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Multi-scale Assessment of Rock Barrens Turtle Nesting Habitat: Effects of Moisture and Temperature on Hatch Success

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Understanding thermal and moisture regimes in nesting habitat is an important step in management and restoration of at-risk turtle habitat because anthropogenic stressors that affect these key properties impact hatch success. In rock barrens landscapes, freshwater turtles are known to nest in unique shallow-soil deposits in depressions in the bedrock. Our objective was to provide the first comprehensive multi-scale assessment of turtle nesting habitat in a rock barrens landscape. At the nest-site scale, we characterized nesting habitat, tested for evidence of nest-site selection by the Blanding's Turtle (*Emydoidea blandingii*), Spotted Turtle (*Clemmys guttata*), and Midland Painted Turtle (*Chrysemys picta marginata*), and examined the effects of nest temperature and moisture on egg hatching success. At the landscape-scale, we conducted a systematic survey across 660 ha to assess the availability of nesting habitat. Although rock barrens were the second most dominant land cover type, the availability of suitable nesting habitat with deeper soil and an open canopy was limited to 11% of the rocky outcrops and <3% of the study area. We found that shallow rock barrens nesting habitat had unique soil temperature and moisture dynamics that were linked to soil properties and bedrock morphology to provide successful incubation conditions. In particular, mean daily temperature, variance of soil saturation during incubation, and their interaction had a significant effect on egg hatching success, regardless of egg mass. There was also evidence that turtles selected sites that were warmer and drained faster than paired haphazard sites despite having other similar characteristics. Given that the loss and degradation of nesting habitat is of conservation concern for the survival and recovery of at-risk turtle species, we recommend that key management strategies should include stronger protection of critical rock barrens nesting habitat and the development of landscape-appropriate strategies for restoration and creation of nesting habitat.

REPTILE species are decreasing globally due in part to habitat loss and degradation, invasive species, and climate change (Gibbons et al., 2000; Lesbarrères et al., 2014; Stanford et al., 2020). These anthropogenic stressors are detrimental for freshwater turtle species, and habitat alterations can affect the species' aquatic habitats in addition to the upland habitat that supports travel corridors, nesting, thermoregulation, and hatchling dispersal from nests. Thus, the availability and suitability of terrestrial habitat is essential for freshwater turtles, especially during the nesting season (Congdon et al., 2011). Some species traverse long distances (>6 km) to reach suitable nesting sites (e.g., Edge et al., 2010; Millar and Blouin-Demers, 2011). If natural nesting habitat is limited, turtles may nest in anthropogenic sites such as road shoulders or agricultural fields which can negatively affect hatch success (e.g., Kolbe and Janzen, 2002; Mui et al., 2015; Thompson et al., 2018). Protecting nest habitat and understanding the factors contributing to hatch success is an important component of managing populations of at-risk turtles because nest success can be as low as 0% in some Ontario populations (Environment and Climate Change Canada [ECCC], 2018a) and population recruitment rates are low due to delayed sexual maturity (Congdon et al., 1993), high nest predation rates (Marchand and Litvaitis, 2004), and dependence on nest incubation conditions (e.g., Kolbe and Janzen, 2002).

Freshwater turtles nest in beaches (Bowen and Janzen, 2008; Hughes et al., 2009), agricultural fields (Mui et al., 2015; Thompson et al., 2017), soil deposits in rocky landscapes (Petokas and Alexander, 1980; Litzgus and Brooks,

1998, 2000; Beaudry et al., 2010; Markle and Chow-Fraser, 2014; Francis et al., 2019), small clearings (Thompson et al., 2017; Piczak and Chow-Fraser, 2019), and even beaver lodges (Obbard and Brooks, 1980; Francis et al., 2019). Female nest-site selection is critical because it influences hatch success through site-specific characteristics that affect nest moisture and temperature including canopy cover, slope, substrate type, and nest depth (e.g., Kolbe and Janzen, 2002; Morjan, 2003; Hughes and Brooks, 2006; Mitchell and Janzen, 2019). Nest sites usually have an open canopy because a high percent canopy cover is likely to decrease incubation temperatures, and completely shaded nests may result in no successful hatchlings (Janzen, 1994; Congdon et al., 2000). Similarly, females often nest on south-facing slopes presumably because of their increased exposure to solar radiation (Schwarzkopf and Brooks, 1987; Hughes and Brooks, 2006). Nest depth also affects incubation temperature, the magnitude of temperature variations, and soil moisture (Nelson et al., 2004; Refsnider et al., 2013). Eggs closer to the soil surface are often exposed to increased temperatures for longer periods and a larger range of daily temperature fluctuations compared to deeper eggs (Wilhoft et al., 1983; Shine and Harlow, 1996; Harlow and Taylor, 2000; Morjan, 2003). Nest temperatures are also affected by moisture conditions where wetter soils experience cooler temperatures and dampened temperature fluctuations (Packard et al., 1985; Morjan, 2003). While soil-water content is important for embryonic development (Cagle et al., 1993) and hatch success (Packard et al., 1987), too much moisture

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or flooding can inhibit development and hatching (Ratterman and Ackerman, 1989).

Understanding soil thermal and moisture regimes in nesting habitat is an important step in habitat management and restoration because any habitat alterations or changes that affect nest temperature and moisture can impact hatch success and hatchling phenotype (e.g., Bolton and Brooks, 2010; Riley et al., 2014; Mui et al., 2015; Thompson et al., 2018; Markle et al., 2020). For example, agricultural fields can act as ecological sinks because vegetation growth occurs after female site-selection and oviposition that subsequently alters incubation temperatures through shading (Mui et al., 2015; Thompson et al., 2018). Although wildfire can be a natural landscape disturbance that creates newly open microhabitats which benefit some species (Litzgus and Mousseau, 2004; Dovčiak et al., 2013), high severity wildfires that result in deep burning substantially reduce the availability of shallow soil deposits used for nesting in rock barrens landscapes and have the potential to negatively affect the suitability of remaining nesting habitat (Markle et al., 2020). In addition to physical alterations to nesting habitat, contemporary climate change poses threats to turtle species with temperature-dependent sex determination (Schwanz and Janzen, 2008; Mitchell and Janzen, 2010; Refsnider et al., 2013; Valenzuela et al., 2019). Not only do increases in mean temperature alter sex ratios (Janzen, 1994), but increased temperature fluctuations could lead to skewed sex ratios and demographic collapse (Mitchell and Janzen, 2010; Valenzuela et al., 2019).

The rock barrens landscape along eastern Georgian Bay, Ontario, Canada is a biodiversity hotspot providing habitat for over 50 species at risk (Burke et al., 2018), including the Blanding's Turtle (*Emydoidea blandingii*), Spotted Turtle (*Clemmys guttata*), Eastern Musk Turtle (*Sternotherus odoratus*), Snapping Turtle (*Chelydra serpentina*), and Midland Painted Turtle (*Chrysemys picta marginata*). In this landscape, turtles nest in shallow soil on the open, rocky outcrops that are dominated by moss (*Polytrichum* spp.) and lichen (*Cladonia* spp.; Litzgus and Brooks, 1998, 2000; Markle and Chow-Fraser, 2014). While this natural rocky nesting habitat must provide similar incubation conditions to other nesting habitat (e.g., beaches, open fields) to permit successful egg incubation, the shallow soils overlaid on granite bedrock are subject to highly variable temperature and moisture fluctuations (Moore et al., 2019). Despite this variability, nesting on rock outcrops may be suitable because of the exposure to sunlight and ability of the underlying granite to maintain higher temperatures for extended periods (Litzgus and Brooks, 1998) to compensate for a shorter incubation duration at northern sites (Bobyn and Brooks, 1994). Little is known about the unique soil thermal and moisture regimes in rock barrens nesting habitat and the effects on hatch success. This lack of knowledge limits our ability to predict climate change impacts on nesting habitat and hatch success and create suitable artificial nesting habitat characteristic of natural rock barrens nesting habitat. Addressing this knowledge gap is vital because any further reduction or alteration to available suitable nesting habitat could have consequences for turtle population persistence (ECCC, 2018a, 2018b) especially in the Ontario rock barrens where turtle populations occur near the species' northern range limit.

Our objective was to provide the first comprehensive multi-scale assessment of turtle nesting habitat in a rock

barrens landscape. At the nest-site scale, we characterized nesting habitat and tested for evidence of nest-site selection. We expected that turtle nests would have different physical characteristics, soil thermal, and soil moisture regimes compared to haphazard sites, indicating nest-site selection by females. Even if females did select for nest sites, there would likely be natural variability in incubation conditions; therefore, we examined the effects of nest temperature and moisture on egg hatching success. Lastly, based on the characteristics of turtle nest sites, we conducted a landscape-scale systematic survey to assess the availability of turtle nesting habitat and predicted that soil depth would be the primary physical characteristic limiting nesting habitat in the rock barrens.

MATERIALS AND METHODS

Study site and nest surveys.—The 660 ha study area is located approximately 10–15 km east of Georgian Bay, Lake Huron, Ontario, and supports a diverse turtle community including the Blanding's Turtle, Spotted Turtle, Snapping Turtle, and Midland Painted Turtle. The Blanding's Turtle is listed as Threatened under Canada's federal Species at Risk Act (SARA, 2002) and Ontario's provincial Endangered Species Act (ESA, 2007), and considered Endangered by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC, 2016). Both federally and provincially, the Spotted Turtle is listed as Endangered and the Snapping Turtle is listed as Special Concern (SARA, 2002; ESA, 2007). The Midland Painted Turtle is considered a species of Special Concern by COSEWIC (2018). The Ontario rock barrens landscape is characterized by a mosaic of open rock, wetlands, and forest underlain by Canadian Shield granitic bedrock (Wester et al., 2018). The shallow soil found on the open rocky outcrops is the natural nesting habitat for turtles within this region (Fig. 1A; Litzgus and Brooks, 1998, 2000; Markle and Chow-Fraser, 2014; Francis et al., 2019).

Beginning in late May or early June 2018 and 2019, open rock barrens were monitored for turtle nesting activity from 1700 h until dark. Female turtles were monitored from a distance during oviposition to minimize disturbance. The turtle species and exact location of the nest site was recorded. After oviposition, we carefully excavated nests and measured egg length, width, and mass. We recorded nest chamber characteristics including depth to eggs, depth to chamber bottom, chamber width, and depth to bedrock. We reburied eggs in their original orientation and position within the nest chamber and installed an above-ground hardware cloth (0.63 cm galvanized wire) nest cage (30 cm diameter) to protect the nests from predators. This style of predator-exclusion cage does not interfere with nest temperature or soil moisture (Riley and Litzgus, 2013) and, because they were applied to all sites, are expected to have consistent effects, if any. At the beginning of August, three openings (5x5 cm) were cut in each predator-exclusion cage to allow hatchlings to escape.

Nest-site monitoring and selection.—We recorded hourly soil temperature and moisture at 12 turtle nests (6 in 2018, 6 in 2019) within 24 hours of oviposition until hatching (Table 1) using temperature loggers (iBwetland iButton, Alpha Mach, Sainte-Julie, Quebec) and 5 cm moisture probes installed horizontally (ECH₂O EC-5, METER Environment, Pullman, WA, logged with a HOBO USB Micro Station, ONSET, Bourne,

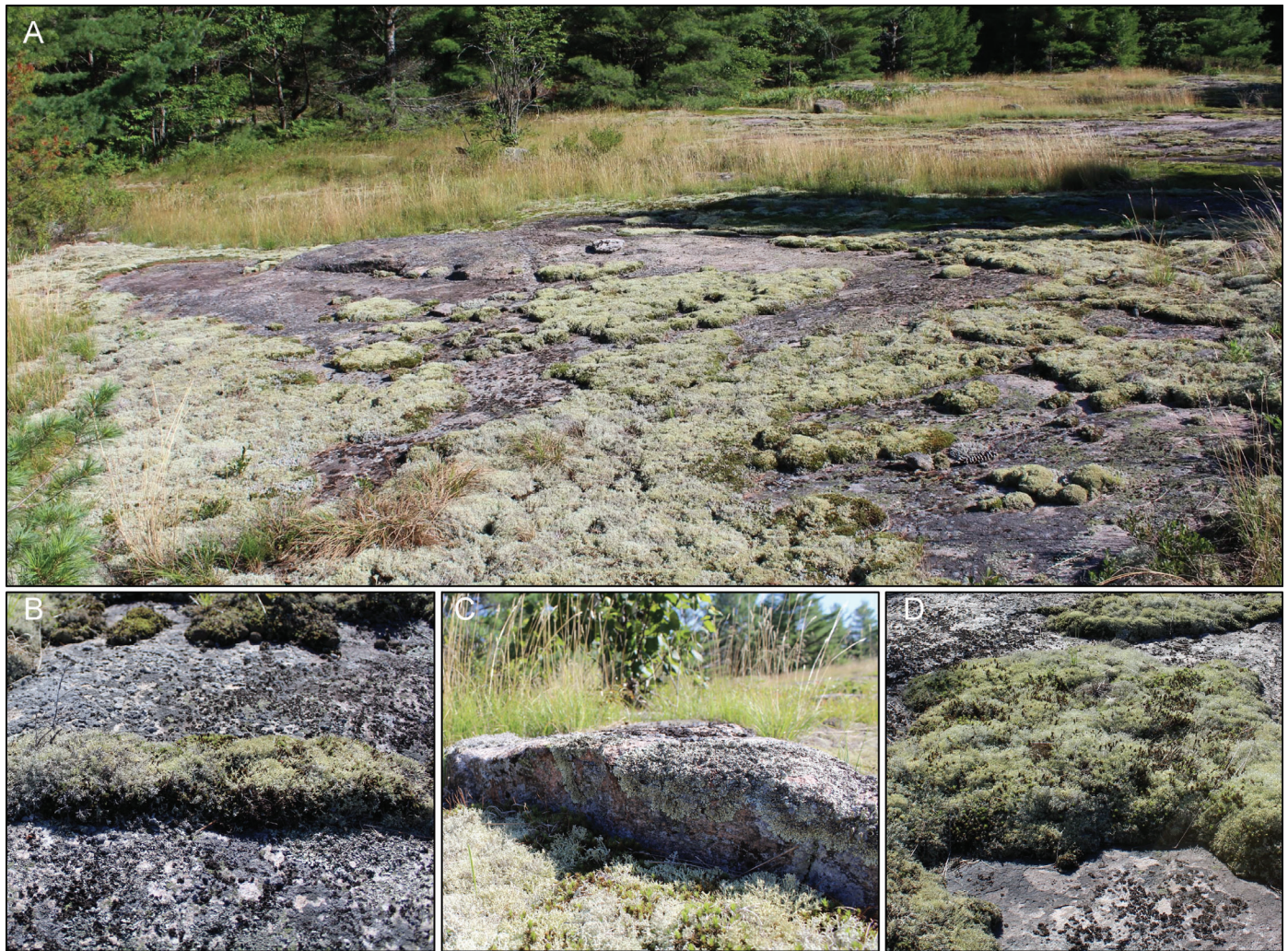


Fig. 1. In a rock barrens landscape in the eastern Georgian Bay region (A), turtles nest in shallow soil deposits underlain by bedrock which can be classified as having either a crevice (B), ledge (C), or flat (D) morphology.

MA) to characterize nesting habitat and assess habitat use. For turtle nests monitored in 2018 only, we also selected a paired haphazard site ($n = 6$) within a 10 m radius of the turtle nest that had a comparable canopy openness and soil depth to bedrock to evaluate nest-site selection. Temperature loggers and moisture probes were buried directly beside each nest chamber at the depth corresponding to the top and bottom of each nest chamber (Table 1) and at the same depths at paired haphazard sites to facilitate comparisons between turtle and haphazard sites (e.g., Massey et al., 2019). Every 10–14 days after oviposition until hatching, we recorded vegetation composition in a 1x1 m quadrat centered on the nest cavity and quantified canopy openness as the proportion of pixels containing sky (hemispherical photos were taken using a Sunex 185 SuperFisheye 5.6 mm F/5.6 lens). The photos were analyzed in Gap Light Analyzer 2.0 (Frazer et al., 1999) using a custom configuration file outlining site-specific details including image orientation, projection distortion, growing-season length, sky region brightness, and atmospheric conditions. A manually derived threshold was used to separate pixels into two categories, sky and vegetation, for image classification. Because turtle nests are laid in shallow soil deposits on the open rock barrens, underlying bedrock morphology was classified as either

crevice, ledge, or flat (Fig. 1). Crevice morphology sites have soil in the cracks of the bedrock (Fig. 1B), ledge sites have soil which accumulated up against the side of the bedrock (Fig. 1C), and flat morphology sites are those where soil has accumulated on gently sloping bedrock (Fig. 1D).

After hatchlings left the nest, soil cores (5 cm diameter) were taken beside each nest chamber at all 12 turtle nests (6 in 2018, 6 in 2019) and haphazard sites (6 in 2018). First, we used the intact soil cores to determine a site-specific calibration curve using the method described by Cobos and Chambers (2010). Calibrated soil moisture data (volumetric water content $\text{m}^3 \text{m}^{-3}$) were temperature-corrected using a multiple linear regression technique (Cobos and Campbell, 2007). Next, we divided each of the 18 soil samples into 5 cm depth increments and processed soil in the lab to determine soil texture, soil bulk density, and percent organic matter. We selected 5 cm depth increments so the soil volume for each sample closely matched the soil volume measured by the moisture probe. Volumetric water content measurements were converted to percent soil saturation (percentage of soil-pore space filled with water) to assess the flooded condition of each nest site. To determine the rate of soil drying after rainfall events, we calculated the recession coefficient (k) 12 hours, 24 hours, and 48 hours after rainfall using an

Table 1. Thermal and moisture regimes were monitored hourly during the incubation period for 12 turtle nests in the eastern Georgian Bay, Ontario region. Evidence of at least one hatchling emerging from the nest was used as the estimated date emerged and to estimate the number of incubation days. Note that no hatchlings overwintered in the nest cavity.

| Species | Clutch size | Eggs hatched | Evening laid | Estimated date emerged | Incubation duration (d) | Depth to top of nest chamber (cm) | Depth to bottom of nest chamber (cm) | Bedrock morphology |
|-----------------------------|-------------|--------------|--------------|---------------------------|-------------------------|-----------------------------------|--------------------------------------|--------------------|
| <i>Clemmys guttata</i> | 4 | 0 | 07 June 2018 | 27 Sept 2018 ^a | 112 | 4.5 | 7.5 | Flat |
| <i>Emydoidea blandingii</i> | 16 | 13 | 11 June 2018 | 31 Aug–11 Sept 2018 | 81–91 (91) | 5.0 | 10.0 | Crevice |
| <i>Chrysemys picta</i> | 8 | 3 | 18 June 2018 | 26 Sept 2018 | 100 | 4.5 | 8.0 | Flat |
| <i>Emydoidea blandingii</i> | 9 | 7 | 20 June 2018 | 31 Aug–11 Sept 2018 | 72–83 (83) | 5.0 | 10.0 | Crevice |
| <i>Chrysemys picta</i> | 6 | 5 | 15 June 2018 | 13 Sept 2018 | 90 | 5.0 | 10.0 | Ledge |
| <i>Chrysemys picta</i> | 6 | 1 | 22 June 2018 | 27 Sept 2018 | 97 | 4.5 | 9.0 | Flat |
| <i>Chrysemys picta</i> | 10 | 2 | 12 June 2019 | 18 Sept 2019 | 98 | 5.5 | 9.0 | Ledge |
| <i>Chrysemys picta</i> | 10 | 9 | 13 June 2019 | 06 Sept 2019 | 85 | 5.5 | 10.0 | Ledge |
| <i>Chrysemys picta</i> | 10 | 2 | 19 June 2019 | 06 Sept 2019 | 79 | 4.5 | 8.0 | Flat |
| <i>Chrysemys picta</i> | 6 | 4 | 24 June 2019 | 06 Sept 2019 | 74 | 5.5 | 9.0 | Ledge |
| <i>Chrysemys picta</i> | 9 | 5 | 24 June 2019 | 06 Sept 2019 | 74 | 5.5 | 10.5 | Ledge |
| <i>Emydoidea blandingii</i> | 11 | 11 | 27 June 2019 | 06 Sept 2019 | 71 | 7.5 | 13.5 | Crevice |

^a Evidence of hatching observed (nest cavity entrance disturbed), but all hatchlings were deceased. The date of this observation was taken as the date emerged to estimate incubation duration.

exponential decay function (Goel, 2011):

$$Q_t = Q_0 k^t$$

where Q_0 is the soil moisture after rainfall (the peak) and Q_t is the soil moisture at time t after rainfall. A larger recession coefficient (k) indicates a slower drying rate. Recession coefficients were compared using a Wilcoxon rank sum test and site properties were compared between turtle and haphazard sites using paired Wilcoxon rank sum tests.

Hatch success.—Towards the end of the incubation period, we monitored nests for signs of hatching. When signs of hatching were observed, all 12 nests (6 in 2018, 6 in 2019) were excavated to determine hatch success. An egg was considered successful if eggshells or hatchlings were present. An egg was considered unsuccessful if the intact egg was found, and it was assessed to determine the potential cause of mortality (e.g., moldy, infertile, late-term mortality, or depredated by ants).

We used a generalized linear mixed model in R 3.6.2 (lme4 package; R Core Team, 2019) to determine the effect of soil temperature and moisture on egg hatching success. We used a binomial distribution (log link) to model the outcome of egg hatching success (successful or unsuccessful) and included egg mass, mean daily temperature, variance of soil saturation during the incubation period, and the interaction between temperature and moisture as fixed effects. Clutch identity was included as a random effect to account for repeated sampling. Although there may be species-specific differences in hatch success, there were only a few eggs and nests for some turtle species and therefore species was not included as a random effect.

We also determined the moisture regime (percent saturation measured hourly during incubation) and rate of soil drying after rainfall events (recession coefficient) for nest sections with 100% hatch success or 0% hatch success. Each nest chamber was divided into two or three nest sections (or vertical layers) depending on egg orientation and placement. As each nest was excavated, the orientation and placement of each egg within the chamber was recorded and drawn. Based on these drawings, eggs were assigned a 'nest section' where eggs at approximately the same depth (or horizontal layer) were grouped together, and groups of eggs at different depths (or vertical layers) were labeled as the top, middle, or bottom nest section. It was common for nests with fewer eggs to only have a top and bottom nest section and no 'middle layer' of eggs. Hatch success for each nest section was calculated as the number of eggs successfully hatched divided by the total number of eggs in that section.

Landscape-scale habitat availability.—We surveyed habitat around eight wetlands, five of which were confirmed to support overwintering turtles (through springtime emergence surveys), to assess the availability and distribution of nesting habitat in the 660 ha study area. These eight focal wetlands were assessed as most likely to support overwintering turtles because they were dominated by aquatic habitats. The remaining wetlands in the study area included small ephemeral wetlands and developed peatlands with no open water. The open rocky outcrops surrounding the eight focal wetlands encompassed the area surveyed for nesting females and the monitored turtle nests were within 200 m of one of the five occupied wetlands.

For each of the eight wetlands, we randomly selected the starting point of six 300 m transects which extended perpendicular from the wetland edge. We walked each transect and measured a suite of habitat characteristics every 1 m for a total of 1,800 points for each of the eight wetlands ($n = 14,400$). At each survey point, we used a 1 m² quadrat to determine the dominant land cover type (e.g., rock barren, forest, wetland). Since our main objective was to quantify rock barrens nesting habitat, we recorded detailed data at open rock barren plots because field surveys have only identified open rocky outcrops as natural nesting habitat (Litzgus and Brooks, 1998, 2000; Markle and Chow-Fraser, 2014). In each 1 m² rock barren quadrat, we measured soil depth, height of lichen or moss cover, slope, aspect, vegetation composition (identified to species), and took a hemispherical photo to quantify canopy openness. The canopy photos were batch processed in MATLAB (MathWorks Inc., Natick, MA) using RGB (red, green, blue) data to classify image pixels as vegetation or sky using a manually derived threshold.

To assess the soil characteristics across the open rock barrens portion of the landscape, we took soil cores (10 cm diameter) according to a stratified random sampling design. Using the landscape-level transect data, quadrats were classified by depth (shallow [3–6 cm], medium [6–10 cm], or deep [10+ cm]) and dominant (>80%) cover type (lichen, moss, or litter). For each depth class, we randomly collected soil from nine locations in each of the three cover types, sampling a total of 81 sites across the landscape. Each of the 81 samples were divided into 2 cm depth increments and processed in the lab to determine soil texture, soil bulk density, and percent organic matter. We used a more detailed depth increment for landscape samples (i.e., 2 cm compared to 5 cm for nest sites) to provide a comprehensive dataset for ongoing research in the region. We tested for a relationship between soil bulk density and soil depth using a linear regression, and for differences among cover types (lichen, moss, or litter) with a Kruskal-Wallis test followed by Steel-Dwass *post hoc* tests.

Laboratory analyses.—Soil bulk density was determined by oven-drying samples at 65°C until their 24-hour weight loss was <0.1 g. Soil bulk density estimates were corrected by removing wood, roots, and large rocks from the sample. Particle density was estimated by determining the organic and inorganic weight fractions of each sample, and assuming an organic and inorganic particle density of 1,470 kg m⁻³ and 2,650 kg m⁻³, respectively (Redding and Devito, 2006). To determine organic and inorganic fractions, we used organic matter loss-on-ignition where a 5 g subsample from each oven-dried sample was placed in a muffle furnace at 550°C for 4 hours. The proportional weight loss after combustion in the muffle furnace was assumed to be the organic fraction of the sample. Soil saturation was calculated by dividing volumetric water content by soil porosity. We calculated porosity using the equation: porosity = 1–bulk density/particle density.

RESULTS

Nest habitat use and site characteristics.—Nest-site characteristics including soil thermal and moisture regimes were monitored for one Spotted Turtle, three Blanding's Turtle, and eight Painted Turtle nests over two seasons (Table 1).

Nest sites were characterized by an average depth to eggs of 5.1±0.2 cm (SE reported unless otherwise indicated; range 4.5–7.5 cm), depth to nest bottom of 9.5±0.5 cm (range 7.5–13.5 cm), nest chamber width of 8.0±0.6 cm (range 6.0–12.0 cm), and depth to bedrock of 13.3±1.6 cm (range 7.5–22.2 cm). Nest chamber size was similar across species, but the deepest nests tended to be laid by Blanding's Turtles (Table 1). Surface slope was an average of 7±1.3° (range 2–15°) with either South, South-East, South-West, or East aspect (no aspect when slope < 5°). In a 1 m² quadrat centered on the nest cavity, lichen (31%), vascular plants (27%; e.g., blueberry [*Vaccinium angustifolium*], grass [*Poaceae*]), and bedrock (23%) were dominant cover types followed by moss (13%) and bare soil (8%). Surface cover at nest sites was consistent throughout the incubation period without much additional vegetation growth. Canopy openness was also fairly consistent throughout the incubation period, changing by only 16±2%, so values were averaged per nest site. Mean canopy openness at turtle nest sites was 70±2% with a range of 56% to 81%.

Although all 12 turtle nests were laid in shallow soil deposits on the open rock barrens, the underlying bedrock morphology varied among the monitored sites. Bedrock morphology affected soil temperatures such that crevice sites maintained temperatures up to 3°C warmer during the evening (1800–2400 h) and night (0000–0600 h; Fig. 2) despite nests being slightly deeper in crevices ($n = 3$; top of chamber, 5.8±0.08 cm; bottom of chamber, 11.2±1.2 cm) compared to flat ($n = 4$; top of chamber, 4.5±0 cm; bottom of chamber, 8.1±0.3 cm) and ledge sites ($n = 5$; top of chamber, 5.4±0.1 cm; bottom of chamber, 9.7±0.3 cm). Regardless of morphology, eggs towards the top of the nest chamber (Fig. 2A) experienced more variable temperatures compared to eggs at the bottom of the chamber (Fig. 2B).

Hatch success.—We monitored hatch success of 36 Blanding's Turtle eggs (3 nests), 4 Spotted Turtle eggs (1 nest), and 65 Painted Turtle eggs (8 nests) in their natural nest sites (105 eggs total; Table 2). Hatch success was comparable between 2018 (59%) and 2019 (59%), although individual nest success ranged between 0% and 100%. Blanding's Turtle eggs had the highest hatching success (86%) compared to Painted Turtle (48%) and Spotted Turtle eggs (0%). One of the eight Painted Turtle nests was located after the female had already left the nest, so egg mass was not recorded to avoid handling of eggs that had been laid an unknown number of hours prior to discovery (Table 2). Therefore, the mass of the six unknown Painted Turtle eggs were assigned the mean Painted Turtle egg mass (7.6 g) for modeling purposes.

Mean daily temperature (Estimate ± SE [Est.] = 0.901±0.347, $Z = 2.60$, $P = 0.009$), variance of soil saturation during incubation (Est. = -0.850±0.355, $Z = -2.40$, $P = 0.016$), and their interaction (Est. = -0.835±0.421, $Z = -1.98$, $P = 0.047$) had a significant effect on egg hatching success ($n = 105$). Egg mass did not significantly influence hatch success (Est. = 0.118±0.141, $Z = 0.84$, $P = 0.40$). When the variability in soil saturation during the incubation period was high (standard deviation of 20% saturation), and temperature was <23°C or >23.5°C, mean hatch success ranged between 41–46%, but large confidence intervals indicate hatch success was highly variable (10–85% [95% CI]; Fig. 3). When mean daily soil temperature was between 23–23.5°C, mean hatch success was only 43% but slightly less variable (25–66% [95%

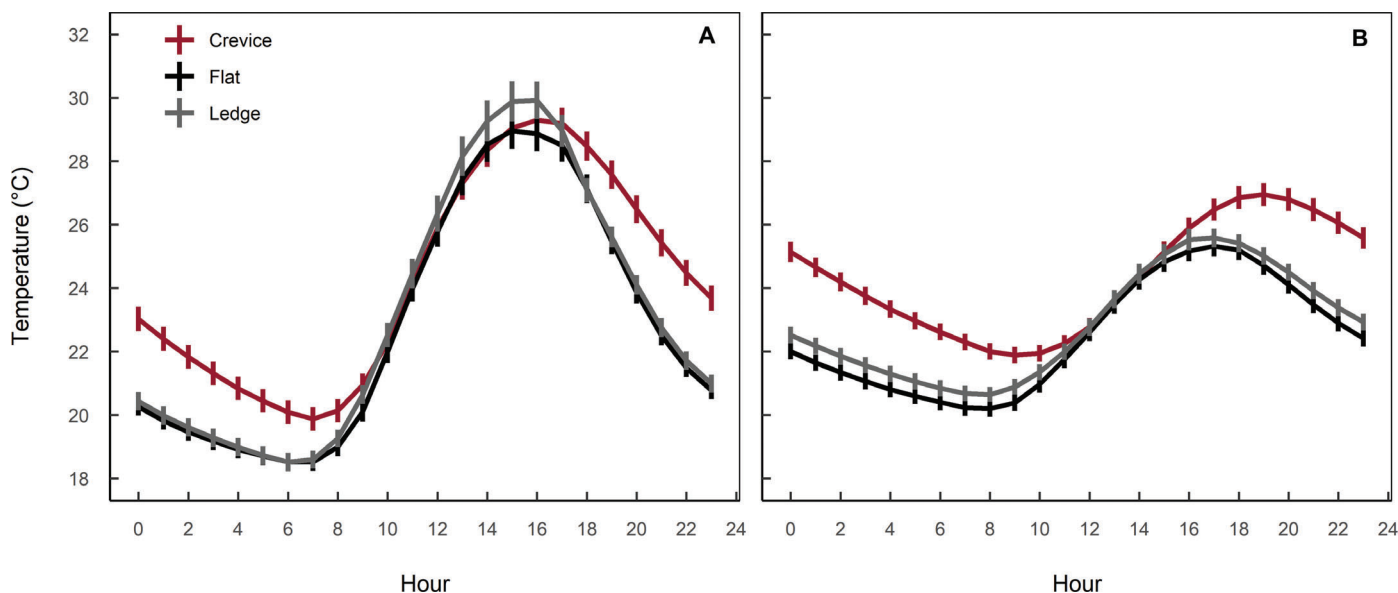


Fig. 2. Mean ($\pm 95\%$ confidence interval) hourly soil temperature ($^{\circ}\text{C}$) at the depth of the nest chamber top (A) and bottom (B) for turtle nests during the 2018 ($n = 6$) and 2019 ($n = 6$) incubation period. Nests were laid in sites with a crevice (red line, $n = 3$), ledge (gray line, $n = 5$), or flat (black line, $n = 4$) bedrock morphology.

CI]. On the other hand, when there was low variability in soil saturation (standard deviation of 10% saturation), mean hatch success increased with increasing mean daily soil temperature. When mean daily soil temperature was $>23.8^{\circ}\text{C}$, mean hatch success was predicted to be $>90\%$ (72–100% [95% CI]; Fig. 3) and was up to 100% when soil temperature was $>24^{\circ}\text{C}$.

In the wetter incubation season (2018, 248.7 mm total rainfall), nest sections with 100% hatch success maintained drier conditions by an average of $32 \pm 11\%$ (SD; Fig. 4A). In comparison, in the drier incubation season (2019, 126.3 mm total rainfall), nest sections with 100% hatch success maintained drier conditions but only by an average of $5 \pm 4\%$ (SD; Fig. 4B). Across both years, nest drying followed an exponential decay after rainfall events, where nest sections with 100% hatch success drained quicker and maintained an approximately 20% lower soil saturation than sections with 0% hatch success (Fig. 5A). Nest sections with 100% hatch success also maintained a significantly higher rate of drying, assessed through the recession coefficient, compared to sections with 0% hatch success 12 hours (0.64 ± 0.02 vs. 0.76 ± 0.02 , respectively; $X^2 = 16.6$, $P < 0.0001$), one day (0.72 ± 0.02 vs. 0.81 ± 0.01 , respectively; X^2

$= 13.7$, $P = 0.0002$), and two days after rainfall (0.79 ± 0.01 vs. 0.85 ± 0.01 , respectively; $X^2 = 13.9$, $P = 0.0002$).

Nest-site selection.—In 2018, we monitored continuous soil thermal and moisture regimes at six turtle nests (three Painted Turtle, two Blanding's Turtle, one Spotted Turtle; Table 1) and six paired haphazard sites to examine nest-site selection. Mean daily temperature at turtle nests ($22.6 \pm 2.9^{\circ}\text{C}$ [SD]) was consistently warmer than paired sites ($21.1 \pm 2.3^{\circ}\text{C}$ [SD], $S = 73585$, $P < 0.0001$; Fig. 6) despite having similar canopy openness and soil properties, and comprising all three bedrock morphologies. At turtle nests and paired sites, canopy openness was comparable when measured at oviposition ($73 \pm 3\%$ vs. $69 \pm 4\%$, respectively, $S = 3.5$, $P = 0.6$) and at hatching ($64 \pm 6\%$ vs. $59 \pm 4\%$, respectively, $S = -8.5$, $P = 0.09$). Both turtle sites and paired sites also had similar soil depth to bedrock (14.2 ± 2.3 cm vs. 12.5 ± 1.5 cm, respectively, $S = -9$, $P = 0.13$) and comparable soil bulk density (1060 ± 99 kg m^{-3} vs. 927 ± 75 kg m^{-3} , respectively) and porosity with depth (0.58 ± 0.04 vs. 0.64 ± 0.03 , respectively; Supplemental Fig. 1; see Data Accessibility). Soil organic content was similar at near-surface depths ($8.1 \pm 1.3\%$ haphazard vs. $9.4 \pm 2.2\%$ turtle) but tended to differ between turtle nests and

Table 2. Morphological characteristics of turtle eggs monitored in the eastern Georgian Bay, Ontario region.

| Species | Mass (g) \pm SD (range) | Width (cm) \pm SD (range) | Length (cm) \pm SD (range) | Number of eggs | Number of nests |
|-----------------------------|------------------------------|--------------------------------|---------------------------------|-----------------|-----------------|
| <i>Clemmys guttata</i> | 6.7 ± 0.4 (5.67–7.09) | 1.45 ± 0.13 (1.10–1.70) | 3.27 ± 0.07 (3.08–3.40) | 4 | 1 |
| <i>Emydoidea blandingii</i> | 12.5 ± 0.2 (10–15) | 2.42 ± 0.04 (2.00–2.96) | 3.45 ± 0.05 (2.76–3.98) | 36 | 3 |
| <i>Chrysemys picta</i> | 7.6 ± 0.2 (5–11) | 1.86 ± 0.05 (1.10–2.70) | 3.12 ± 0.05 (2.10–3.78) | 59 ^a | 7 ^a |

^a Morphological characteristics were only measured for 59 of the 65 *Chrysemys picta* eggs monitored for hatching success because one of the eight Painted Turtle nests was located after the female had already left the nest. Eggs were not handled since they were laid an unknown number of hours prior to discovery.

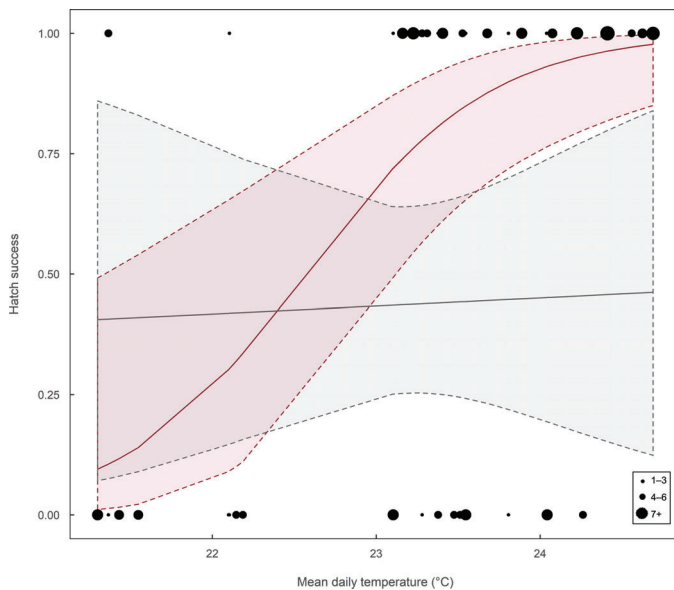


Fig. 3. Predicted probability ($\pm 95\%$ confidence intervals) of turtle egg hatch success ($n = 105$) in relation to mean daily soil temperature ($^{\circ}\text{C}$) when variance of percent soil saturation during incubation was high (standard deviation of 20% saturation, gray) compared to low (standard deviation of 10% saturation, red). Mean daily incubation temperature is shown for each turtle egg and black circles represent sample size (1–3 eggs [small circle], 4–6 eggs [medium circle], or 7+ eggs [large circle]).

haphazard sites into the soil column (Supplemental Fig. 1; see Data Accessibility).

As expected, soil temperatures closer to the surface, measured at depths representing the top of the nest chamber, were more variable and temperatures at some haphazard sites exceeded 50°C and dropped below 10°C (Fig. 7). The mean temperature difference between nests and paired sites was greatest in the afternoon ($2.32 \pm 0.05^{\circ}\text{C}$) and evening ($2.01 \pm 0.02^{\circ}\text{C}$) when turtle nests were up to 17.8°C and 15.8°C warmer than the paired site, respectively (Fig. 7). Warmer temperatures during the afternoon were driven by warmer surface temperatures, whereas warmer evening temperatures occurred at the bottom of the nest. Although to a lesser degree, turtle nests were still warmer in the morning ($1.13 \pm 0.02^{\circ}\text{C}$) and night ($1.23 \pm 0.02^{\circ}\text{C}$), reaching up to 10.7°C and 6.4°C warmer compared to the paired site,

respectively (Fig. 7). During both the morning and night, warmer temperatures occurred at the bottom of the nest chamber.

In the first half of the 2018 incubation period, when there were fewer rainfall events, the bottom of turtle nests tended to stay slightly more saturated compared to the top and bottom of the haphazard sites, whereas the top of the turtle nests dried quite rapidly despite all sites reaching similar maximum soil saturation during rainfall events (Fig. 8). However, beginning in August 2018, when rainfall events were more frequent, turtle nests (top and bottom) continued to drain following rainfall, whereas haphazard sites (top and bottom) drained slower, staying approximately 15–20% more saturated (Fig. 8). Overall, nest drying followed an exponential decay with turtle nests draining significantly faster than haphazard sites (Fig. 5B), and the greatest rate of drying (recession coefficient) for turtle nests compared to haphazard nests occurred 12 hours (0.66 ± 0.02 vs. 0.77 ± 0.02 , respectively; $X^2 = 19.4$, $P < 0.0001$), one day (0.74 ± 0.01 vs. 0.82 ± 0.01 , respectively; $X^2 = 17.0$, $P < 0.0001$), and two days after rainfall (0.79 ± 0.01 vs. 0.87 ± 0.01 , respectively; $X^2 = 17.8$, $P < 0.0001$).

Landscape-scale.—Approximately 26% of the landscape was classified as rock barrens, 66% as forest cover, and 7% as wetlands. Of the 3,781 quadrats assessed on rock barrens (i.e., potential nest habitat), 10% were dominated by juniper (*Juniperus* spp., $n = 384$) and the remaining 90% were considered open habitat potentially available for nesting ($n = 3,397$). At the potential nesting sites, mean soil depth was 7.9 ± 6.9 cm (SD, range 0–64 cm, $n = 3,389$), height of lichen or moss cover was 3.0 ± 2.0 cm (SD, range 0.5–28 cm, $n = 2,030$), canopy openness was $47 \pm 13\%$ (SD, range 4–88%, $n = 2,147$), and slope was $10 \pm 5^{\circ}$ (SD, range 3–43°, $n = 1,017$). Dominant cover types ($>80\%$ surface cover in 1 m^2 quadrat) across the open habitats were litter (38% of plots, $n = 684$), bedrock (27% of plots, $n = 483$), lichen (21% of plots, $n = 376$), and moss (10% of plots, $n = 186$). The aspect of surveyed plots was approximately equally distributed in all directions. Around the five wetlands confirmed to support overwintering turtles, the distribution of potential nest habitat (rocky outcrops) was typically within 200 m of the wetland edge.

Based on data from the 2018 and 2019 turtle nest sites, nest chambers required a minimum of 3–6 cm of soil, but eggs were typically laid 4.5–7.5 cm from the soil surface;

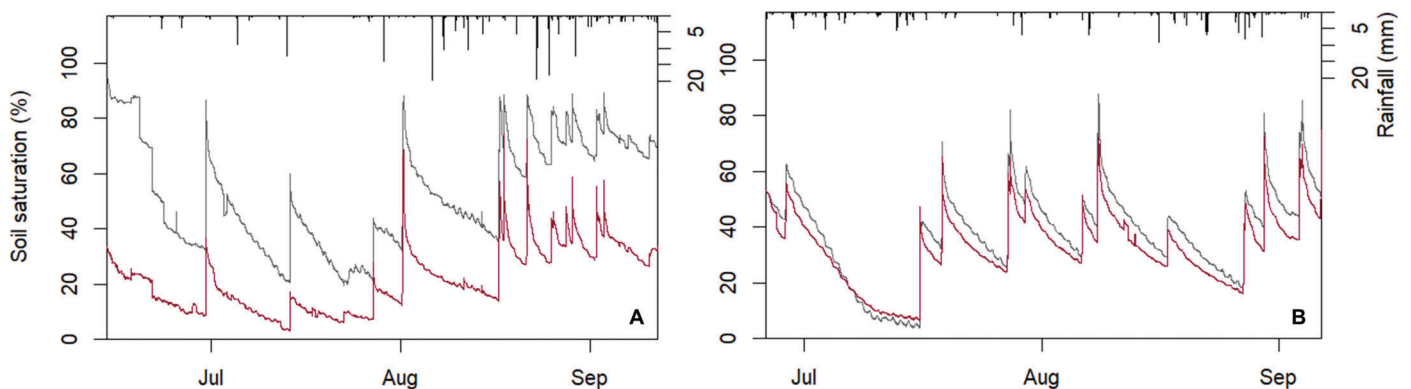


Fig. 4. Daily rainfall (mm) during the 2018 (A) and 2019 (B) incubation periods and average 15-minute soil saturation (%) for sections of the nest cavities with 100% hatch success (red line; $n = 3$, 2018; $n = 5$, 2019) and 0% hatch success (black line; $n = 5$, 2018; $n = 4$, 2019).

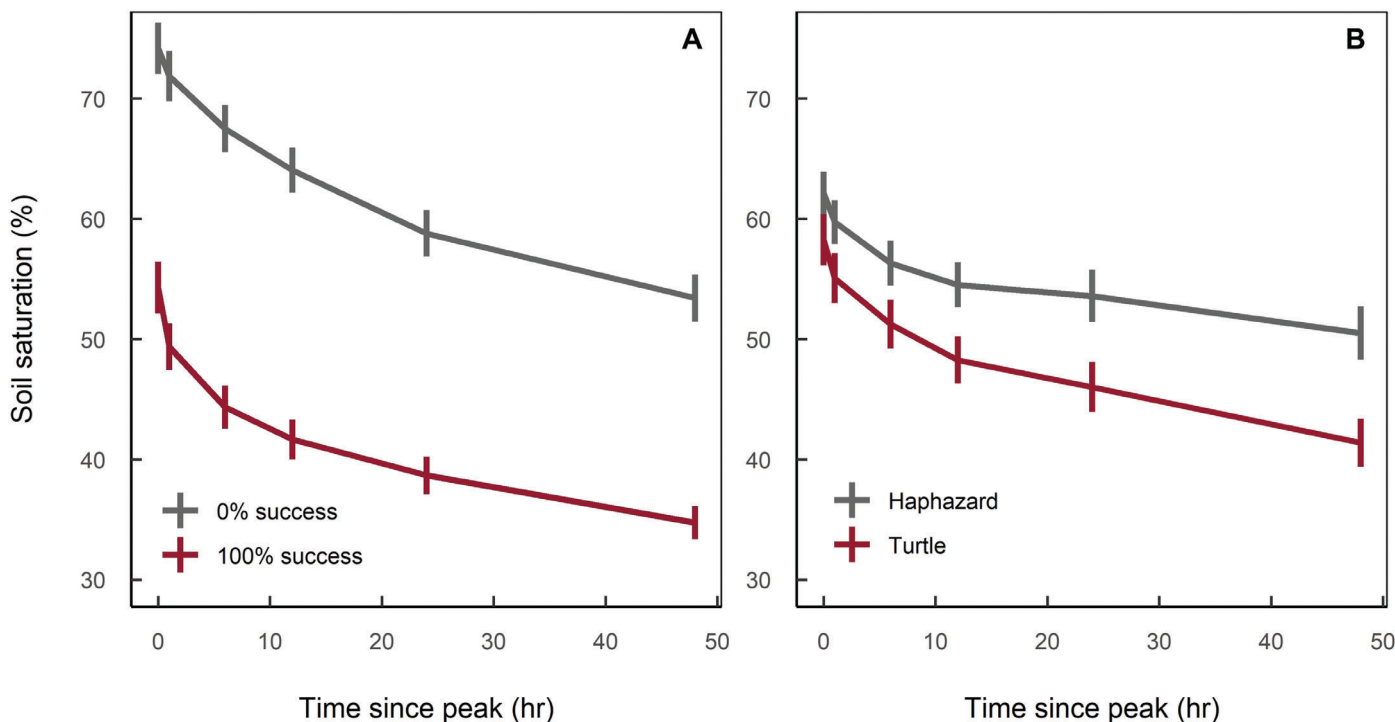


Fig. 5. Mean (\pm SE) soil saturation (%) recession curves after rainfall events for sections of the turtle nest cavities with 100% hatch success (red line, $n = 8$) and 0% hatch success (gray line, $n = 9$) during the 2018 and 2019 incubation periods (A). Mean (\pm SE) soil saturation (%) recession curves after rainfall events for turtle nests (red line, $n = 6$) and paired haphazard sites (gray line, $n = 6$) during the 2018 incubation period (B).

therefore, the bottom of the nest chambers were 7.5 to 13.5 cm below the soil surface in soil deposits that had an average depth-to-bedrock of 13.3 cm (range 7.5–22.2 cm; Table 1). Despite these relatively shallow nest requirements, only 29% ($n = 988/3,389$) of the open rock barren quadrats had soil depths ≥ 10 cm, 13% ($n = 450/3,389$) had soil depths ≥ 15 cm, and only 7% ($n = 232/3,389$) had soil depths ≥ 20 cm. Using the lowest canopy openness recorded for a turtle nest site at hatching (55%), nest-site availability was limited on the landscape where 11% ($n = 240/2,140$) of sites had a soil depth ≥ 7.5 cm. As soil depth requirements increase, nesting habitat availability decreases. The availability of nest sites with a canopy openness $\geq 55\%$ and soil depths ≥ 10 cm was

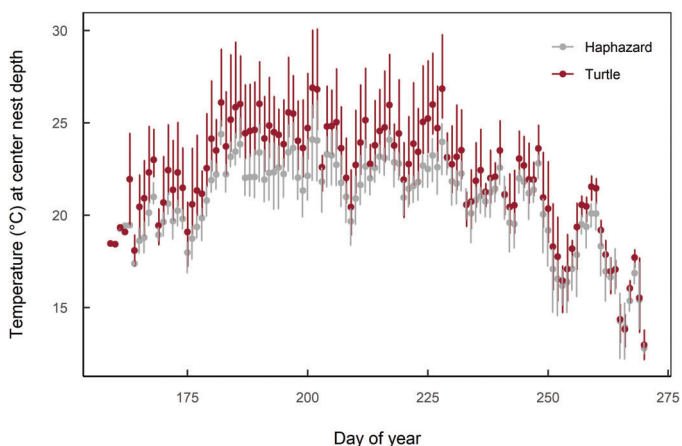


Fig. 6. Mean (\pm range) daily soil temperature ($^{\circ}\text{C}$) at the depth of the nest chamber center during the 2018 incubation season for turtle nests ($n = 6$, red) and paired haphazard sites ($n = 6$, light gray).

8% ($n = 166/2,140$) and was only 4% ($n = 78/2,140$) for soil depths ≥ 15 cm.

Soil bulk density on the landscape ranged from 119 kg m^{-3} to $1,806 \text{ kg m}^{-3}$, averaging $774 \pm 17 \text{ kg m}^{-3}$ and was lower than the soil bulk density at turtle nest sites ($1060 \pm 99 \text{ kg m}^{-3}$; Supplemental Fig. 1; see Data Accessibility). Landscape soil bulk density differed based on cover type ($X^2 = 13.1$, $P = 0.001$) and increased with depth ($R^2 = 0.15$, $F_{1,314} = 54.7$, $P < 0.0001$). Soil samples that were extracted under lichen-dominated ($754 \pm 29 \text{ kg m}^{-3}$, $n = 103$) and moss-dominated quadrats ($722 \pm 30 \text{ kg m}^{-3}$, $n = 107$) had similar bulk densities ($Z = -1.03$, $P = 0.56$) but were significantly less than the bulk density of soil in litter-dominated sites ($847 \pm 27 \text{ kg m}^{-3}$, $n = 106$; $Z = 2.61$, $P = 0.02$; $Z = -3.4$, $P = 0.002$, respectively). Organic matter content varied substantially, ranging from 2.9% to 80.4%. The average soil organic matter content was $12.1 \pm 0.5\%$, with 85% of soils having less than 20% organic matter, which was similar to the organic content at turtle nesting sites (Supplemental Fig. 1; see Data Accessibility). Lastly, the majority of the soil texture was classified as sandy loam (73%), and sandy clay loam, loamy sand, and loam were less common.

DISCUSSION

Over 25% of the 660 ha study landscape was open rock barrens providing a large availability of potential turtle nesting habitat. The remaining 75% of the landscape was dominated by forest and wetlands. Although Spotted Turtles have been found to nest on wetland hummocks, this was confirmed in southern locations (Joyal et al., 2001; Beaudry et al., 2010) where incubation temperatures are not a limiting factor (Bobyn and Brooks, 1994). In a rock barrens landscape, a natural disturbance (e.g., wildfire) that increases canopy

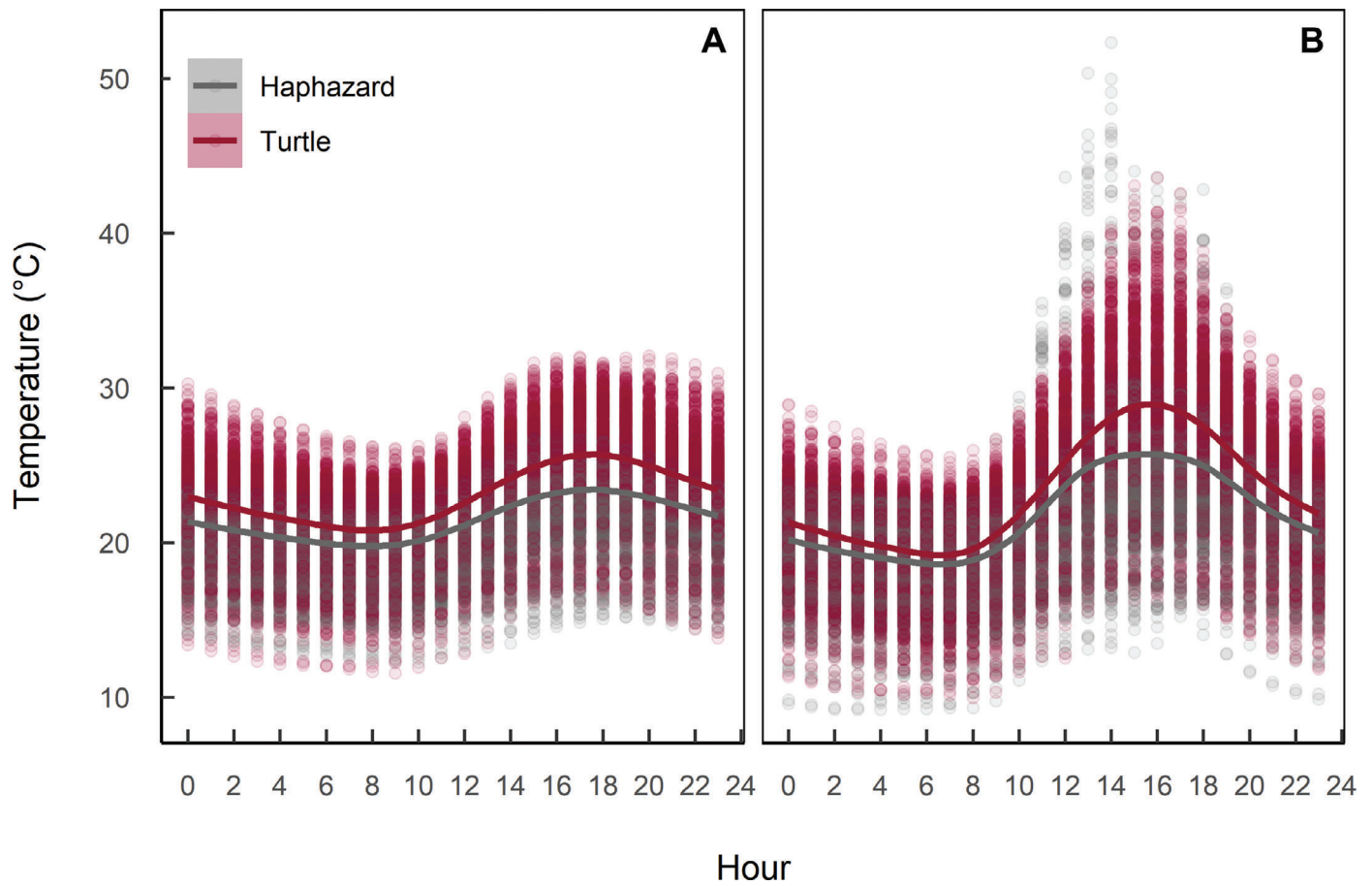


Fig. 7. Diel soil temperature (°C) pattern for turtle nests ($n = 6$, red line) and paired haphazard sites ($n = 6$, gray line) measured hourly (points) at depths equivalent to the bottom (A) and top (B) of the nest chambers during the 2018 summer incubation period.

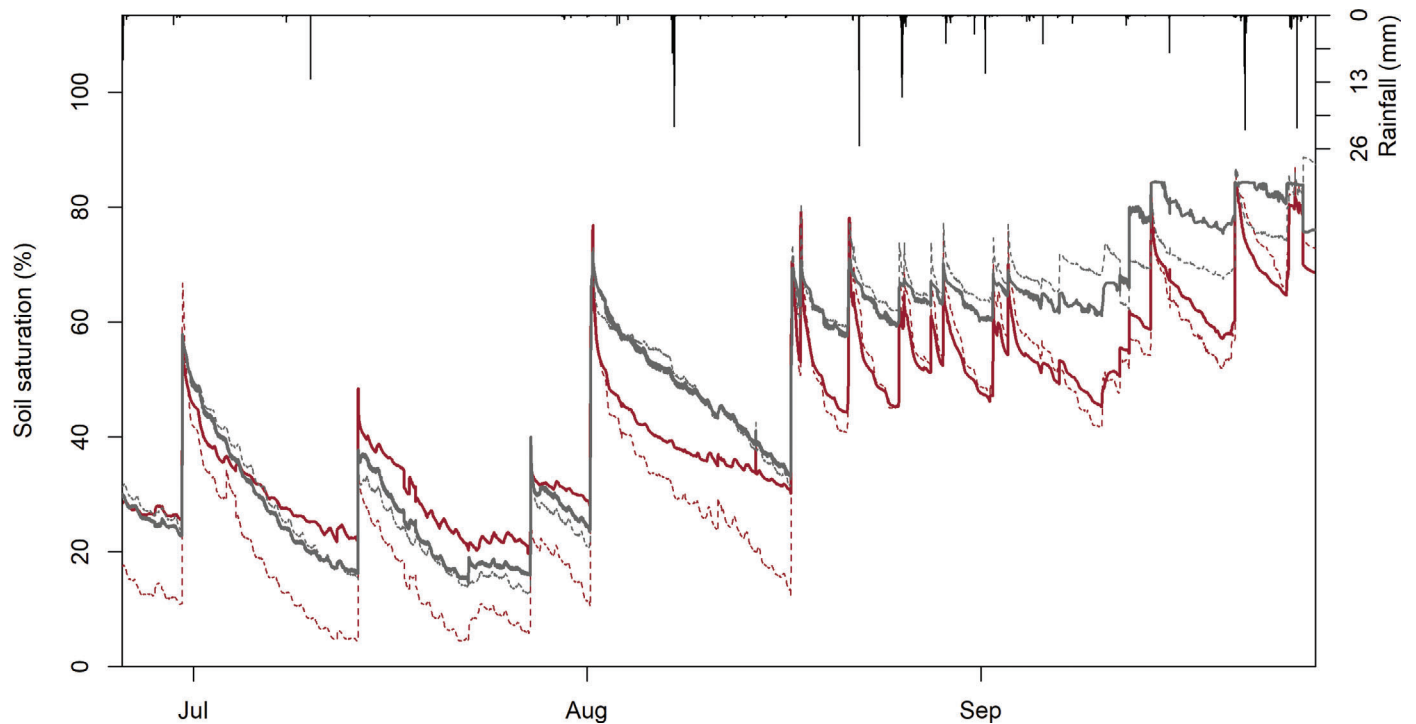


Fig. 8. Daily rainfall (mm) during the 2018 incubation period and average 15-minute soil saturation (%) at the bottom (solid line) and top (dashed line) of turtle nests (red, $n = 6$) and haphazard sites (gray, $n = 6$).

openness without impacting other nest habitat properties (e.g., volume or depth of soil, drainage rates) could create temporary nesting habitat in previously forested areas (Beaudry et al., 2009; Markle et al., 2020). However, in the Georgian Bay rock barrens, surveys have consistently shown that turtles nest in soil deposits in cracks and crevices in the bedrock and not elsewhere (Litzgus and Brooks, 1998, 2000; Markle and Chow-Fraser, 2014; this study). This is likely due to the open canopy and ability for the rock to maintain incubation temperatures, especially at northern latitudes where the active season is constrained, limiting natural nesting habitat to the open rock barrens (Bobyne and Brooks, 1994; Litzgus and Brooks, 2000; this study).

Although rock barrens were the second most dominant land cover type and primarily located within 200 m of overwintering wetlands, the availability of nesting habitat with deeper soil deposits and an open canopy was limited. Only 11% ($n=240/2,140$) of the rock barrens and <3% of the study area provided suitable nesting habitat on rocky outcrops with soil depths ≥ 7.5 cm and canopy openness $\geq 55\%$. The limited availability of deeper nesting sites is expected in a landscape characterized by shallow soils (Wester et al., 2018), but the average soil depth across the rock barrens (7.9 ± 6.9 cm) was less than the nest depths recorded for Painted Turtles ($10.1 \pm \text{SD } 1.2$ cm, Schwarzkopf and Brooks, 1987; 6–13 cm, Morjan, 2003; 8.0–10.5 cm, this study), Blanding's Turtles (12 cm, Standing et al., 1999; 10–13.5 cm, this study), and Snapping Turtles (12–18 cm, Congdon et al., 1987; 14–21.25 cm to middle of nest; Francis et al., 2019) throughout their range. For smaller-bodied species such as Spotted Turtles that can nest in shallower soils (4.5–5.9 cm, Ernst, 1970; 2–6 cm, Rasmussen and Litzgus, 2010; 7.5 cm, this study), nest-site availability was primarily limited by canopy openness. Canopy openness was slightly lower on the landscape ($47 \pm 13\%$) compared to the lowest openness recorded (55%) at a turtle nesting site in 2018 and 2019. On the other hand, for larger-bodied species such as Snapping Turtles, which require deeper soils for nesting, suitable habitat was limited to only 4% of sites that had deeper soils (≥ 15 cm soil) and an average canopy openness $\geq 55\%$.

We expected suitable nesting habitat to be limited by the availability of deeper soils but did not expect nesting habitat to also be limited by canopy openness in a rock barrens landscape. Other studies have found nest-site selection was limited by habitat openness (Litzgus and Brooks, 2000), and the requirement for little canopy and vegetation cover is well established (e.g., ECCC, 2018a, 2018b) because of its direct influence on the thermal incubation environment. Turtles in our study selected nest sites with a minimum canopy openness of 55% up to a maximum of 94%. Similar to other landscapes, canopy openness at selected sites averaged 83% for Painted Turtle nests (Hughes and Brooks, 2006), and ranged from 46–100% and 63–100% for Painted Turtle and Snapping Turtle nests, respectively (Riley et al., 2014). The rock barrens landscape is known for its open, rocky habitat (Wester et al., 2018); however, the occurrence of deeper soils in areas with open canopy appear to be limited possibly due to larger shrubs and trees occupying the deeper soils. This suggests that low severity fire that burns the canopy but doesn't result in soil loss may be an important natural process in maintaining open rock barrens and increasing nest habitat availability.

Given the limited range of soil depths on the rock barrens landscape, it is likely that turtles are constructing nests in sites where the total soil depth is shallower compared to anthropogenic nest sites or in landscapes where natural nesting habitat is beaches and open fields. In all turtle nests we monitored, eggs were close to (<10 cm) or even sitting on the bedrock. For clutches that are laid in shallower soils, temperature and moisture dynamics are more variable. In shallower nests, there is an increase in temperature and amplitude of fluctuation, creating more variable temperature conditions (Figs. 2, 7; Wilson, 1998; Booth and Astill, 2001). In turn, the impact of soil depth on temperature variation influences hatching speed, incubation length, mortality, and sex ratio (Schwarzkopf and Brooks, 1985; Ashmore and Janzen, 2003; Paitz et al., 2010; Neuwald and Valenzuela, 2011; Refsnider, 2012). Moreover, nests are vulnerable to soil desiccation due to limited water storage in shallower soils, especially if nest sites are exposed to warm and dry conditions (Moore et al., 2019).

Despite the unique challenges of nesting on a rock barrens landscape, nest success was 59% in both years and nest sites were warmer (Fig. 7) and had faster drainage rates (Fig. 5B) than haphazard sites, providing evidence of nest-site selection. Although we used predator exclusion cages, 67% of the unsuccessful eggs were moldy when the nest was excavated. This suggests that incubation conditions were too wet at these sites and further emphasizes the importance of soil drainage in this landscape. Although we only examined nest-site selection in 2018 for a limited number of nests, we found that turtle nests were consistently warmer than the paired haphazard sites despite similar canopy openness, depth to bedrock, and soil properties (Fig. 7). Selecting for warmer nest sites was found in other turtle populations (Schwarzkopf and Brooks, 1987; Hughes et al., 2009; Francis et al., 2019) which is thought to be favorable for northern populations that are thermally constrained (Bobyne and Brooks, 1994; Holman and Andrews, 1994). However, the direct contact of the shallow soil with the underlying granite is unique to a rock barrens landscape. Here, we found that turtle nests laid in crevice bedrock morphologies were up to 3°C warmer than other turtle nests (with flat and ledge morphologies) during the evening and night (Fig. 2). At a nearby site where temperature profiles are up to 15 cm deep in the bedrock, the granite temperatures are consistently warmer than air temperatures (up to 20°C warmer, Supplemental Fig. 2; see Data Accessibility). Because crevices have more soil-granite contact, heat from the bedrock prevents a drop in soil temperatures at night (Fig. 2; Clauser, 2009, 2011), and we suggest that this could be a critical process for maintaining incubation temperatures and minimizing fluctuations in natural nests laid at the northern range limit of at-risk turtles. Since crevice rock barrens sites do provide a thermally suitable incubation environment, evident by successful hatching (Table 1), they provide a benefit over thermally suitable anthropogenic sites (e.g., Francis et al., 2019) that may act as ecological traps (Mui et al., 2015; Hale and Swearer, 2016).

In addition to temperature, moisture conditions influence the success and life history traits of the embryo (Packard et al., 1987). We found that mean daily soil temperature, variance of soil saturation during incubation, and their interaction had a significant effect on hatch success. Hatch success was highly variable when the variability in soil

saturation during the incubation period was high (SD of 20% saturation). Variable hatch success is likely because high variability in soil saturation indicates that the site experiences a wide range of moisture conditions. For instance, after rainfall, a site that drains slowly prolongs the duration of wetter soils but does eventually reach drier conditions. Furthermore, periods of flooding may be prolonged in shallower nests where eggs are deposited directly on the bedrock. On the other hand, when there was low variability in soil saturation (SD of 10% saturation), mean hatch success increased with increasing mean daily temperature. Moreover, hatch success was predicted to be up to 100% when mean daily soil temperature was $>24^{\circ}\text{C}$ (Fig. 3). Low variability in soil saturation indicates that although saturation may peak after rainfall the site drains quickly, so soil saturation values are more tightly distributed around the mean. For example, where soil depth is sufficient, eggs can be positioned above the bedrock allowing water to pool below the nest cavity avoiding waterlogged soils and reducing exposure to extended periods of flooding (Ratterman and Ackerman, 1989), resulting in limited variability in soil saturation within the nest cavity itself.

The effect of soil saturation on hatch success was also supported by the continuous soil moisture data and drainage analysis which revealed that nest sections with 100% hatch success drained quicker following rainfall and maintained drier conditions by an average of $32\pm 11\%$ (SD; Fig. 4A) in the wetter season and $5\pm 4\%$ (SD; Fig. 4B) in the drier season. Similar to our results, other studies have also shown greater success in well-drained (Dowling et al., 2010) but moist soils (Packard et al., 1987; Cagle et al., 1993; Wilson, 1998). The moisture regime within a nest site is strongly dependent on the ability of the site to respond to water inputs, because turtle eggs must be incubated in moist soils without oversaturation (Packard et al., 1987; Packard, 1999; Bodensteiner et al., 2015) while also retaining enough moisture to prevent desiccation (Ratterman and Ackerman, 1989). In addition to the impact of moisture regimes on hatch success, turtles also selected nest sites that drained significantly faster than haphazard sites (Figs. 4, 5B). In particular, in August and September 2018 when rainfall events were more frequent, turtle nests remained 15–20% less saturated than paired haphazard sites.

Management implications.—The interaction between nest temperature and moisture dynamics are strongly influenced by soil properties such as texture, organic content, and bulk density and thus are important to consider when restoring or creating nesting habitat. Although sand mounds have been used in other landscapes to successfully create nesting habitat (Buhlmann and Osborn, 2011; Paterson et al., 2013; Quinn et al., 2015), they do not replicate the natural nesting habitat for turtles in rocky landscapes (Litzgus and Brooks, 1998; Beaudry et al., 2010; Markle and Chow-Fraser, 2014; Francis et al., 2019; this study). Sand mounds will also erode in a rocky landscape and could become predation hotspots (Robinson and Bider, 1988; Quinn et al., 2015) because natural nests are typically dispersed in the rock barrens (Zagorski et al., 2019; this study) compared to other landscapes (Robinson and Bider, 1988; Kell, 2018). Therefore, it is critical to inform nest habitat restoration and creation based on the properties of natural rock barrens nesting habitat. Here, we identified that natural nesting sites for the

Blanding's Turtle, Spotted Turtle, and Midland Painted Turtle included an open canopy ($70\pm 2\%$), soil depths ranging between 7.5–22 cm depending on species, soil properties (sandy loam with intermediate bulk density and soil organic matter) and site characteristics (e.g., slope, bedrock morphology, soil depth) that allowed for adequate drainage, and lichen as the dominant surface cover. We also found that crevice bedrock morphologies were able to maintain stable incubation temperatures compared to flat and ledge morphologies, avoiding drops in temperature during the evening and night, and is an important consideration for nest habitat restoration and creation.

Across our rock barrens landscape and at nest sites, sandy loam was the dominant soil texture and is generally characterized as having moderate drainage. Soil properties play an important role in a nest site's ability to respond to changes in moisture, and water exchange by the eggs is also affected by soil type (Ratterman and Ackerman, 1989; Milton et al., 1997; Mitchell and Janzen, 2019). Finer texture soils are more likely to be classified as poorly drained, whereas soils with a higher sand content (Zhao et al., 2008; Government of Canada, 2013) and lower organic matter can increase drainage (Gupta and Larson, 1979; Hudson, 1994; Minasny and McBratney, 2018). On the rock barrens landscape, sandy loam is likely favorable because soil depth is naturally limited and the ability to hold some moisture is necessary to prevent egg desiccation since water availability influences hatch success (Packard et al., 1987; Cagle et al., 1993; Wilson, 1998; this study). Furthermore, bulk density is inversely related to soil organic matter where, in sandy and sandy loam soils, a higher bulk density soil (and lower organic content) has decreased drainage (Thomasson, 1978). Soil bulk density and organic matter content were comparable between turtle and haphazard sites (Supplemental Fig. 1; see Data Accessibility), and the landscape-scale assessment revealed low organic matter content on the landscape where 85% of sites had less than 20% organic matter, particularly in depths suitable for turtle nest sites. Overall, soil texture, organic content, and bulk density used by nesting turtles is not limited and suggests that a sandy loam with intermediate bulk density ($1,000\text{ kg m}^{-3}$) and soil organic matter (10–15%) would be best for restored or constructed sites on this landscape.

We found evidence that nesting habitat was limited by canopy openness on the rock barrens. The natural fire regime for this landscape is considered to be low intensity (Van Sleetwen, 2006) and is an important natural process for maintaining open rock barrens (Asselin et al., 2006). However, the frequency and severity of fires are predicted to increase with climate change (Flannigan et al., 2009), and severe fires resulting in soil loss and erosion compromise nesting availability and suitability (Markle et al., 2020). Techniques such as removing dead trees, clearing understory vegetation, and hand thinning the overstory have been used in other landscapes dominated by Jack Pine (*Pinus banksiana*) to reduce fuel load as a strategy to manage fire severity (Schroeder, 2010). Thinning also results in increasing canopy openness, which could be investigated as a technique for increasing nesting habitat availability. The integration of Indigenous ecological knowledge on the use of fire to manage landscapes is critical. Cultural burning provides important management strategies that manage understory vegetation through controlled fires (Crafts, 2020), and because high frequency, low severity fires are believed to be

critical to sustaining unforested rock barrens (Asselin et al., 2006), it also likely played a vital role maintaining open rock barrens and availability of natural turtle nesting habitat.

The loss and degradation of nesting habitat is of conservation concern for the survival and recovery of at-risk turtle species (e.g., ECCC, 2018a, 2018b). In a relatively undistributed rock barrens landscape, we found that nesting habitat was naturally limited. Therefore, impacts to the landscape such as anthropogenic alterations (Kolbe and Janzen, 2002; Thompson et al., 2017; Piczak and Chow-Fraser, 2019), climate change (Refsnider et al., 2013; Butler, 2019; Valenzuela et al., 2019), and severe wildfire (Markle et al., 2020) that alter the amount or function of natural nesting habitat could negatively affect sensitive turtle populations. Our study reveals that the shallow rock barrens nesting habitat has unique soil temperature and moisture dynamics that are tightly coupled with soil properties and bedrock morphology to provide successful incubation conditions. The increased development pressures in the eastern Georgian Bay region and expansion of a highway that intersects species-at-risk habitat can further impact limited nesting habitat (Ontario Ministry of Natural Resources and Forestry, 2016; Rogers, 2016). Therefore, we recommend that key management strategies should include stronger protection of critical rock barrens nesting habitat and development of landscape-appropriate strategies for restoration and creation of nesting habitat.

DATA ACCESSIBILITY

Supplemental material is available at <https://www.ichthyologyandherpetology.org/h2020125>. Unless an alternative copyright or statement noting that a figure is reprinted from a previous source is noted in a figure caption, the published images and illustrations in this article are licensed by the American Society of Ichthyologists and Herpetologists for use if the use includes a citation to the original source (American Society of Ichthyologists and Herpetologists, the DOI of the *Ichthyology & Herpetology* article, and any individual image credits listed in the figure caption) in accordance with the Creative Commons Attribution CC BY License.

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