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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*)

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Abstract

Context. Turtles are one of the most imperilled taxonomic groups worldwide and information about population ecology is essential to species recovery. Although the spatial ecology and demography of adults of several turtle species have been well studied, little is known about early life stages. The small size, soft shell, and limited mobility of hatchling turtles may cause differences in survivorship and habitat selection compared with adults.

Aims. We tested the hypothesis that hatchling turtles select habitat as they move away from nests, so as to reduce the risk of predation and desiccation.

Methods. We examined survivorship, behaviour and habitat selection at two spatial scales in hatchling Blanding's turtles (*Emydoidea blandingii*) and wood turtles (*Glyptemys insculpta*) in 2009 and 2010, using radio-telemetry in Algonquin Provincial Park, Ontario, Canada. In addition, temperatures of sites used by hatchlings during winter were compared with those at haphazard stations in various habitats.

Key results. The mortality rate was high, with 42% of *E. blandingii* and 11% of *G. insculpta* hatchlings surviving to winter; most mortality was caused by predation. Most behavioural observations for both species were of individuals hiding under cover. Both species showed evidence of macrohabitat and microhabitat selection as they dispersed from nests towards overwintering sites, and important variables in the models differed between species. Likewise, the adult stages of these two species differ in their macrohabitat specialisation. There was also evidence that hatchlings chose overwintering sites on the basis of temperature.

Conclusions. Despite significant differences in survivorship between hatchlings and adults, resource selection was similar between these two demographic stages, and conservation plans based on adult habitat use should simultaneously protect hatchlings.

Implications. Understanding habitat selection by juveniles is important for testing hypotheses about ontogenetic shifts in resource selection and for protecting habitat for species at risk.

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Introduction

Understanding the spatial ecology and habitat use of an organism is required for a basic knowledge of that species' resource requirements (Johnson 1980; Alldredge and Griswold 2006), and for testing hypotheses about life-history evolution, competition and habitat patch dynamics. Habitat selection occurs as a result of a 'choice' by an organism to use one patch type over another, and this choice is influenced by population density, habitat quality and the relative availability of habitat types (Rosenzweig 1981; Thomas *et al*. 2001; Gunnarsson *et al*. 2005). Most habitat-selection studies test preferences for habitat types by comparing use to availability at predefined spatial and or temporal scales (Johnson 1980; Orians and Wittenberger 1991), and reasons organisms select specific habitats may be related to fitness via food quality or density, physiology (e.g. water loss), predators, thermoregulation and reproduction (Huey 1991; Alldredge and Griswold 2006).

In organisms without parental care, preferred habitats are likely to differ between juveniles and adults because of differences in selective pressures on different size classes that result from predation risk, physiology and resource requirements (Stamps 1983; Werner and Hall 1988; Janzen *et al*. 2000*a*, 2000*b*; Kolbe and Janzen 2002; Imansyah *et al*. 2008). Immature life stages are often more at risk of predation and may select habitats that increase crypsis or have lower densities of predators (Keren-Rotem *et al*. 2006; Imansyah *et al*. 2008).

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Juveniles may also be more at risk of mortality from environmental factors because of their physiology and limited mobility (Kolbe and Janzen 2002; Rothermel and Semlitsch 2002). Differences in food resources also affect habitat selection because juveniles may be unable to catch or restrain certain food items (Moermond 1979), or they may be gape-limited to smaller food types than are adults (Lind and Welsh 1994). Together, these factors influence habitat selection by juvenile organisms through a trade-off between pressures to reduce mortality risk and maximise foraging return and growth (Gilliam and Fraser 1987; Werner and Hall 1988; Gotceitas and Colgan 1990).

Considering only adults in conservation of habitats and resources for species at risk may reduce recruitment if juvenile resources are different from those of adults and are not by chance simultaneously protected via management plans to protect adult resources. Turtles experience relatively little anatomical reorganisation between juvenile and adult stages, but large differences in size between hatchlings and adults may explain changes in survivorship and behaviour because of changes in selective pressures. Therefore, turtles are good model organisms to examine differences in habitat selection among life stages, especially in the context of conservation biology, because the majority of turtle species is at risk of extinction (Klemens 2000). Whereas habitat selection by adult freshwater turtles has been well studied (e.g. Compton *et al*. 2002; Arvisais *et al*. 2004; Edge *et al*. 2010), very little is known about the ecology of hatchlings (but see McNeil *et al*. 2000; Tuttle and Carroll 2005; Ultsch *et al*. 2007), partly because of technological limitations of radio-transmitter size and difficulty in locating individuals of this cryptic life stage.

We studied habitat selection and survivorship from nest emergence to overwintering in hatchlings of two freshwater turtles, *Glyptemys insculpta* and *Emydoidea blandingii*, over two field seasons at the same site. Both species are of conservation concern in eastern North America (COSEWIC 2005, 2007) and adults of both species are considered habitat specialists, with *G. insculpta* using cold-water creeks and the surrounding floodplains, forests and fields (Compton *et al*. 2002; Arvisais *et al*. 2004), and *E. blandingii* specialising on wetland complexes, with large terrestrial movements between bodies of water (Ross and Anderson 1990; Edge *et al*. 2010). We tested the hypothesis that hatchlings select habitat as they move away from nests so as to reduce the risk of predation and desiccation. At the macrohabitat scale, we predicted that hatchlings would move to aquatic habitats that would provide cover from predators and desiccation. At the microhabitat scale, we predicted that hatchlings would choose sites that have proportionately more cover and cooler temperatures that would increase crypsis and allow more efficient thermoregulation. We also predicted that there would be differences in habitat selection between hatchlings and adults because of differences in resource requirements and pressure from predators. Finally, we predicted that hatchlings would choose aquatic overwintering sites that were colder than the surrounding environments, as found for adults in both of these species (Greaves and Litzgus 2007, 2008; Edge *et al*. 2009). Comparisons between *G. insculpta* and *E. blandingii*, which have very different habitat preferences as adults, provided insight into resource requirements and mortality sources of similar-sized organisms in different environments.

Materials and methods

Study site, nests and hatchlings

The study site was in Algonquin Provincial Park, Ontario, Canada, and consisted of a mosaic of wetlands in an upland softwood forest. The exact location of the site is not revealed herein to protect the populations from poaching. Known nesting locations of *G. insculpta* and *E. blandingii* were monitored on foot during May and June of 2009 and 2010. Once females oviposited, nests were protected from predation with hardware cloth cages. Nests of *G. insculpta* were 32 ± 4 m (mean $\pm$ s.e.) from water and nests of *E. blandingii* were 115 ± 25 m from water. Beginning in early August, all nests were monitored daily for emerging hatchlings. Carapace lengths of hatchlings were measured to the nearest 0.01 cm with 15-cm calipers (Scherr-Tumico, St James, Minnesota, USA), and masses were measured ($\pm$0.1 g) using Pesola spring scales. Hatchlings greater than 8 g that emerged naturally from nests were outfitted with radio-transmitters (Model A2245, Advanced Telemetry Systems, Isanti, Minnesota, 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, Ontario, Canada); the package was 5–8% of hatchling body mass. Hatchlings were released directly at their nest site because the first movement to aquatic habitats is important in homing behaviour of freshwater and sea turtles (Lohmann and Lohmann 1996; Pappas *et al*. 2009). Hatchlings were tracked every 1–3 days, from emergence until they died or until 15 October 2009 or 6 October 2010, by using a three-element Yagi antenna and a R410 Scanning Receiver (Advanced Telemetry Systems, Isanti, Minnesota, USA). By these dates, all living turtles were at overwintering sites. Transmitters were expected to last 60 days. Transmitters were replaced before overwintering each year and hatchlings were tracked once per month from November to March. The coordinates of radio-telemetry locations were recorded with a hand-held GPS unit (GPSmap 76CSx, Garmin, Kansas City, Kansas, USA).

Survivorship and behaviour

The fates of all hatchlings were recorded during both field seasons. Each hatchling was assigned to one of the following six categories: alive, predated, desiccated, drowned, dead on road, or lost. Turtles were considered predated when remains were found using telemetry that showed evidence of predators. This included empty carapaces with the transmitter still intact, dead hatchlings with limbs and/or organs removed, or just the transmitter with obvious signs of predator activity (e.g. missing antenna, body of transmitter crushed or chewed on, found in the burrow of potential predators). Desiccated turtles were those found dead in open habitat without any signs of being attacked by a predator. Drowned turtles were those found dead at the bottom of a body of water with no signs of trauma. Turtles dead on a road were found with obvious damage from a vehicle. Lost individuals could not be

definitively assigned to any other category, and may sometimes have included turtles whose radios failed. Each time a turtle was located alive, its behaviour was classified as resting under cover, basking, foraging, or moving. Resting turtles were found under cover and were inactive. Basking turtles were found in sunlight in the open and did not show evidence of movement. Foraging hatchlings were those actively biting at plant or animal material. Moving turtles were those that were actively walking or swimming but showed no evidence of food searching.

Macrohabitat selection

Macrohabitat selection by hatchlings was examined using a modification of the Euclidean distance method (Conner and Plowman 2001), using individual turtles as replicates. Only turtles with at least 10 locations were used in the analysis, and both cohorts (2009 and 2010) were pooled together. Because of differences in natural history and spatial ecology between the two species (Ernst and Lovich 2009); their habitat selection data were analysed separately. Wetlands were classified into one of five categories based on the Canadian Wetland Classification System (Warner and Rubec 1997), and the remaining habitats were categorised on the basis of water source, substrate and vegetation into five additional habitat types not described by the classification system (Table 1). The entire site was mapped using ArcGIS 9.2 (ESRI, Redlands, California, USA) and a combination of existing mapping databases, orthophotographs and ground truthing with a handheld GPS (GPSmap 76CSx, Garmin, Kansas City, Kansas, USA).

The Euclidean distance method compares distances from turtle locations to different habitat types, with the distances from random points to different habitat types (Conner and Plowman 2001). The null hypothesis (random habitat use) is that the distribution of distances for turtle location points is the same as a distribution of distances for random points. Normally, the distance method would use the population range or an individual home range as the defined available habitat (Conner and Plowman 2001; Edge *et al*. 2010). However, hatchling turtles are constrained by limited mobility and a pre-defined starting point (their nest) such that habitats available to some individuals in the population may not be realistically available to others. We defined the available habitat for each nest (i.e. nest range) as a circle with a radius equal to the maximum seasonal path length for hatchlings of each species in our study. Maximum seasonal path lengths were calculated as the sum of straight-line distances between consecutive telemetry points for individuals using the HAWTHS Tools extension (Beyer 2004) in ArcGIS. The maximum path lengths were 195 m for *G. insculpta* and 449 m for *E. blandingii*. We assumed that hatchlings, if travelling in a straight line from their nest, could not physically reach habitat beyond this radius before the onset of winter. All telemetry points for a given nest were within the radius of these circles and this method accounted for differences in habitat availability among nests.

Habitat use was quantified as the average distance from telemetry points to each habitat type (u_{ij}) for each habitat (j) by individual (i). Habitat availability was quantified by generating random points within a nest range and then measuring the average distance from random points to each habitat type (r_{ij}) in the nest range, for each habitat (j) by individual (i). The number of random points generated for a nest range was the same as the number of telemetry points for all hatchlings from that nest. A matrix of ratios was calculated for each habitat for each hatchling ($d_{ij} = u_{ij}/r_{ij}$), and if turtles were selecting habitat randomly, then the expected mean ratio for each habitat would be one. Values <1 represent preference for a habitat, and values >1 indicate avoidance of that habitat. If a habitat type was not available to a hatchling (not inside the nest range), a ratio of one was assigned because the turtle could neither select nor avoid habitat that was unavailable to it. A MANOVA was used to test whether the mean ratio ($\bar{d}$) for all habitats (each habitat was a dependent variable) was significantly different from one (random habitat use) using individual turtles as the replicates ($n = 16$ for *G. insculpta*, and $n = 30$ for *E. blandingii*). A separate MANOVA was performed for each species. *Post hoc* analyses tested which habitats were being used disproportionately to availability. To test which

Table 1. Classification of habitat types used for analyses of macrohabitat selection by hatchling *Glyptemys insculpta* and *Emydoidea blandingii* in Algonquin Provincial Park, Ontario

Wetlands were classified using the Canadian Wetland Classification System (CWCS; Warner and Rubec 1997), and the remaining landscape was divided into five habitats using the CWCS criteria (indicated by an asterisk)

Habitat	Substrate	Water source	Watertable	Vegetation
Creek*	Variable	Variable	Above the surface, flowing	Variable, confined to shoreline
Fen	Peat	Groundwater	Fluctuating	Graminoid species and brown mosses
Lake*	Variable	Variable	Above surface >2 m	Variable, but confined mainly to shorelines and bays
Marsh	Mineral	Variable	Shallow and fluctuates dramatically	Emergent aquatic macrophytes
Floodplain*	Variable	Precipitation or overflow	Close to surface; varies throughout year	Alders, graminoid, sedges
Swamp	Peatland and/or mineral	Groundwater	At or below the surface	Woody plants often >1 m high (shrubs, trees)
Pond	Mineral	Variable	Free surface water up to 2 m deep	Submerged or floating aquatic plants (<25% of area)
Upland open*	Sand or gravel	Precipitation	Below surface	Sparse trees and/or forbs
Upland forest*	Variable	Precipitation	Below surface	Dominated by trees

habitat ratios were significantly different from one, Student's *t*-tests with a Bonferroni correction for multiple comparisons ($\alpha = 0.05/9$ habitats $= 0.0056$) were used. Habitats were then ranked using pair-wise comparisons with a Tukey HSD test.

Microhabitat selection

Microhabitat selection was quantified by comparing habitat features at turtle locations with those in random plots using paired logistic regression models. Only data from the 2010 field season were used because of the addition of several microhabitat variables during this season. Eight microhabitat characteristics (Table 2) that are likely to be related to water loss and predation risk were quantified within a 1-m^2 quadrat surrounding each hatchling at each radio-location to examine selection of locations at a small spatial scale. So as to compare habitat use to availability, the same eight characteristics were measured in a 1-m^2 plot at a random distance (1–30 m away) and compass bearing from each turtle location at the same time as measurements were taken at the turtle location. The maximum of 30 m was chosen because this distance is within the range of average daily distances travelled by hatchlings of both species (Standing *et al*. 1997; Castellano *et al*. 2008). Pairing random and turtle locations accounted for temporal variation in the availability of microhabitat variables (such as temperature). Random plots were always positioned within the same macrohabitat type as their corresponding turtle location so as not to cross the spatial scale at which selection was being assessed (macrohabitat *versus* microhabitat selection). If the transect for the random plot required going further than the border of the current macrohabitat type, then transects were reflected off the border to remain in the same macrohabitat type. Logistic regression models were based on a binary response (turtle or random point) that used coefficients ($\beta_{0.n}$) of habitat characteristics as predictors of the transformed logit response (Z) (Hosmer and Lemeshow 2000). Paired logistic regression models predict responses on the basis of relative changes in variables (analogous to paired Student's *t*-tests). Interpretation of such models relies on relative changes in variables between controls (random points with no turtles) and cases (locations with turtles). Larger coefficients have a larger influence on the logit response variable (turtle *versus* random location) and probability of habitat selection. Positive coefficients indicate that the probability of selection increases with a variable, and negative coefficients indicate the probability of selection decreases with that variable. For each species, paired logistic regression models were developed using stepwise backwards regression, starting with all the variables in Table 2. Initial analyses and data exploration resulted in five models for each species. Only models for which all main-effect coefficients were significant (as determined by individual Wilcoxon signed-rank tests) were used. The candidate models were ranked on the basis of Akaike's information criterion (AIC) and the models with the smallest AIC values were considered to be most supported (Burnham and Anderson 1998). The relative probability (RP) that hatchlings would select a microhabitat on the basis of the difference between turtle and paired random locations for significant variables was modelled using the relationship between relative probability and the logit response variable (Z):

$$RP = Z/(1 + e^{Z})$$

The predictive power (fit) of the best models were assessed with McFadden's p^2, which is analogous to the multiple correlation coefficient (R^2) used in linear regression (McFadden 1974).

Table 2. Descriptions of variables measured in the assessment of microhabitat selection by hatchling *Glyptemys insculpta* and *Emydoidea blandingii* in Algonquin Provincial Park, Ontario, using paired logistic regression

Variable	Description
GC	Percentage of quadrat that is not open ground (includes leaf litter, emergent vegetation and woody vegetation)
LL	Percentage of quadrat covered by leaf litter
EV	Percentage of quadrat covered by emergent vegetation
WV	Percentage of quadrat covered by woody vegetation (including shrubs and trees that are alive or dead)
Temp	Air temperature at the exact location of the turtle. In centre of plot for random points
Canopy	The percentage of over story canopy cover (above hip height) measured using a densitometer
WtrD	The average water depth in the quadrat (cm) of four cardinal directions
SubD	The substrate depth (cm) at the centre of the quadrat using a meter stick

Winter site selection

During the inactive season from November to April, temperatures of hatchling overwintering sites, as determined from turtles outfitted with transmitters, were compared with temperatures of haphazard stations in a variety of habitats. In October (2009 and 2010) temperature data loggers (iButton, Maxim, Sunnydale, California, USA) were attached to 5 cm × 2.5 cm × 100 cm pine stakes and placed directly beside the turtles so that the data logger would be at the same depth, and therefore same temperature, as the hatchling. To determine whether hatchlings were selecting overwintering sites on the basis of temperatures, 43 haphazard stations in five different habitats (creek, lake, marsh, pond and upland forest) within the study site were deployed in December of 2009 and 2010. At least three stations were placed in each water body, and if possible, more than one of each habitat type was used. In 2009, 10 stations were placed in three creeks, with four stations being placed in one, and three each in two others. Three stations were placed in the one lake in the study area. Nine stations were placed in three marshes (three each), and 15 stations were placed in five ponds (three each). In 2010, eight stations were placed in three creeks (three each in two, two in the third), eight in marshes (five in one, three in another), eight in ponds (three each in two, and two in another) and eight in upland open habitats (five in one site, three in another). The temperature data loggers at the stations were synchronised with the data loggers at turtle locations and recorded temperatures every 120 min. The data loggers were waterproofed with Plasti-Dip (Plasti-Dip International, Blaine, Minnesota, USA) and then attached with epoxy to either a brick or pine strapping.

Although covering data loggers in plastic has been shown to alter temperatures (Roznik and Alford 2012), the differences in temperature are typically small (0–1.3°C), and all data loggers in our study were coated so that any effects would be equally applied to turtle and haphazard stations. The temperature loggers were buried 2–5 cm into the substrate at each station, which was similar to depths that young turtles bury themselves before overwintering (J. E. Paterson, pers. obs.). Average monthly temperatures were compared between hatchling turtle sites and haphazard stations in different habitat types by using a repeated-measures ANOVA (Type III). A separate test was performed for each winter (2009–10 and 2010–11). For *post hoc* analyses, Wald-tests (Wald 1943) were used to compare linear models of turtle-site temperatures to linear models of haphazard-station temperatures in each habitat.

Results

Survivorship and behaviour

Over two cohorts (2009 and 2010), radio-transmitters were attached to 93 hatchlings (45 *G. insculpta* and 48 *E. blandingii* ones) from 24 nests for a total of 879 radio-locations. Survivorship rates from fall emergence until the onset of winter were low; 42% of *E. blandingii* and 11% of *G. insculpta* individuals survived until winter (Fig. 1). The majority of *G. insculpta* hatchlings was eaten, presumably by small mammals because the transmitters and remains were recovered from small burrows ($n = 13$); however, in several cases ($n = 6$) remains and transmitters were recovered above ground. Although *E. blandingii* hatchlings were also recovered from mammal burrows ($n = 3$), at least one individual appeared to be killed by an avian predator, and three others were recovered dead above ground. One *E. blandingii* hatchling was hit by a car. Hatchlings that were lost may have been the result of transmitter failure, predators that destroyed the transmitter, or predators that moved the turtle and transmitter out of signal-reception range (<500 m, depending on landscape).

Recorded behaviours were similar between species, and hatchlings were inactive the majority of the time. Using 295 observations of behaviour of *G. insculpta*, hatchlings were found resting under cover 75% of the time, basking 12% of the time, and moving 13% of the time ($\chi^2 = 409.45$, d.f. = 3, $P < 0.00001$). Using 468 observations of behaviour for *E. blandingii*, hatchlings were found resting under cover 83% of the time, basking 3% of the time, and moving 14% of the time ($\chi^2 = 851.23$, d.f. = 3, $P < 0.00001$). There were no observations of hatchlings foraging.

Macrohabitat selection

Hatchling *G. insculpta* locations differed significantly from random points within the four available habitats surrounding nests (MANOVA, $F_{3,15} = 47.59$, $P < 0.0001$). All four available habitats were used non-randomly and had $\bar{d}$ values significantly different from one ($P < 0.0056$). Tukey HSD comparisons between habitats grouped upland open, creek and floodplain habitats together (summarised in Table 3). These three habitats were significantly ($P < 0.05$) preferred over upland forest.

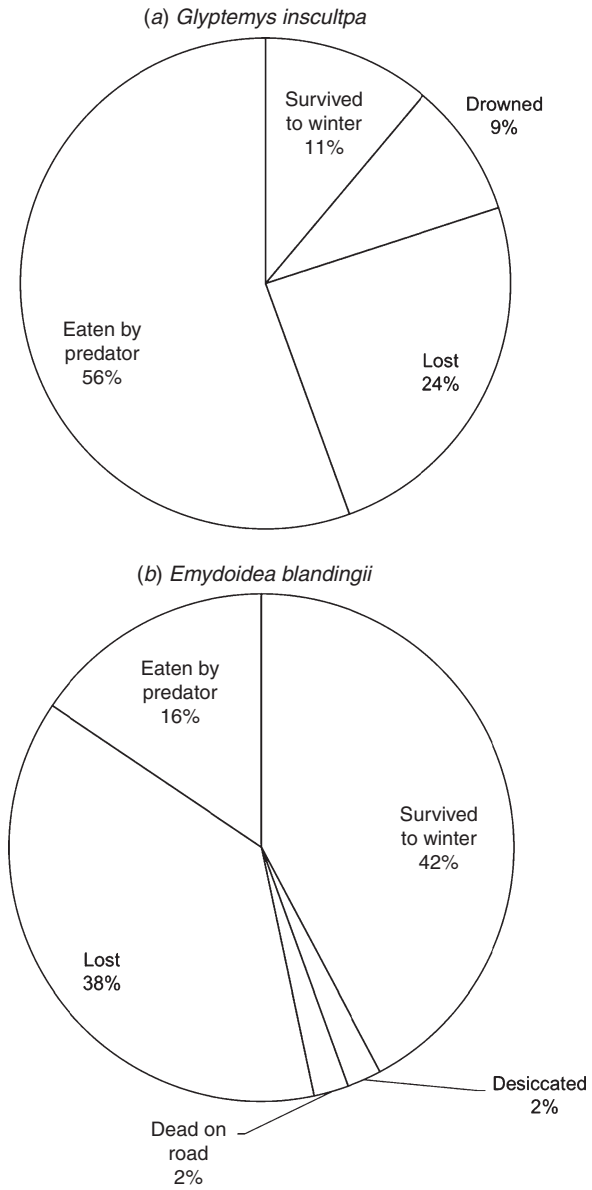

Fig. 1. Fates of (*a*) *Glyptemys insculpta* ($n = 45$) and (*b*) *Emydoidea blandingii* ($n = 48$) hatchlings tracked in Algonquin Provincial Park, Ontario, in 2009 and 2010.

Hatchling *E. blandingii* locations also differed in their distances to habitats (8 available types) from random points available to each nest ($F_{8,22} = 26.83$, $P < 0.00001$). Upland open, marsh and swamp all had $\bar{d}$ values significantly (preferred, $P < 0.0056$) lower than one, whereas all other habitats had $\bar{d}$ values similar to one (random habitat use, $P > 0.0056$). Pair-wise comparisons found differences only between upland forest and other habitats (summarised in Table 4), and this was due to the very large range of d values for upland forest (1.98–48.13). Therefore, Tukey HSD comparisons were also performed with upland forest removed (summarised in Table 4), and this re-analysis indicated that

Table 3. Adjusted *P*-values (significantly different comparisons bolded) from pair-wise comparisons (Tukey HSD) of mean distance ratios ($\bar{d}$) for macrohabitat selection by hatchling *Glyptemys insculpta* ($n = 16$) in Algonquin Provincial Park, Ontario, during 2009 and 2010
Habitats are ranked from most preferred (low $\bar{d}$ values) to least preferred (high $\bar{d}$ values)

Habitat	$\bar{d}$	Floodplain	Creek	Upland open
Floodplain	0.175			
Creek	0.280	0.991		
Upland open	0.380	0.936	0.992	
Upland forest	3.699	**0.00001**	**0.00001**	**0.00001**

upland open, marsh and swamp habitats were significantly ($P < 0.05$) preferred over all other habitat types.

Microhabitat selection

Logistic regression models were created using 101 paired turtle–random points for *G. insculpta* and 202 paired points for *E. blandingii* during the 2010 field season. For each species, at least five models with significant ($P < 0.05$) coefficients were generated and ranked on the basis of AIC (Tables 5, 6). The best models differed between *G. insculpta* (*LL*temp*) and *E. blandingii* hatchlings (*GC*WV*). Coefficients for the best model of *G. insculpta* suggested hatchlings selected microhabitats that were cooler than the surrounding areas, and had less leaf litter. For every 1% increase in leaf litter, there was an 11% reduction in the odds of a hatchling being in that 1-m^2 plot (Table 7). In addition, a 1°C increase in temperature resulted in a 14% decrease in the odds of selection. Coefficients for the best model of *E. blandingii* suggested that hatchlings selected microhabitats that had more ground cover and woody vegetation than did the surrounding area (Table 7). For every 5% increase in percentage of ground cover, there was a 16% increase in the odds of selection, and for every 1% increase in woody vegetation, there was a 17% increase in the odds of selection. For both species, the best model had a significant interaction term between the two strongest predictive variables. The relative probability that a hatchling would select microhabitat on the basis of differences in variables between turtle locations and random points is shown for the best model in each species in Fig. 2. Wide variation in habitat selection both within and among individuals resulted in an overall low predictive power of the best models ($p^2 = 0.13$ for *G. insculpta*, and $p^2 = 0.08$ for *E. blandingii*).

Winter site selection

In 2009–10, *E. blandingii* hatchlings overwintered in upland open ($n = 5$ turtles) and marsh ($n = 3$ turtles) habitats. The *G. insculpta* hatchlings overwintered on the shores of a creek ($n = 3$ turtles). All transmitters failed by March and no live hatchlings were found at any overwintering sites in early spring (April 2010), so it is unknown what proportion of hatchlings survived the winter. Two *E. blandingii* individuals that overwintered terrestrially were recovered dead. Heavy rainfall and snow melt flooded overwintering sites and made locating hatchlings in spring improbable.

The overwintering sites of *E. blandingii* hatchlings in 2009–10 differed in temperature from haphazard stations in marshes, ponds and creeks ($F_{3,32} = 3.26$, $P < 0.0007$, Fig. 3*a*). Overwintering sites of *E. blandingii* individuals were significantly colder than haphazard stations in marshes ($F_{3,30} = 4.64$, $P < 0.01$) and ponds ($F_{3,30} = 8.78$, $P < 0.0003$), but not creeks ($F_{3,30} = 2.00$, $P = 0.13$). Of the three *G. insculpta* hatchlings that survived until the onset of winter, only two temperature loggers were recovered from their hibernation sites, so variance could not be estimated to compare with haphazard stations.

In 2010–11, hatchling *E. blandingii* overwintered in upland open ($n = 3$ turtles), swamp ($n = 3$ turtles) and marsh ($n = 5$ turtles) habitats. The overwintering sites of *E. blandingii* hatchlings in 2010–11 also differed in temperature from haphazard stations ($F_{4,33} = 5.97$, $P < 0.0001$, Fig. 3*b*). Overwintering sites of turtles were significantly colder than haphazard stations in ponds ($F_{3,31} = 10.81$, $P < 0.0001$) and creeks ($F_{3,31} = 5.97$, $P < 0.001$), but not marshes ($F_{3,31} = 0.98$, $P = 0.41$). Overwintering sites of turtles were warmer than stations in upland open habitats, but the difference was not significant ($F_{3,31} = 2.31$, $P = 0.09$). All *G. insculpta* ($n = 2$) individuals that survived to winter

Table 4. Adjusted *P*-values (significantly different comparisons bolded) from pair-wise comparisons (Tukey HSD) of mean distance ratios ($\bar{d}$) for macrohabitat selection by hatchling *Emydoidea blandingii* ($n = 30$) in Algonquin Provincial Park, Ontario, during 2009 and 2010 for all habitats and with upland forest removed
Habitats are ranked from most preferred (low $\bar{d}$ values) to least preferred (high $\bar{d}$ values)

Habitat	All habitats								Upland forest removed						
	$\bar{d}$	Upland open	Swamp	Marsh	Fen	Lake	Creek	Pond	$\bar{d}$	Upland open	Swamp	Marsh	Fen	Lake	Creek
Upland open	0.42								0.42						
Swamp	0.47	1.00							0.47	10.95					
Marsh	0.53	1.00	1.00						0.53	0.75	0.98				
Fen	0.98	1.00	1.00	1.00					0.98	**<0.001**	**<0.001**	**<0.001**			
Lake	0.99	1.00	1.00	1.00	1.00				0.99	**<0.001**	**<0.001**	**<0.001**	0.99		
Creek	1.03	1.00	1.00	1.00	1.00	1.00			1.03	**<0.001**	**<0.001**	**<0.001**	0.99	1.00	
Pond	1.05	1.00	1.00	1.00	1.00	1.00	1.00		1.05	**<0.001**	**<0.001**	**<0.001**	0.96	0.99	1.00
Upland forest	4.92	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**							

Table 5. Akaike's information criterion (AIC) rankings and fitted parameter estimates for paired logistic regression models relating *Glyptemys insculpta* hatchling microhabitat selection to various microhabitat characteristics (defined in Table 4) in Algonquin Provincial Park, Ontario, in 2010

Model	AIC	Coefficient (β)					
		LL	*GC*	*LL*: *GC*	*temp*	*LL*: *temp*	*GC*: *temp*
*LL*temp*	117.31	–0.1190			–0.1393	0.0049	
*GC*temp*	118.21		–0.1186		–0.2631		0.0052
*LL*GC*	124.88	0.0445	0.0231	–0.0007			
LL	132.10	–0.013					

Table 6. Akaike's information criterion (AIC) rankings and fitted parameter estimates for paired logistic regression models relating *Emydoidea blandingii* hatchling microhabitat selection to various microhabitat characteristics (defined in Table 4) in Algonquin Provincial Park, Ontario, in 2010

Model	AIC	Coefficient (β)					
		LL	*GC*	*Canopy*	*WV*	*GC*: *WV*	*LL*: *GC*
*GC*WV*	225.43		0.0340		0.1565	–0.0016	
*LL*GC*	230.46	0.0613	0.0249				–0.0005
LL	235.41	0.0169					
GC	237.70		0.022				
WV	244.03				0.0148		
Canopy	244.76			0.0121			

Table 7. Coefficients and the corresponding odds ratios (given change *x* in variable between two locations) for the best models for microhabitat selection by *Glyptemys insculpta* and *Emydoidea blandingii* hatchlings in Algonquin Provincial Park, Ontario, in 2010

Species	Variable	Coefficent (β)	Odds ratio ($e^{(\beta * x)}$)
G. insculpta	*LL*	–0.12	0.89 (1%)
	Temp	–0.14	0.87 (1°C)
	LL:*Temp*	0.005	1.005 (1% * 1°C)
E. blandingii	*GC*	0.03	1.16 (5%)
	WV	0.16	1.17 (1%)
	GC:*WV*	–0.0016	0.998 (1% * 1%)

overwintered in water along the creek shore, and similar to the previous year, variance could not be calculated for only two samples. No turtles were recovered the following spring, and the percentage surviving winter was not determined.

Discussion

Survivorship and behaviour

The rate of survival from nest emergence until winter was much lower for *G. insculpta* than for *E. blandingii*. This difference was present even though *G. insculpta* nests were closer to water than were *E. blandingii* nests. An increased distance to travel through terrestrial habitats would increase

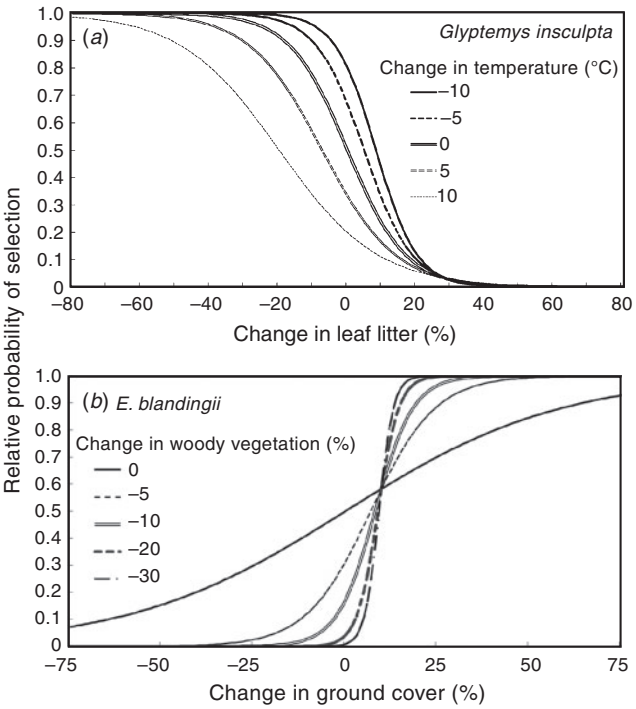

Fig. 2. Relative probability (*RP*) of habitat selection using the best paired logistic regression models for changes in variables between two microhabitat plots in Algonquin Provincial Park, Ontario, in 2010 for (*a*) *Glyptemys insculpta* hatchlings (*LL*temp*) and (*b*) *Emydoidea blandingii* hatchlings (*GC*WV*). See Table 4 for definition of acronyms.

exposure to predators and the risk of desiccation (McNeil *et al*. 2000; Tucker 2000; Tuttle and Carroll 2005), indicating that *E. blandingii* in our study should have experienced higher mortality than *G. insculpta*. The main source of mortality for *G. insculpta* was predation, suggesting that predator density or type is causing at least part of the observed difference in mortality rate between the two species. Although the populations of both species were more-or-less sympatric, the available habitats were quite different because *G. insculpta* nests were located around a creek and associated floodplains, whereas *E. blandingii* nests were located around marshes and swamps surrounded by upland forest. Therefore, predator species or their success in these respective habitats could be different. Predators may have a larger impact on *G. insculpta* hatchlings because linear habitat types, such as creeks, often have elevated predation rates (Simberloff and Cox 1987; Major *et al*. 1999). Our estimate of mortality for *E. blandingii* could be an underestimate if some fraction of the 'lost' hatchlings were taken by avian predators that carried the turtles from the study site and out of telemetry reception. In contrast, the mortality estimate could be an overestimate if a significant number of the 'lost' turtles were still alive but were out of telemetry range (i.e. they may have left the study site, given the high mobility we observed in *E. blandingii* hatchlings) or carried failed transmitters. Although an automobile struck only one hatchling in the present study, cars may be a significant source of mortality for hatchlings in populations with higher traffic and road densities. Future work should identify

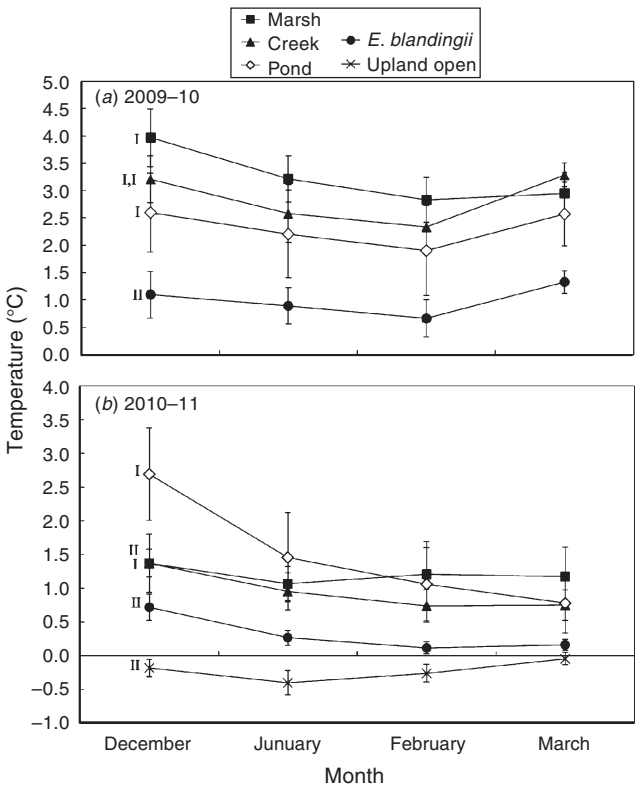

Fig. 3. Temperatures at overwintering sites used by hatchling *Emydoidea blandingii* compared with haphazard stations at Algonquin Provincial Park, Ontario, in (*a*) three habitats during 2009–10 and (*b*) four habitats in 2010–11. Different Roman numerals indicate significantly ($P < 0.05$) different temperatures between categories.

important predator species, possibly through trail cameras, and the effect of their density and spatial distribution on hatchling survival.

Macrohabitat selection

Hatchlings of both species moved from nests in upland habitat towards overwintering sites, selecting habitats non-randomly at the macro-spatial scale on route. Hatchling *G. insculpta* remained in upland open habitat after emerging from nests, and then moved to pools in alder (*Alnus incana rugosa*) floodplains or to the shoreline of a creek. Although all turtles had to move through upland forest to disperse from their nests to reach aquatic habitats, they used forests less than if they were moving randomly within available habitats surrounding their nests, and the analysis suggested avoidance of upland forests. Hatchling *E. blandingii* preferred upland open, marsh and swamp habitats. Although many other habitats were available, they were all used in proportion to their availability and not preferred. In general, there was very little movement once hatchlings reached aquatic habitats. We did not test what cues turtles used to select habitat; however, other studies have suggested that visual cues, a sun-compass, positive geotaxis and auditory cues may all be important in the detection and selection of suitable aquatic habitat (Tuttle and Carroll 2005; Castellano *et al*. 2008; Pappas *et al*. 2009).

Both species of hatchlings used aquatic habitat types that are also selected by conspecific adults. Adult *G. insculpta* individuals select areas that are close to streams and rivers, and also use forest edges for foraging (Compton *et al*. 2002). Hatchling *G. insculpta* showed a strong preference for open upland habitat (low $\bar{d}$ value) and often spent several days resting under cover such as woody debris, shrubs or leaf litter, before moving to aquatic habitats to overwinter. Adult turtles also extensively use upland habitat for foraging in the summer (Compton *et al*. 2002; Arvisais *et al*. 2004; Walde *et al*. 2007). We found aquatic habitats used by *G. insculpta* hatchlings to be the same as those used by adult turtles. Protecting nesting areas of adults would include the areas utilised by hatchlings in the fall. As long as safe corridors exist between nesting habitats and these aquatic habitats (rivers, creeks or brooks), then protecting habitats for *G. insculpta* adults should be sufficient for protection of post-emergent hatchlings. However, future work should test whether hatchlings and juveniles move into habitats that are not used by adults during their first active seasons; we only tracked hatchlings until their first winter.

Adult *E. blandingii* at our Algonquin Park site preferred swamp, marsh and pond habitats and avoided upland habitats (Edge *et al*. 2010). Marsh and swamp habitats were also preferred by hatchlings, and they moved to overwinter in these aquatic habitats. However, in contrast to conspecific adults, several hatchlings extensively used the open upland habitat surrounding the nest, and selected this habitat for refuge before moving to either a marsh or swamp for overwintering. All water bodies that were used by *E. blandingii* hatchlings during the present study were also used by adults at the same site (Edge *et al*. 2010; J. E. Paterson, unpubl. data), suggesting that protection of wetlands for adults would also protect aquatic habitat for hatchlings. Importantly, the use of upland habitats in the fall by hatchlings may require additional protection of upland dispersal routes from nest habitats to nearby wetlands. The two critical periods where upland open habitat would be most important to *E. blandingii* are during nesting by adult females (May–June in Ontario), and again as hatchlings emerge from nests and disperse to overwintering sites (August–October).

Microhabitat selection

We found evidence that hatchlings select habitat at the micro-scale. The important variables used to select microhabitat differed between species, likely reflecting differences in both the habitats available to hatchlings of each species and also differences in species-specific selective pressures influencing hatchling behaviour. The available microhabitats surrounding a creek and floodplain (for *G. insculpta*) were probably different from available microhabitats in marshes, swamps and the surrounding forest (*E. blandingii*). However, temporal differences in emergence of each species, approximately a week earlier in *G. insculpta* than in *E. blandingii*, inhibit direct comparisons of microhabitat availability between the species because availability of different resources (such as temperature) changes through time. Hatchling *G. insculpta* selected microhabitats with cooler temperatures than random plots, which would reduce water loss and the risk of desiccation. We predicted that hatchlings would use

microhabitats with more ground cover than random plots, but instead hatchlings chose sites with less leaf litter than expected. These microhabitats may have been further away from the forest edge, which hatchlings strongly avoided at the macrohabitat spatial scale. Hatchling *E. blandingii* selected microhabitats with more total ground cover and more woody vegetation than random plots. This cover, which turtles used for refuge, would both reduce their exposure to visual predators and also reduce water loss. Hatchlings were not only selecting macrohabitat types, but they also selected microhabitat within these broader-scale classifications that likely reduced their risk of mortality.

Winter site selection

Hatchlings showed evidence of selecting specific overwintering sites on the basis of temperature. In winter 2009–10, *E. blandingii* selected overwintering sites that were significantly colder than haphazard stations. In winter 2010–11, there was also some evidence of temperature selection, although temperatures were similar between marsh, upland open and turtle overwintering sites. The selection of cold temperatures compared with the surrounding environment appears to be a widespread strategy among adult turtles in northern temperate environments (Litzgus *et al*. 1999; Greaves and Litzgus 2007, 2008; Edge *et al*. 2009; Rasmussen and Litzgus 2010; Paterson *et al*. 2012). Adult *E. blandingii* congregated for winter at our study site (Edge *et al*. 2009), but hatchlings were rarely found overwintering in groups. Although some habitats were even colder than where turtles overwintered (specifically upland open in 2010–11), the present study is the first to suggest that hatchlings may move to specific sites in aquatic habitats that are colder than the surrounding areas, similar to conspecific adults at the same site (Edge *et al*. 2009). However, we did not quantify other physical characteristics (e.g. water depth) that may be correlated with temperature, so the relationship between site selection and temperature may represent a correlation and not a cause and effect relationship.

Several *E. blandingii* hatchlings attempted to overwinter in upland habitats, especially in 2009–10. Terrestrial overwintering has been suggested for *E. blandingii* (Standing *et al*. 1997; McNeil *et al*. 2000), but no studies to our knowledge have concretely documented hatchlings that remained upland over winter outside of nest cavities. Hatchlings emerged from nests later in 2009–10 (first emergence 28 August) than in 2010–11 (first emergence 14 August), and hatchlings may simply have not had sufficient time to move to aquatic habitats (which are thermally buffered) before air temperatures dropped to levels that precluded further terrestrial movements in 2009–10. However, because of transmitter failure and difficulty in reaching the remote site in the early spring, it is unknown whether terrestrially overwintering hatchlings survived. In 2010–11, only two *E. blandingii* hatchlings overwintered in terrestrial habitats, although they were both close to open water (<50 m) and their fate was not determined the following spring. Future work should identify whether hatchling *E. blandingii* can overwinter successfully on land because this may have strong implications for the conservation of upland habitat adjacent to nesting sites.

Conclusions and management implications

Hatchlings of both *G. insculpta* and *E. blandingii* selected habitat at macro- and micro-spatial scales as they dispersed from nesting sites to their overwintering sites, which may decrease the risk of environmental exposure and predation; however, the habitats selected differed between species as a result of female nest-site choice. Because of their higher mobility (i.e. maximum path lengths), eight different macrohabitat types were available to *E. blandingii* hatchlings in their nest ranges, whereas only four different macrohabitats were available to *G. insculpta* hatchlings, and the limited habitat heterogeneity for *G. insculpta* may have contributed to their relatively higher mortality rate. Female nest-site selection is known to have a powerful influence on the fitness of emerging hatchlings (O'Steen 1998; Kolbe and Janzen 2002). Our findings suggest that female nest-site selection also influences the habitats that are available to these small and relatively immobile hatchlings; this is significant because habitat selection presumably plays a large role in survival. We also found evidence that, like conspecific adults, hatchling *E. blandingii* individuals select overwintering sites on the basis of temperature. Despite occurring more-or-less sympatrically, habitats selected for overwintering differed between the two species. Future work should compare the fitness (survival) consequences for hatchlings selecting different macro- and microhabitat features.

Despite significant differences in survivorship and mobility between hatchlings and adults, comparisons of our data with those of published studies on conspecific adults revealed no evidence of an ontogenetic shift in habitat selection. Our results indicated that habitat protection based on adult preferences of aquatic habitats and nesting sites would also protect habitat for post-emergent hatchlings. However, terrestrial dispersal from nests to overwintering sites and potential terrestrial overwintering behaviour in *E. blandingii* suggested that upland areas that differ from those used by adults may also need to be protected. To our knowledge, our study is the first to successfully follow and test habitat selection by a large number of hatchling turtles; thus, our study provides an important first step in understanding how resource requirements differ between life stages within species and between species, and is important for establishing management plans to protect multiple life stages of species at risk.

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