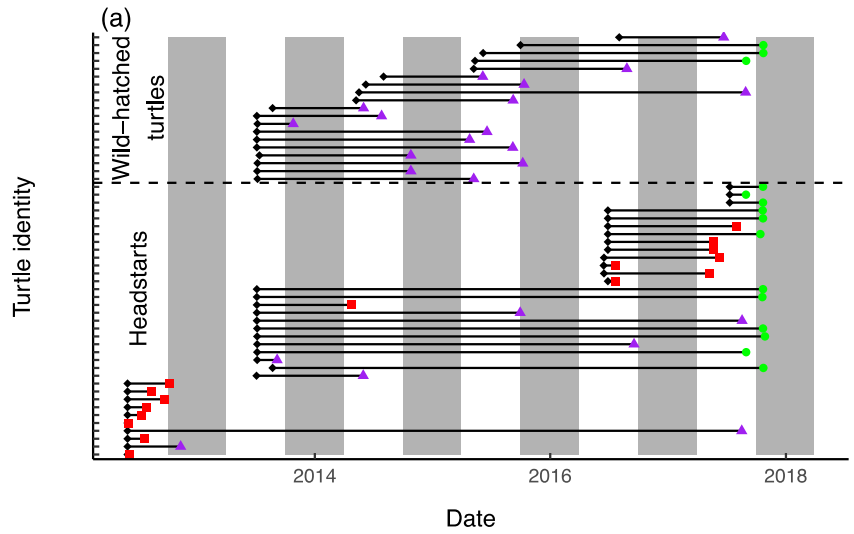
650 **Figure Legends & Figures**

651 **Figure 1.** (a) Timeline of the headstarting study, showing 19 wild-hatched and 35
652 headstarted, released Blanding's Turtles (*Emydoidea blandingii*; 2012-2017). Gray bars
653 represent winters (October – March). (b) Predicted monthly survival probability (\pm 95%
654 CI) of headstarts and wild-hatched turtles during the active season (April - September),
655 derived from model-averaging known-fate models within 4 AIC_c of the most-supported
656 model.

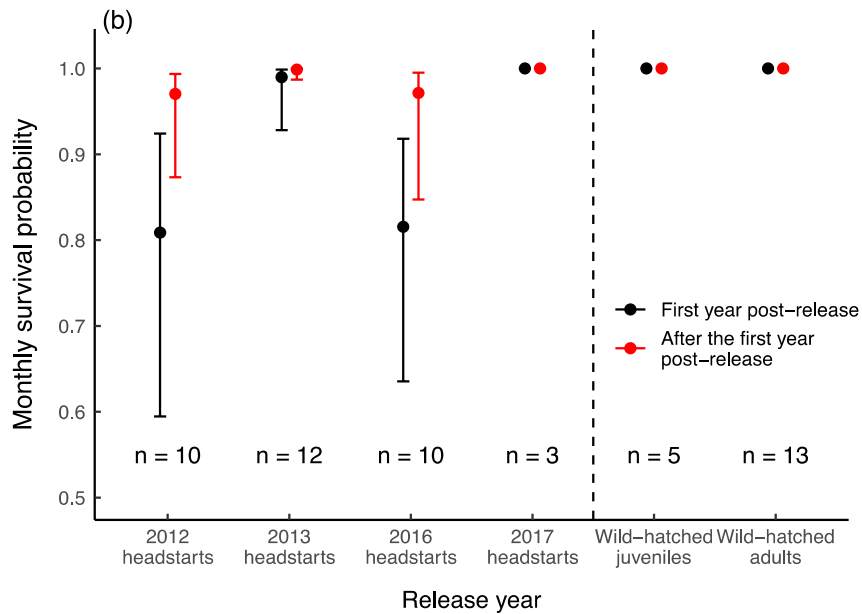
657 **Figure 2.** (a) Post-release size (carapace length; mm) of headstarted and wild-hatched
658 Blanding's Turtles (*Emydoidea blandingii*). (b) Carapace length growth rate (mm/day) of
659 headstarts and wild-hatched juveniles (Δ carapace length/day). Thick horizontal lines:
660 medians; box outlines: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

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

664 **Figure 4.** The mean distance travelled per day by headstarts, wild-hatched juveniles,
665 and wild-hatched adult Blanding's Turtles (*Emydoidea blandingii*). Thick horizontal lines:
666 medians; box outlines: 25th and 75th percentiles.



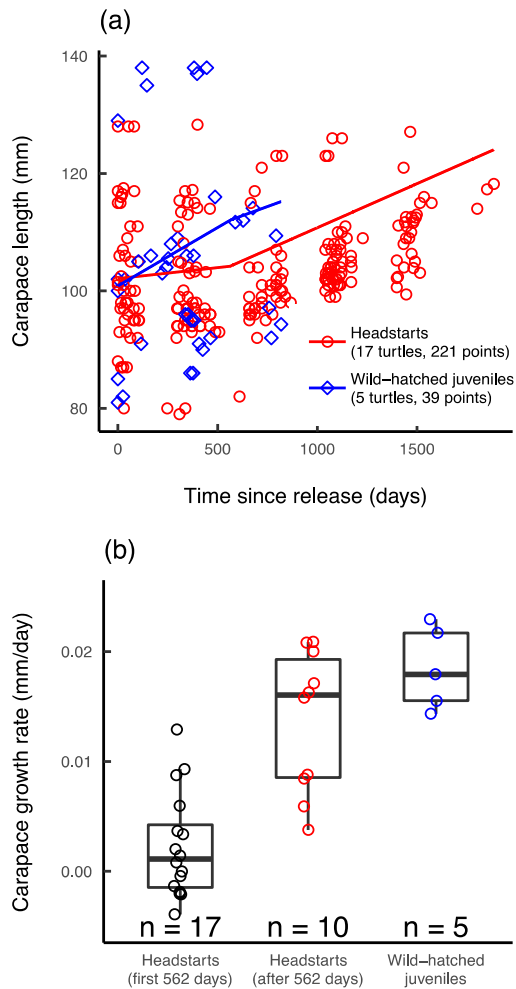
Legend ● alive ■ dead ▲ lost ◆ release



667
 668 **Figure 1.** (a) Timeline of the headstarting study, showing 19 wild-hatched and 35
 669 headstarted, released Blanding’s Turtles (*Emydoidea blandingii*; 2012-2017). Gray bars
 670 represent winters (October – March). (b) Predicted monthly survival probability (± 95%
 671 CI) of headstarts and wild-hatched turtles during the active season (April - September),

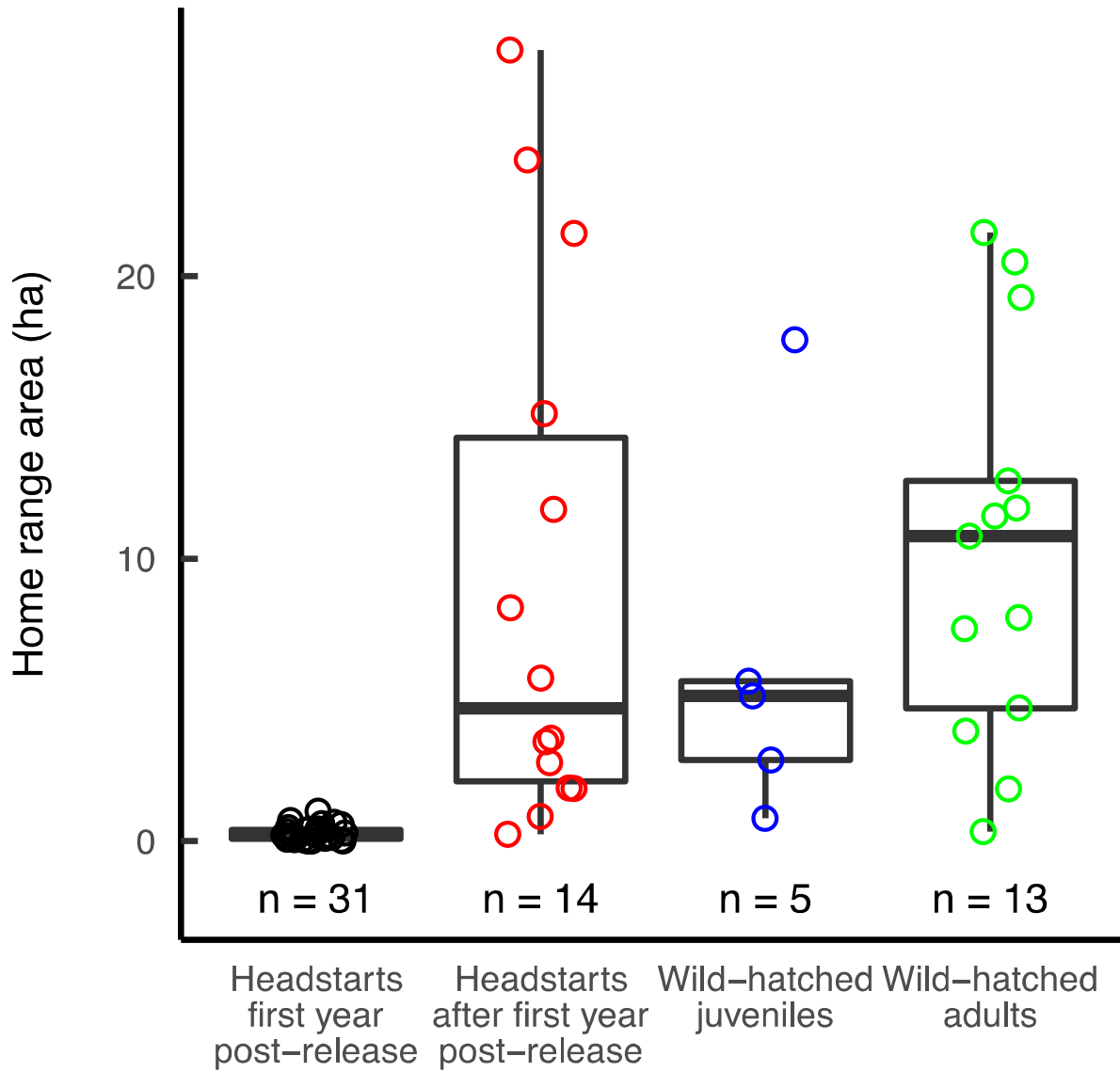
672 derived from model-averaging known-fate models within 4 AIC_c of the most-supported
673 model.

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675

676 **Figure 2.** (a) Post-release size (carapace length; mm) of headstarted and wild-hatched
677 Blanding's Turtles (*Emydoidea blandingii*). (b) Carapace length growth rate (mm/day) of
678 headstarts and wild-hatched juveniles. Thick horizontal lines: medians; box outlines:
679 25th and 75th percentiles.

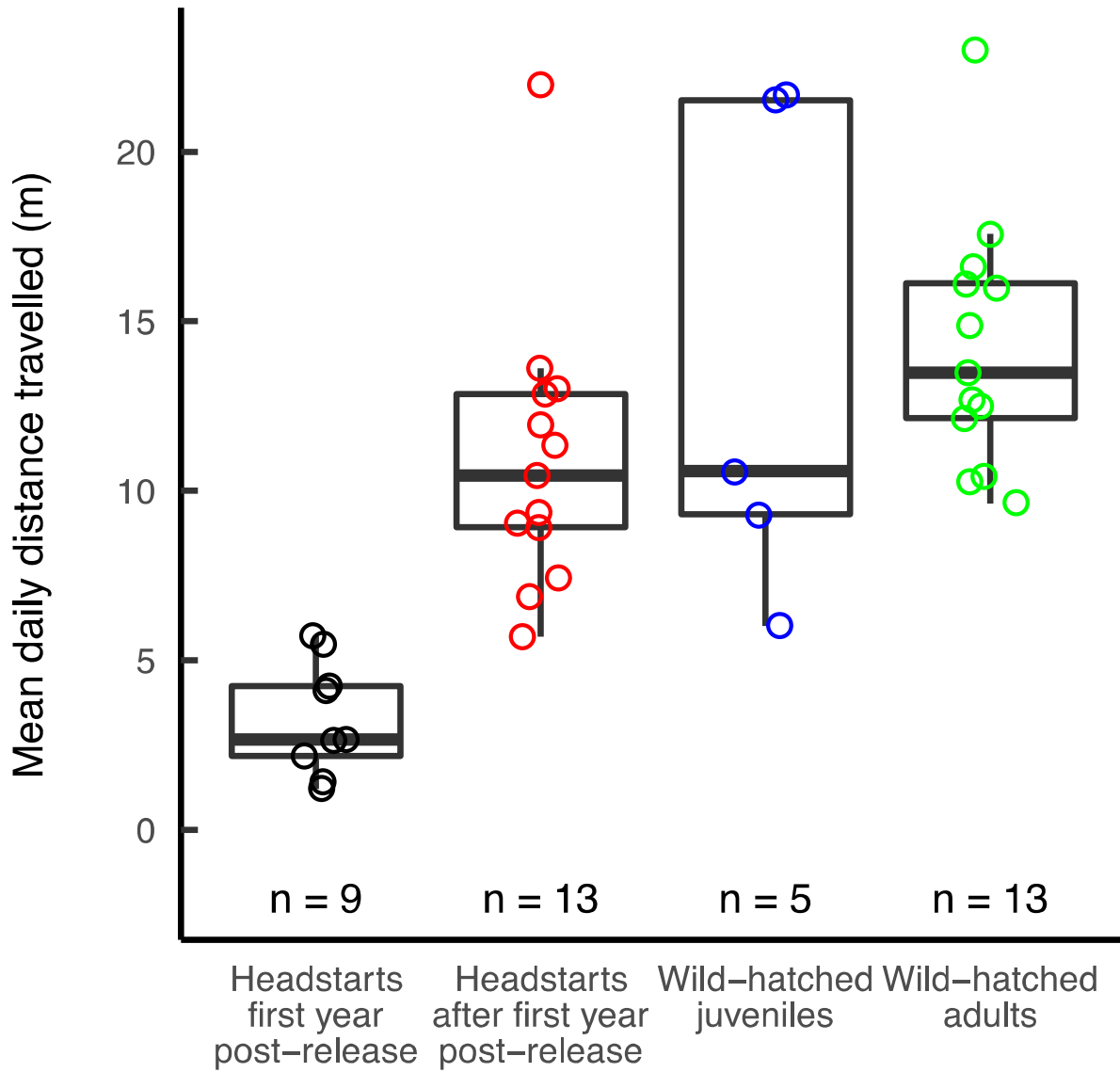


680

681 **Figure 3.** Home range size of headstarted, wild-hatched juvenile, and wild-hatched

682 adult Blanding's Turtles (*Emydoidea blandingii*). Thick horizontal lines: medians; box

683 outlines: 25th and 75th percentiles.



684

685 **Figure 4.** The mean distance travelled per day by headstarts, wild-hatched juveniles,
 686 and wild-hatched adult Blanding's Turtles (*Emydoidea blandingii*). Thick horizontal lines:
 687 medians; box outlines: 25th and 75th percentiles.