

Effects of body size, habitat selection and exposure on hatchling turtle survival

J. E. Paterson^{1*}, B. D. Steinberg² & J. D. Litzgus¹

¹ Department of Biology, Laurentian University, Sudbury, Canada

² Ontario Parks, Ontario Ministry of Natural Resources, Peterborough, Ontario, Canada

Keywords

ectotherm; mortality; reptile; bigger is better; survivorship.

Correspondence

James E. Paterson, Department of Biology, Laurentian University, Sudbury, P3E 2C6 Canada. Email: james.earle.paterson@gmail.com

*Current address: Department of Biology, University of Ottawa, Ottawa, Canada.

Editor: Mark-Oliver Rödel

Received 13 January 2014; revised 12 August 2014; accepted 15 August 2014

doi:10.1111/jzo.12176

Abstract

Iteroparous species invest little energy into annual reproduction and tend to experience low and variable survivorship in young life stages. However, juveniles with traits that increase survival will have a fitness advantage over conspecifics, and usually bigger is better for juvenile vertebrates. Understanding behavioural and morphological characteristics that increase fitness is important for our understanding of the evolution of life-history strategies. We outfitted naturally emerging hatchlings of two species of turtles (Blanding's turtles *Emydoidea blandingii* and wood turtles *Glyptemys insculpta*) with radio transmitters to test five hypotheses related to survival from nests to overwintering sites using logistic regression models. In contrast to the widely supported hypothesis that bigger is better for survival of juveniles, we found that smaller hatchlings of both species were more likely to survive from emergence to overwintering. In *E. blandingii*, hatchlings that emerged later in the year, which reduced exposure time to predators and environmental risks, and spent less time in upland open habitat, were also more likely to survive. Our results demonstrate that bigger is not always better in juvenile ectotherms. Assuming bigger is better without observations of survival can lead to erroneous conclusions related to fitness proxies and the ontogeny of body size in populations. The observed relationship between habitat selection and survival in *E. blandingii* indicates a direct link between behaviour (habitat selection) and fitness through mortality caused by predators and environmental stressors.

Introduction

Variation in stage-specific survivorship and reproductive success may shape evolutionary changes and the evolution of life histories in organisms (Stearns, 1977; Michod, 1979). Therefore, phenotypic variation in adult populations may arise from differential fitness of juvenile stages. For example, Lailvaux *et al.* (2004) observed alternative male phenotypes in *Anolis* lizards and attributed them to differences in selective pressure arising from male–male combat at transition sizes between small and large lizards. Lindell, Forsman & Merila (1993) examined ventral scale counts in adders *Vipera berus*, which were correlated to body size. They found that the mean number of ventral scales was lower in juveniles than adults and that growth rate was positively correlated with scale count, suggesting that scale counts of the adults result from selection for fast-growing and larger juveniles. In these cases, observed differences in phenotype frequencies arise from selection for a trait at earlier life stages. In long-lived species, variation in survival is often low in adults, and this lowers the strength of natural selection to modify phenotypic traits. However, in juvenile life stages for which survival is low or

extremely variable, there are stronger selective pressures acting on behavioural or physical traits that maximize fitness.

Freshwater turtles typically have high adult survivorship and long lifespans (Congdon, Dunham & van Loben Sels, 1993; Heppell, 1998), and these traits present challenges for testing hypotheses regarding mortality sources and the evolution of life-history strategies for adults. However, hatchling turtles undergo a period of extremely high mortality resulting from predators and environmental stressors, such as water loss and thermal stress, when moving from nests to aquatic habitats (Myers, Tucker & Chandler, 2007; Castellano, Behler & Ultsch, 2008). These mortality sources could impose strong selective pressure for heritable behavioural and physical characteristics that maximize juvenile survival. Several field experiments have examined variation and selection for body size of turtles during the hatchling life stage (Tucker, 2000; Kolbe & Janzen, 2002; Janzen, Tucker & Paukstis, 2007), but none have used natural variation in emergence time or radio-telemetry to directly measure mortality at natural population densities. Understanding major sources of mortality and their timing is important for conservation actions regarding turtles, including nest protection, headstarting and habitat

management, and for understanding distributions of phenotypes in later life stages.

We used hatchlings emerging from natural nests to test five hypotheses that could explain observed patterns of survival for two freshwater turtle species [*Emydoidea blandingii* (Holbrook, 1836) and *Glyptemys insculpta* (Agassiz, 1857)] in Canada. First, the early emergence hypothesis (H1) suggests that survival is higher at thermally buffered overwintering sites than in habitats surrounding the nest because there is less risk of predation and thermal extremes. Therefore, hatchlings that emerge earlier to move to overwintering sites are more likely to survive because they avoid predators that cue in to the presence of hatchlings at or near the nest (prey switching mechanism; Tucker, Paukstis & Janzen, 2008) and they avoid risks of thermal extremes that occur later in the season, such as fall cold snaps. Second, under the reduced exposure hypothesis (H2), probability of survival is inversely related to the amount of time spent above ground between emergence from the nest and overwintering (length of exposure). Therefore, hatchlings that emerge later are more likely to survive because of a lower cumulative probability of mortality from predators and exposure to unfavourable environmental conditions. Third, the bigger is better hypothesis (H3) predicts that larger hatchlings are more likely to survive because size gives an advantage against predators and water loss, either directly via gape-limited predation or indirectly through effects on performance, such as speed or endurance (Janzen *et al.*, 2007). Fourth, in the habitat use hypothesis (H4), hatchling survival is directly related to the types of habitats that hatchlings choose to occupy after emerging from the nest. If certain surrounding habitats provide a fitness benefit, then hatchling survival will be positively related to the amount of time spent in those habitats. Finally, in the null hypothesis (H5), hatchling survival is a stochastic event and not related to size, exposure time or habitat use. Our study is unique because it uses wild hatchlings incubated in natural nests and follows survival at natural abundance levels rather than survival following release experiments (Janzen, Tucker & Paukstis, 2000a,b; Janzen *et al.*, 2007) where high hatchling density and low variance in release times may not reflect natural ecosystem patterns.

Materials and methods

Study site and hatchlings

The study site was in Algonquin Provincial Park, Ontario, Canada. Land cover is a mosaic of wetlands in a primarily coniferous forest. The exact location is not revealed to protect the populations from poaching. Nesting sites of *E. blandingii* and *G. insculpta* were monitored in 2009 and 2010. Nests were protected from predation with hardware cloth cages and monitored daily from August to October for emerging hatchlings. Two cohorts (2009 and 2010) of each species were tracked. Carapace lengths of hatchlings were measured to the nearest 0.01 cm with 15-cm calipers (Scherr-Tumico, St James, MN, USA). Hatchlings greater than 8 g that emerged naturally from nests were outfitted with radio transmitters

(Model A2245, Advanced Telemetry Systems, Isanti, MN, USA; 0.55 g). Of all hatchlings, 25% of *E. blandingii* and 35% of *G. insculpta* hatchlings were too small for transmitters. Transmitters were attached to the mid-carapace using epoxy (LePage, Brampton, ON, Canada); the package was 5–8% of hatchling body mass. Hatchlings were released at their nest site within 1 h of processing. Although the attachment of transmitters may alter the behaviour of animals (White & Garrott, 1990), all individuals received the same manipulation and were not recaptured after release. We believe that hatchling turtle behaviour with transmitters is comparable with non-manipulated animals. Hatchlings were tracked every 1–3 days, from emergence until they died or until 15 October 2009 or 6 October 2010, using a three-element Yagi antenna and a R410 Scanning Receiver (Advanced Telemetry Systems). By these dates, all living turtles were at overwintering sites. Transmitters were expected to last 60 days. The coordinates of radio-telemetry locations were recorded with a handheld global positioning system (GPS) unit (GPSmap 76CSx, Garmin, Kansas City, KS, USA). The telemetry data were used for a habitat selection study (Paterson, Steinberg & Litzgus, 2012), and the current study used those data to test H4. At each radio location, hatchlings were classified as alive, dead or lost. Lost hatchlings were assumed to be dead if they were not relocated within 2 weeks. For all analyses below, 90 hatchlings were used: 48 *E. blandingii* and 42 *G. insculpta*.

Habitat use, exposure time and survival

To test whether habitat use significantly affected hatchling survival to winter (H4), we quantified the proportion of locations in different habitat types for each hatchling. Habitats were classified into one of 10 categories based on water source, substrate and vegetation (Paterson *et al.*, 2012). The entire site was mapped using ArcGIS 9.2 (ESRI, Redlands, CA, USA) and a combination of existing mapping databases, orthophotographs and ground-truthing with a handheld GPS (GPSmap 76CSx, Garmin). We conducted a principal component analysis (PCA) on the proportion of telemetry points in each habitat type to summarize habitat use into simplified variables. The first component was used as the numerical description of habitat use for each hatchling. Separate PCAs were performed for each species because of the differences in habitat types available to each species.

Exposure time was calculated as the difference between the last day of tracking and when a turtle emerged from its nest. In the first sampling year, the last day of tracking was 15 October 2009. In the second year, the last day was 6 October 2010. Turtles that emerged earlier in the year had longer exposure times.

We used mixed-effects logistic regression to test whether survival of hatchlings was related to body size, exposure time and habitat use. We used the three explanatory variables as fixed effects. Clutch and year (2009 and 2010) were included as random effects to control for maternal (genetic) effects and weather differences, respectively. We used linear regressions to test whether explanatory variables were independent. Because the habitat use, biology and emergence dates varied between

species, separate analyses were conducted for *E. blandingii* and *G. insculpta*. We constructed seven regression models using combinations and subsets of the three fixed effects and one null model (eight total models per species) and used Akaike's information criterion, corrected for small sample sizes (AIC_c) to evaluate models (Burnham & Anderson, 2002). Only models for which main fixed effects were significant ($P < 0.05$) were considered supported. All models were initially constructed as fully factorial, but interaction terms are shown only when significant. Cubic splines were also estimated (Schluter, 1988) to visualize the relationship between survival and explanatory variables for the best model of each species. Estimated splines are presented with 95% confidence intervals calculated using 100 bootstraps. All statistical analyses were performed using R (R Development Core Team, 2012) and logistic regression models were constructed using the 'lme4' package (Bates, Maechler & Bolker, 2011).

Results

Survival of *E. blandingii*

Of the 48 *E. blandingii* hatchlings tracked, 30 did not survive (62.5% mortality rate). Carapace length of radio-tagged *E. blandingii* hatchlings was 3.37 ± 0.01 cm (range 3.06–3.49 cm). Radio-tagged hatchlings were larger than non-tagged hatchlings (3.27 ± 0.01 cm; range 2.73–3.58 cm). Emergence time, and therefore exposure time, varied widely. In the first sampling year, hatchlings emerged from 28 August 2009 to 27 September 2009. In the second year, hatchlings emerged from 14 August 2010 to 22 September 2010. The first

principal component of habitat use (PC1) explained 73% of the variation in habitat use among individuals. More positive values of PC1 indicated hatchlings spent more time in upland open habitat, and more negative values indicated hatchlings spent more time in forest and marsh habitats (Fig. 1a). The first two principal components cumulatively explained 99% of the variance in habitat use among hatchlings.

Carapace length was not related to exposure time [$F = 0.23$, degrees of freedom (d.f.) = 1, 46, $P = 0.64$, $r^2 = 0.005$], or habitat use ($F = 2.45$, d.f. = 1, 46, $P = 0.12$, $r^2 = 0.05$). However, exposure time was negatively correlated with the first principal component of habitat use ($F = 9.10$, d.f. = 1, 46, $P = 0.0042$, $r^2 = 0.16$). All but one logistic regression model performed significantly better than the null model, where survival was not related to size, exposure time or habitat (Table 1). In the best logistic regression model ($AIC_c = 57.12$), hatchling survival was significantly inversely related to carapace length (coefficient = -11.24 , $z = 1.91$, $P = 0.05$, Fig. 2a), inversely related to exposure time (coefficient = -0.15 , $z = 2.17$, $P = 0.030$) and inversely related to PC1 of habitat use (coefficient = -4.21 , $z = 2.97$, $P = 0.0030$, Fig. 2b).

Survival of *G. insculpta*

Of the 42 *G. insculpta* hatchlings tracked, 36 did not survive (85.7% mortality rate). Carapace length of radio-tagged *G. insculpta* hatchlings was 3.37 ± 0.02 cm (range 3.10–3.59 cm). Tracked hatchlings were larger than those not tracked (3.27 ± 0.02 cm; range 2.94–3.58 cm). In the first sampling year, hatchlings emerged from 24 August 2009 to 28 September 2010. In the second year, hatchlings emerged

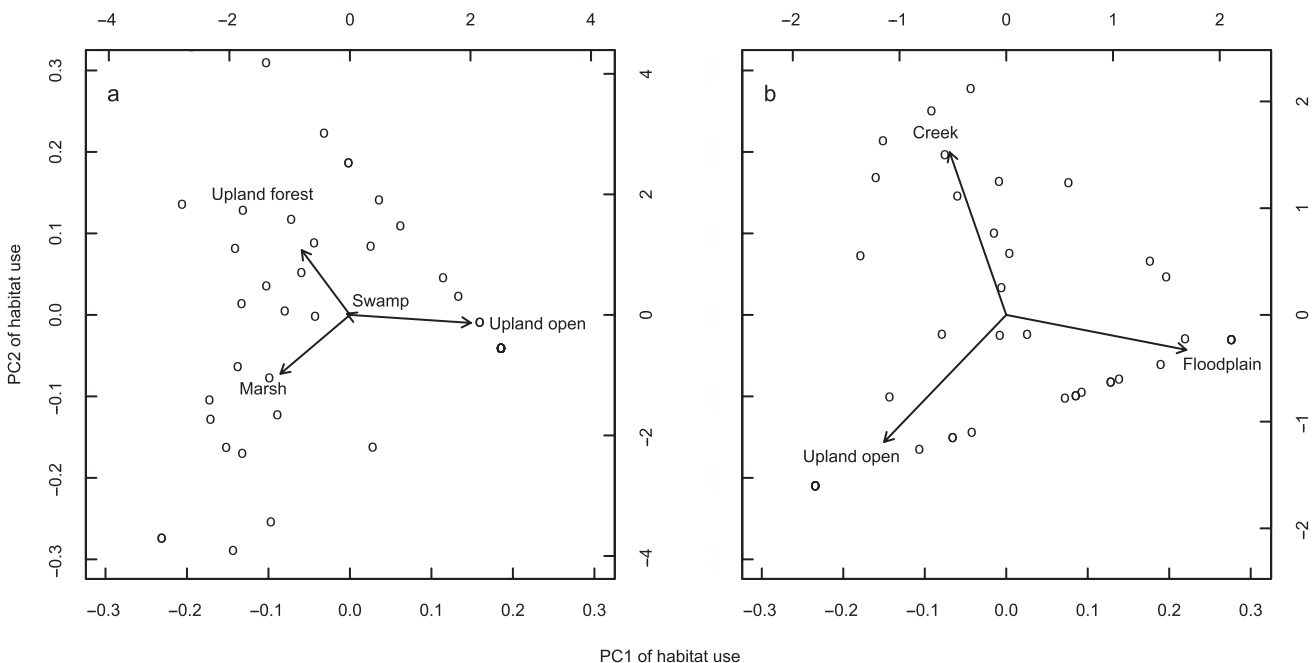


Figure 1 Biplot of principal component analyses for habitat use by hatchling (a) *Emydoidea blandingii* ($n = 48$) and (b) *Glyptemys insculpta* ($n = 42$).

Table 1 Summary of the eight logistic regression models constructed to explain survival patterns of hatchling turtles using carapace length (CL; cm), exposure time (exposure; days) and the first principal component of habitat use (habitat)

Species	Model ^a	AIC _c	Δ AIC _c
<i>Emydoidea blandingii</i>	Survive $\sim(-11.24)$ CL + (-0.15) Exposure + (-4.21) Habitat	57.12	
	Survive $\sim(-3.98)$ Habitat + (-0.13) Exposure	58.92	1.80
	Survive $\sim(-11.20)$ CL + (-2.96) Habitat	60.70	3.58
	Survive $\sim(-3.06)$ Habitat	63.40	6.28
	Survive $\sim(-10.56)$ CL	64.73	7.61
	Survive $\sim(-10.51)$ CL + (-0.04) Exposure	65.54	8.42
	Survive ~ 1	70.02	12.90
	Survive $\sim(-0.05)$ Exposure	70.57	13.45
<i>Glyptemys insculpta</i>	Survive $\sim(-10.28)$ CL	33.37	
	Survive $\sim(-10.44)$ CL + (1.06) Habitat	34.93	1.56
	Survive $\sim(-8.98)$ CL + (-0.03) Exposure	35.20	1.83
	Survive $\sim(-0.07)$ Exposure	36.00	2.63
	Survive ~ 1	36.31	2.94
	Survive $\sim(-8.30)$ CL + (-0.05) Exposure + (1.59) Habitat	36.35	2.98
	Survive $\sim(-2.13)$ Habitat + (-0.10) Exposure	36.39	3.02
	Survive $\sim(-1.36)$ Habitat	37.64	4.27

^aAll models include clutch and year (2009 or 2010) as random effects.

For each species, Survive ~ 1 is the null model where survival is not related to CL, exposure or habitat. Coefficients are presented for each independent variable in the models, and bolded coefficients are significantly different than zero ($P < 0.05$). Akaike's information criterion, corrected for small sample size (AIC_c), evaluated the performance of models, and models for each species are arranged from best to worst. Only models where all the main effects were significant were considered supported.

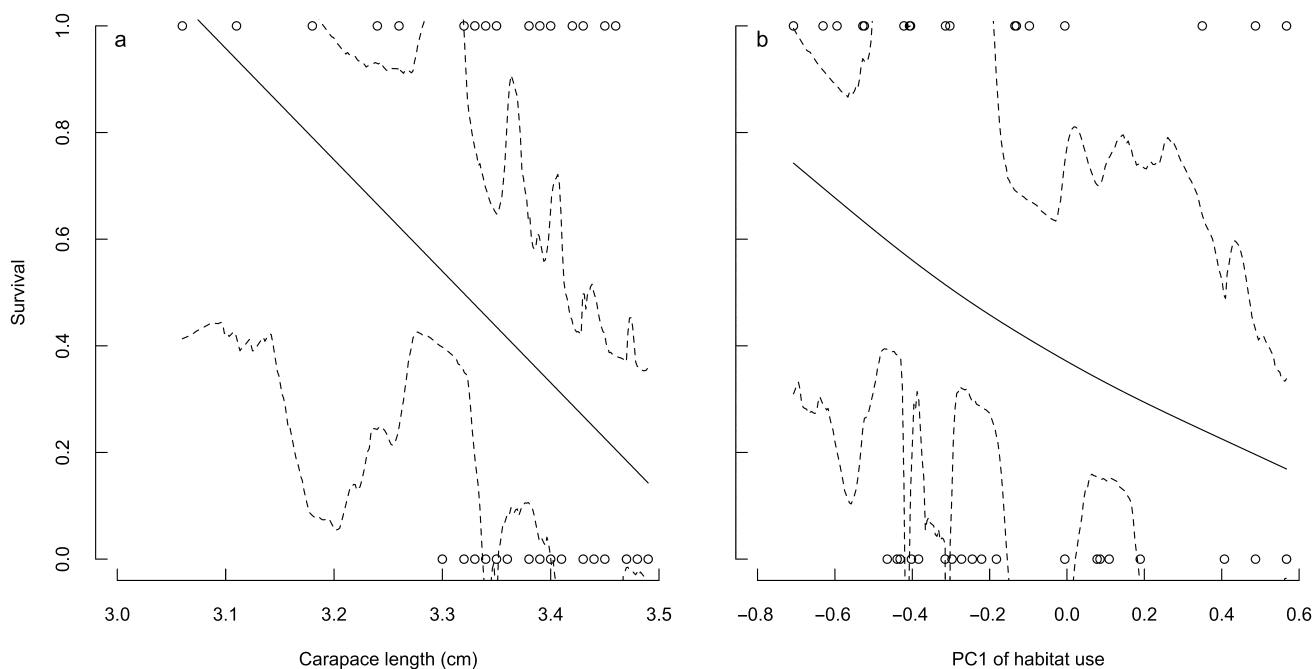


Figure 2 Fitness functions based on cubic spline analyses for *Emydoidea blandingii* hatchlings ($n = 48$). Survival was negatively related to (a) carapace length (cm; $P = 0.05$) and (b) the first principal component (PC1) of habitat use ($P = 0.0030$) with clutch and year (2009 and 2010) included as random effects. Curves are cubic splines (solid lines) with 95% confidence intervals (dashed lines) calculated using 100 bootstraps.

from 9 August 2010 to 13 August 2010. The first principal component of habitat use (PC1) explained 54% of the variation in habitat use among individuals. More positive values of PC1 indicated that hatchlings spent more time in floodplain habitat, and more negative values indicated that hatchlings

spent more time in upland open and creek habitats (Fig. 1b). The first two principal components cumulatively explained 99% of the variance in habitat use among hatchlings.

Carapace length was positively related to exposure time ($F = 19.93$, d.f. = 1, 40, $P < 0.0001$, $r^2 = 0.33$), but not habitat

use ($F = 0.53$, d.f. = 1, 40, $P = 0.50$, $r^2 = 0.01$). Exposure time was slightly positively correlated with the first principal component of habitat use ($F = 4.05$, d.f. = 1, 40, $P = 0.051$, $r^2 = 0.09$). Only one logistic regression model performed significantly better than the null model. In the best logistic regression model for *G. insculpta* ($AIC_c = 33.37$; Table 1), hatchling survival was significantly inversely related to carapace length (coefficient = -10.28 , $z = 2.11$, $P = 0.035$, Fig. 3). Survival was not related to exposure time ($P > 0.05$) or PC1 of habitat use ($P > 0.05$) in any of the models.

Discussion

Survival of *E. blandingii*

Using the best model, size, exposure time and habitat use were all significant predictors of hatchling survival. Hatchlings that were more likely to survive were smaller, emerged later in the season (reduced exposure) and spent less time in upland open habitats. These findings support the reduced exposure (H3) and habitat use (H4) hypotheses. Interestingly, smaller hatchlings (within the size range constraints of the animals that were examined) were more likely to survive, which contradicts the bigger is better hypothesis (H1).

Habitat is likely to have a strong influence on survival because of variation in food abundance, susceptibility to predators and environmental conditions in different habitats. While the mechanism for habitat-mediated differences in survival may be driven by food limitations (Kennedy, Nislow & Folt, 2008), hatchling turtles in the fall were not observed

foraging and likely relied on yolk reserves for the majority of their energetic needs. As a consequence of the high mortality rate from predators, it is more likely that habitat use affected survival because of differences in predator density or susceptibility to predation between habitats. King *et al.* (2006) found that survival of fledgling songbirds was related to the vegetation complexity of the habitat after they left the nest. As with turtles, the preferred nesting habitat of the songbirds was not the habitat with the highest survivorship of juveniles after leaving the nest, resulting in mortality from predators as birds dispersed from nesting sites. Gilliam & Fraser (1987) demonstrated experimentally that juvenile creek chubs *Semotilus atromaculatus* change habitat choice to balance maximizing energy acquisition through food resources and minimizing predation risk. Hatchling *E. blandingii* that spent proportionally less time in upland open habitats and more time in marsh and upland forest habitats were more likely to survive. Upland open habitat is structurally less complex than marsh, upland forest and swamp where large amounts of vegetation provide shelter and refuge from predators. Because we have demonstrated that these hatchlings disperse non-randomly from nests relative to the availability of habitat types (Paterson *et al.*, 2012), there should be a fitness benefit to selecting habitat. By leaving upland open habitat, where all nests were situated, hatchlings may have experienced reduced risk of predation in habitats that provide more structural complexity.

Emergence time, and therefore length of exposure to predators and environmental stressors, may be important for survival if mortality is largely random (Janzen *et al.*, 2007). Reducing the time of exposure above ground to predators and unfavourable environmental conditions would reduce the cumulative probability of mortality. Among *E. blandingii* hatchlings, we observed a large variation in the number of days exposed to predators after emerging from nests and before the onset of winter. Hatchlings that emerged later in the season had reduced exposure times and were more likely to survive, supporting the idea that longer exposure times reduce survival, although both habitat use and size also affected survival. Importantly, our consideration of survival began after emergence from nests, and most freshwater turtle nests are depredated before emergence (Congdon *et al.*, 1987; Spencer, 2002). There may be differing selective pressures to maximize egg survival versus survival of hatchling turtles post emergence, and we suggest that future work should evaluate survival patterns from oviposition to overwintering and beyond.

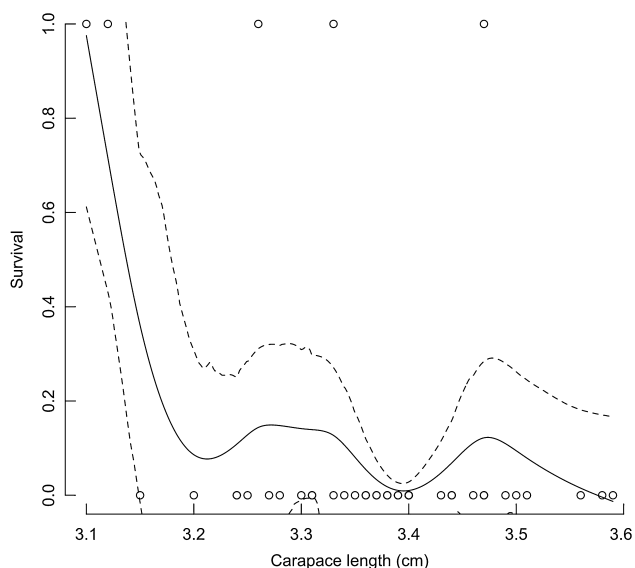


Figure 3 Fitness function based on cubic spline analysis carapace length (cm) of *Glyptemys insculpta* hatchlings ($n = 42$) showing a decrease in survival in larger hatchlings ($P = 0.035$). Curves are cubic splines (solid line) with 95% confidence intervals (dashed lines) calculated using 100 bootstraps.

Survival of *G. insculpta*

The only variable significantly related to survivorship of *G. insculpta* hatchlings was body size, with smaller individuals within the size range constraints of the animals that were examined being more likely to survive. This is in contrast to the bigger is better hypothesis (H3), and there was no support for our hypotheses about emergence time (H1 and H2) or habitat use (H4). The best model, where size was inversely related to survival, performed better than the null model in which survivorship was stochastic (H5).

Post-hatching habitat use may not be as important for survival in the few weeks before overwintering for *G. insculpta*. However, the lack of a relationship between survival and habitat use may also be due to a lack of variation in available habitats at our site. Nest sites were all situated in upland open areas and separated from a creek by a narrow strip of forest and floodplain. Because the surrounding habitat composition was fairly uniform among nests (Paterson *et al.*, 2012), it is possible that habitat homogeneity masked the importance of habitat use for survival of hatchlings.

Emergence date, which affects exposure time to predators and environmental risks, was not related to survival of hatchling *G. insculpta*. The largest source of mortality was from predators (Paterson *et al.*, 2012), but probability of survival did not decrease with increased exposure. However, it should be noted that because most nests of this species were laid in similar habitat around the same date, there was reduced variation in the emergence time, and therefore exposure time, for hatchlings. In 2010, the emergence times only varied by 4 days, from 9 to 13 August; it is possible this lack of variation masked any potential effect of exposure time on hatchling survival.

Conclusions

For both species, body size was a significant predictor of survival from nests to overwintering when controlling for year and clutch. However, contrary to the bigger is better hypothesis, smaller hatchlings of both species were more likely to survive. While previous authors have found support for the bigger is better hypothesis in aquatic turtle hatchlings (Janzen *et al.*, 2000a,b, 2007; O'Brien, Robert & Tiandray, 2005), others have found no support for directional selection on hatchling body size (Congdon *et al.*, 1999). In previous release experiments that found larger hatchling turtles had higher survivorship (Janzen *et al.*, 2000a,b, 2007), larger hatchlings had a selective advantage because of increased performance in moving to aquatic habitats; this decreased the exposure time of hatchlings to predators in terrestrial habitats. In those studies, avian predators drove the observed indirect selection on body size, and it is possible that at our study site, mammalian predators are a stronger influence than avian fauna. Indeed, at our site 10% of *E. blandingii* and 10% of *G. insculpta* hatchlings tracked were found dead inside small mammal burrows, including those of *Tamias striatus* and *Blarina brevicauda* (Paterson *et al.*, 2012). It is possible that larger hatchlings do not have a performance advantage at our site because of differences in foraging methods among predator types. In contrast, the bigger is better hypothesis has been supported in other taxa, including birds (Magrath, 1991), mammals (O'Donoghue, 1994) and fish (reviewed in Sogard 1997).

Mortality risk does not appear to be lower once hatchlings reach aquatic habitats, and most mortality occurred after *G. insculpta* hatchlings reached the floodplain or creek habitats. Gape-limited predators at our study site include fish and bullfrogs *Lithobates catesbeianus* that can only influence survival after hatchlings reach aquatic habitats. However, many

avian and mammalian predators are not limited by gape size. As in both species, smaller hatchlings had higher chances of surviving; gape-limited predation does not appear to have a strong influence on the survival of hatchlings in our study. Both species in our study are considered semi-aquatic, but because of the limited possible activity time from emergence until the onset of cold winter temperatures, individuals of both species needed to move to aquatic habitats to avoid lethally cold temperatures. This behaviour makes our survival data similar and more comparable with previous experiments with aquatic species, such as *T. scripta* and *Chrysemys picta* that experience high mortality during movements from nests to aquatic habitats. However, most experiments with aquatic species assume there is safety for individuals that can reach aquatic habitats.

Although our sample sizes are not exhaustive (48 *E. blandingii* and 42 *G. insculpta*), we believe that our conclusions are robust because (1) we found support for higher survival in smaller hatchlings in both species using independent models; (2) we used a direct measure of survival through telemetry as opposed to recapture rates; (3) we used naturally emerging nests so that density levels of hatchlings were in the normal range for this system.

We can only hypothesize on the mechanism that gives an advantage to smaller hatchlings, but it may be related to retreat site selection, size-specific differences in detectability by predators or a performance advantage to smaller or differently shaped hatchlings. It is possible that smaller hatchlings have significantly different detectability to predators, but the range in hatchling size in our population is small (range 3.06–3.59 cm, both species pooled). It seems more plausible that size-influenced survival is linked to performance. Usually size is directly proportional to performance (Azevedo, French & Partridge, 1997; Janzen *et al.*, 2000a,b, 2007). However, for specific locomotory traits, such as gliding by arboreal snakes (Socha and LaBarbera 2005) or sustained swimming in salmon (Brett, 2011), size may be inversely proportional to performance. It is possible that small size in hatchlings at our site is favorable for some survival-related performance attribute in young turtles. It is also possible that size is inversely proportional to another morphometric trait related to survival. Myers *et al.* (2007) found that *Trachemys scripta elegans* hatchling body shape was correlated to swimming performance, and it is possible that smaller hatchlings have a more hydrodynamic shape than larger hatchlings. However, the mechanism for this possible relationship is unknown for terrestrial dispersal from nests to overwintering sites. In a release experiment with two aquatic species, Tucker (2000) found that the smaller species (*C. picta*) was faster and more likely to survive. However, within each species, larger individuals were more likely to survive. The mechanisms driving size-specific mortality in young life stages should be addressed using performance experiments and survival data on the same individuals.

It is also possible that hatchlings of an intermediate size, and not the smallest, were most likely to survive, and our removal of hatchlings less than 8 g from the study created this bias. Although our criterion to remove hatchlings was based

on mass, tracked hatchlings of both species had significantly larger carapace lengths (the measure of size that predicted survivorship) than non-tracked hatchlings. Our data show that individuals smaller than the maximum are more likely to survive, but we could not evaluate the survival success of the smallest individuals in the population because of our *a priori* transmitter to body mass limitations. Nonetheless, our sample still captured the majority of variation in size in each species' population of hatchlings (73% of the size variation in *E. blandingii*; 75% of size variation in *G. insculpta*).

Understanding the influence of body size, habitat use and emergence time on survival is important for testing hypotheses about life-history evolution and for managing populations of these two declining species. Populations of both species have been managed through headstarting and body size, release location and release time can all be chosen to maximize survival of juveniles reared in the laboratory using data from juveniles in the wild. Caution must be used when assuming correlations between size and survival, as we found that smaller individuals were more likely to survive dispersal from nests to overwintering sites. Future work should identify factors related to survival of juveniles in their first active seasons and functional links between size and performance related to survival of hatchling turtles.

Acknowledgements

Financial support was provided by the Environment Canada's Habitat Stewardship Program, the Ontario Ministry of Natural Resources' (OMNR) Species at Risk Stewardship Fund, the Natural Sciences and Engineering Research Council of Canada (PGS-M Scholarship to JEP and Discovery Grant to JDL) and the Laurentian University. Extensive in-kind and financial contributions were provided by Algonquin Park. The authors are grateful to E. Newton, E. Upham-Mills, M. McDermott, M. Keevil, A. Bennett, M. Rasmussen, E. Huner, T. Cameron, J. Riley and A. Leifso who assisted in the field. All work was carried out under an approved Laurentian University Animal Care protocol and was authorized by permits from OMNR.

References

- Azevedo, R.B.R., French, V. & Partridge, L. (1997). Life-history consequences of egg size in *Drosophila melanogaster*. *Am. Nat.* **150**, 250–282.
- Bates, D., Maechler, M. & Bolker, B. (2011). lme4: linear mixed-effects models using Eigen and Eigen. R package version 0.999375-42. <http://CRAN.R-project.org/package=lme4>
- Brett, J.R. (2011). The relation of size to rate of oxygen consumption and sustained swimming speed of sockeye salmon (*Oncorhynchus nerka*). *J. Fish Res. Board Can.* **22**, 1491–1501.
- Burnham, K.P. & Anderson, D.R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach*. 2nd edn. New York: Springer-Verlag.
- Castellano, C.M., Behler, J.L. & Ultsch, G.R. (2008). Terrestrial movements of hatchling wood turtles (*Glyptemys insculpta*) in agricultural fields in New Jersey. *Chelonian Conserv. Biol.* **7**, 113–118.
- Congdon, J.D., Breitenbach, G.L., van Loben Sels, R.C. & Tinkle, D.W. (1987). Reproduction and nesting ecology of snapping turtles (*Chelydra serpentina*) in southeastern Michigan. *Herpetologica* **43**, 39–54.
- Congdon, J.D., Dunham, A.E. & van Loben Sels, R.C. (1993). Delayed sexual maturity and demographics of Blanding's turtles (*Emydoidea blandingii*): implications for conservation and management of long-lived organisms. *Conserv. Biol.* **7**, 826–833.
- Congdon, J.D., Nagle, R.D., Dunham, A.E., Beck, C.W., Kinney, O.M. & Yeomans, S.R. (1999). The relationship of body size to survivorship of hatchling snapping turtles (*Chelydra serpentina*): an evaluation of the 'bigger is better' hypothesis. *Oecologia* **121**, 224–235.
- Gilliam, J.F. & Fraser, D.F. (1987). Habitat selection under predation hazard: test of a model with foraging minnows. *Ecology* **68**, 1856–1862.
- Heppell, S.S. (1998). Application of life-history theory and population model analysis to turtle conservation. *Copeia* **1998**, 367–375.
- Janzen, F.J., Tucker, J.K. & Paukstis, G.L. (2000a). Experimental analysis of an early life-history stage: selection on size of hatchling turtles. *Ecology* **81**, 2290–2304.
- Janzen, F.J., Tucker, J.K. & Paukstis, G.L. (2000b). Experimental analysis of an early life-history stage: avian predation selects for larger body size of hatchling turtles. *J. Evolution. Biol.* **13**, 947–954.
- Janzen, F.J., Tucker, J.K. & Paukstis, G.L. (2007). Experimental analysis of an early life-history stage: direct or indirect selection on body size of hatchling turtles?. *Funct. Ecol.* **21**, 162–170.
- Kennedy, B.P., Nislow, K.H. & Folt, C.L. (2008). Habitat-mediated foraging limitations drive survival bottlenecks for juvenile salmon. *Ecology* **89**, 2529–2541.
- King, D.I., Degraaf, R.M., Smith, M.-L. & Buonaccorsi, J.P. (2006). Habitat selection and habitat-specific survival of fledgling ovenbirds (*Seiurus aurocapilla*). *J. Zool.* **269**, 1469–1498.
- Kolbe, J.J. & Janzen, F.J. (2002). Experimental analysis of an early life-history stage: water loss and migrating hatchling turtles. *Copeia* **2002**, 220–226.
- Lailvaux, S.P., Herrel, A., Vanhooydonck, B., Meyers, J.J. & Irschick, D.J. (2004). Performance capacity, fighting tactics and the evolution of life-stage male morphs in the green anole lizard (*Anolis carolinensis*). *Proc. Roy. Soc. Lond. Ser. B.* **271**, 2501–2508.
- Lindell, L.E., Forsman, A. & Merila, J. (1993). Variation in number of ventral scales in snakes: effects on body size, growth rate and survival in the adder, *Vipera berus*. *J. Zool.* **230**, 101–115.

- Magrath, R.D. (1991). Nestling weight and juvenile survival in the blackbird, *Turdus merula*. *J. Anim. Ecol.* **60**, 335–351.
- Michod, R.E. (1979). Evolution of life histories in response to age-specific mortality factors. *Am. Nat.* **113**, 531–550.
- Myers, E.M., Tucker, J.K. & Chandler, C.H. (2007). Experimental analysis of body size and shape during critical life-history events of hatchling slider turtles, *Trachemys scripta elegans*. *Funct. Ecol.* **21**, 1106–1114.
- O'Brien, S., Robert, B. & Tiandray, H. (2005). Hatch size, somatic growth rate and size-dependent survival in the endangered ploughshare tortoise. *Biol. Conserv.* **126**, 141–145.
- O'Donoghue, M. (1994). Early survival of juvenile snowshoe hares. *Ecology* **75**, 1582–1592.
- Paterson, J.E., Steinberg, B.D. & Litzgus, J.D. (2012). Revealing a cryptic life-history stage: differences in habitat selection and survivorship between hatchlings of two turtle species at risk (*Glyptemys insculpta* and *Emydoidea blandingii*). *Wildlife Res.* **39**, 408–418.
- R Development Core Team (2012). *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.
- Schluter, D. (1988). Estimating the form of natural selection on a quantitative trait. *Evolution* **42**, 849–861.
- Socha, J.J. & LaBarbera, M. (2005). Effects of size and behavior on aerial performance of two species of flying snakes (*Chrysopelea*). *J. Exp. Biol.* **208**, 1835–1847.
- Sogard, S.M. (1997). Size-selective mortality in the juvenile stage of teleost fishes: a review. *Bull. Mar. Sci.* **60**, 1129–1157.
- Spencer, R.-J. (2002). Experimentally testing nest site selection in turtles: fitness trade-offs and predation risk in turtles. *Ecology* **83**, 2136–2144.
- Stearns, S.C. (1977). The evolution of life history traits: a critique of the theory and a review of the data. *Annu. Rev. Ecol. Syst.* **8**, 145–171.
- Tucker, J.K. (2000). Body size and migration of hatchling turtles: inter- and intraspecific comparisons. *J. Herpetol.* **34**, 541–546.
- Tucker, J.K., Paukstis, G.L. & Janzen, F.J. (2008). Does predator swamping promote synchronous emergence of turtle hatchlings among nests?. *Behav. Ecol.* **19**, 35–40.
- White, G.C. & Garrott, R.A. (1990). *Analysis of wildlife radio-tracking data*. San Diego: Academic Press.