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Effects of temperature heterogeneity on freshwater turtle habitat selection at their northern range limit

are naturally available.

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Keywords: Animal behaviour Ectotherm Thermal biology Spatial scale Thermoregulation	Environmental temperature is a crucial resource for ectotherms, affecting their physiology, behaviour and fitness. To maintain body temperatures within a suitable performance range, ectotherms select thermally-favourable locations, but this selection may be challenging in environments with high spatio-temporal hetero-geneity. We assessed thermal habitat selection in two freshwater turtles (<i>Emydoidea blandingii; Chrysemys picta</i>) within a thermally heterogeneous environment at two spatial scales (selection of home ranges within the landscape, selection of locations within home ranges) and across seasons, by comparing temperatures at turtle locations vs. those available in the environment. Turtles selected warmer locations compared to those available in aquatic and terrestrial habitats only within home ranges, but did not show any temperature preferences when selecting home ranges at the larger scale. Turtles selected locations that were less thermally-variable than their surroundings, both at the home range scale and within home ranges. Thermal habitat selection was strongest during colder and more thermally-variable pre-nesting season compared to later periods. Despite differences in thermal mass between species, both species responded similarly to temperature variation. We conclude that freshwater turtles at their ortherm range margin select suitable microclimates within the suite of conditions that

1. Introduction

For many ectotherms, ambient temperature can be considered as an environmental resource by influencing body temperature, which translates to changes in physiology and behaviour that ultimately shape survival, reproduction, and, thus, fitness (Huey and Stevenson 1979; Huey 1991). To maintain body temperatures within a suitable range that maximizes physiological performance, ectotherms behaviourally thermoregulate by adjusting their body position, timing of activity, and selection of thermally-suitable locations (Christian and Tracy 1981; Stevenson 1985; Parlin et al., 2017). Thermoregulation is thus a major driver of habitat selection in ectotherms, and ambient temperature is often more important in determining ectotherm habitat selection than other resources such as food abundance and quality (Classen et al., 2015; Halliday and Blouin-Demers 2016). Maintaining favourable body temperature is particularly important but may be challenging, especially in regions with climatic extremes such as near species' distribution margins (e.g. Blouin-Demers and Weatherhead, 2001a; Picard et al., 2011) and in areas with high heterogeneity in ambient temperature owing to variation in habitat or sun exposure (e.g. Pincebourde and Suppo 2016; Sears et al., 2016; Scheffers et al., 2017).

Most landscapes are thermally heterogeneous and ectotherms can adjust their behaviour to exploit environmental disparity and avoid less favourable temperature (Huey 1991; Sears et al., 2011; Carroll et al., 2016). In fact, in a heterogeneous landscape, absolute and relative temperature may be equally important in influencing behaviour and physiological performance (Sears and Angilletta 2015). While the link between habitat selection and thermoregulation has been demonstrated in a variety of ectotherms (e.g. Harvey and Weatherhead 2010; Chukwuka et al., 2021), it is less clear how environments with especially high spatial and temporal heterogeneity in ambient temperature can shape ectotherm behaviour.

Environmental heterogeneity and animal sensitivity to spatial variation in ambient temperature are often a matter of scale (e.g. Robson and Blouin-Demers 2021; Verzuh et al., 2023). At which scale habitat selection occurs is related to the biology or physical traits of the species, for example, smaller animals often perceive their surroundings at finer spatial scales (Mech and Zollner 2002; Thornton and Fletcher 2014).

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Received 17 July 2023; Received in revised form 6 October 2023; Accepted 7 October 2023 Available online 21 October 2023 0306-4565/© 2023 Elsevier Ltd. All rights reserved. While there is some evidence that ectotherms select macrohabitats at larger spatial scales such as the home range scale (Edge et al., 2010; Robson and Blouin-Demers 2021), environmental temperature may be more important in determining behaviour at a finer scale. Therefore, responses to temperature heterogeneity within the home range seem plausible (Hughes 2016). Hence, to ensure biologically-relevant interpretation of behavioural observations, habitat selection should be considered across multiple spatial scales (Compton et al., 2002; Markle and Chow-Fraser 2014).

Such scale-sensitive perceptions of the environment may be influenced by body size, but this feature can also influence thermal inertia and the time required for body and ambient temperature to equilibrate: larger species or individuals require more time to heat up or cool down with changes in ambient temperature (Turner and Tracy 1985; Knigge et al., 2017). The relationship between body size and temperature balance can depend on the level of heterogeneity in the environment, through habitat-specific differences in heat transfer and capacity. Environments composed of both aquatic and terrestrial habitats are especially variable in their thermal properties, because water is more efficient in terms of heat transfer and retention than air (Turner 1987). This means that body size and thermal variation are likely to work in tandem to shape ectotherm habitat selection. Further, habitat selection may vary through time due to seasonal differences in mean temperature and varying biological needs of animals (e.g. Arnall et al., 2019; Richter et al., 2020; Hyder et al., 2021). For example, in temperate environments animals may be more sensitive to thermal heterogeneity in spring, when mean ambient temperature is relatively low, compared to other times of the year (Angilletta 2009; Stellatelli et al., 2018). In spring, ectotherms may also be especially sensitive to thermal variation in the environment after their emergence from hibernation, which could prompt basking or other behavioural adjustments to raise their temperature and metabolic rate (e.g. Akins et al., 2014; Erdélyi et al., 2019). These spatial and temporal dynamics remain largely untested, however, especially for species occupying both aquatic and terrestrial habitats.

We assessed patterns of temperature-based (or thermal) site selection in two freshwater turtles (Blanding's turtles: Emydoidea blandingii; painted turtles: Chrysemys picta), in a temperate region of southern Canada. Both species are near their northern range limit in this region, and near the northern range limit of reptiles generally, and are thus good candidates for evaluating our hypothesis that ectotherms respond to environments exhibiting large spatial and temporal variation in temperature. We hypothesized that thermal conditions in our study area dictate how turtles use the landscape, and expected that thermal site selection depends on the spatial scale of analysis and season. Specifically, we predicted that turtles should select locations that are (1) warmer, and (2) less variable in temperature, compared to the surrounding environment. Furthermore, because of their relatively small size and restricted movements, we expected that turtles should exhibit thermal site selection at (3) a relatively fine spatial scale (i.e., locations within home ranges and within habitats, rather than across the landscape). Further, turtle selection for thermal sites should be (4) strongest during pre-nesting season, when mean ambient temperature is lower and animals are more sensitive to thermal heterogeneity. Finally, because both species differ to varying degrees in several traits, particularly body size (Bury and Germano 2003; Ernst and Lovich 2009), we expected that (5) species would differ in thermal habitat selection, with smaller painted turtles having lower thermal inertia resulting in stronger preference for warmer and less-variable thermal habitats compared to larger Blanding's turtles.

2. Methods

2.1. Study species and site

We studied Blanding's and painted turtles in the South March Highlands Conservation Forest in Ottawa, Ontario, Canada (45°20' N,

75°56' W) during April–September 2019–2020. Both species inhabit wetlands and are syntopic in our study area, with painted turtles being more generalist in habitat use compared to Blanding's turtles (Standing et al., 1999; Ernst and Lovich 2009). In general, adult Blanding's turtles are 10-80% larger and 160-420% heavier than painted turtles (Congdon and Loben Sels 1991; Rowe et al., 2003). Both species use aquatic and terrestrial habitats to varying degrees, with the former being used primarily for foraging and basking and the latter serving mainly for inter-wetland travel or searching for nesting or overwintering sites (Bowne et al., 2006; Hartwig and Kiviat 2007). Temperatures at our study location are generally colder than in more temperate parts of the species' range, which could constrain physiological performance (Huey and Slatkin 1976; Addo-Bediako et al., 2002). Consequently, turtles in our area have a short active period (April to October) during which they must acquire sufficient energy and thermal resources for digestion, growth, and reproductive activities (Congdon 1989; Huey 1991). The active season for turtles in our study region can be divided into distinct periods including pre-nesting (April-May) and nesting (June-July), when turtles are more active and bask often (Krawchuk and Brooks 1998; Edwards and Blouin-Demers 2007), and post-nesting (July-October), when animals gradually prepare for hibernation by reducing feeding and activity (Rasmussen and Litzgus 2010; Christensen 2013).

Our study area (~1000 ha) is composed of five main habitats: deciduous and mixed forest (~51%), open field (~25%), marsh (~11%), swamp (\sim 10%), and open water (\sim 3%) (see Supplementary Fig. 1). We captured Blanding's and painted turtles using baited hoop-nets or by hand, weighed turtles and measured their carapace lengths, and fitted each of them with a combined GPS/temperature/water sensor data logger (model AxyTrek, Technosmart, Rome, Italy) and a VHF transmitter (model SI-2T, RI-2B, Holohil, Carp, Canada) bolted to the left and right carapace margins, respectively. Combined, both units comprised <10% of turtle body mass in air. Data loggers recorded water conductivity and temperature at a frequency of 1 Hz (temperature logger accuracy \pm 0.1 °C, Technosmart). GPS transmitters recorded locations every hour, but because animals spent considerable time underwater and GPS data could not be collected when devices were submerged, the realised fix rate averaged across the entire study was 12.3% (12601 total fixes). We tested locational accuracy of GPS transmitters (n = 3) by leaving them stationary in the field for six days and found a 17.4 m accuracy and no habitat-based detection or precision bias. After transmitter attachment, turtles were released at their capture sites and recaptured at the end of the field season to retrieve data loggers. All animals were handled in accordance with guidelines from the Canadian Council on Animal Care (CCAC) (2005) and procedures were approved by the Trent University Animal Care Committee (Protocol No. 24729) and by the Ontario Ministry of Natural Resources and Forestry (OMNRF, Permit No. KV-C-002-14).

2.2. Available and selected environmental temperatures

We collected environmental temperatures in opportunisticallyselected locations in forest (n = 3-8), open field (n = 2-4), marsh (n = 5–8), swamp (n = 4–6), and open water (n = 4–6) using iButton temperature loggers (Maxim model DS1921G-F5, accuracy \pm 0.5 °C, Dallas Semiconductor, Sunnyvale, CA). Temperature loggers were placed in waterproof clear tubing or plastic bags, and were tied to branches or rocks. Most loggers were placed >200 m from each other to reduce autocorrelation (A. Auge, unpubl.), although some locations received multiple loggers (i.e., water surface and ~ 1 m under water). Loggers recorded temperature hourly and were moved weekly several meters within the same site and habitat type to obtain a representative sample. Our preliminary analysis of logger data revealed low spatial autocorrelation in ambient temperature and lower within-habitat than between-habitat temperature variation (A. Auge, unpubl.), reflecting that habitat types had distinct temperature profiles that were captured by our iButton deployment.

We calculated habitat-specific mean daily temperatures by averaging temperature recorded for each day and within each habitat. We tested if mean daily temperatures within each habitat predict temperatures in specific locations within the same habitat type, using linear regression. For this, we randomly divided the dataset into a training data subset (70%) of temperature data, from which we calculated mean daily habitat-specific temperature, and a test data subset (30%) with daily temperatures from individual locations (see Liu and Cocea, 2017). We found strong positive correlation between daily mean habitat temperature calculated from the training and test datasets (forest: $R^2 = 0.94$; field: $R^2 = 0.94$; marsh: $R^2 = 0.72$; swamp: $R^2 = 0.89$; open water: $R^2 =$ 0.89). Differences between recorded mean habitat temperatures were generally consistent through both years of study, except for fields, where undersampling in 2019 led to unreliable estimates (A. Auge, unpubl.). Accordingly, we adjusted estimates for fields by calculating their relative temperature in 2020 compared to forest habitat. We considered both quadratic ($R^2 = 0.83$; AICc = 17679) and linear ($R^2 = 0.81$, AICc = 18048) models when fitting field vs. forest temperatures, and note that the difference between Akaike Information Criterion (AIC) values $(\Delta AIC = 369)$ is large despite relatively small differences in R², which is not uncommon given AIC calculation and interpretation (see Burnham and Anderson, 2002). Accordingly, we chose the more parsimonious model (quadratic) based on AIC. Further, we considered the quadratic relationship between forest and field temperature as being most biologically plausible because at warmer ambient temperatures open field habitat should warm up faster than forest. Thus, we corrected 2019 field temperatures with the following equation:

$T_{field} = 0.0217 T_{forest}^2 + 0.7273 T_{forest} - 0.0045$

Using ArcGIS Pro 2.4.0 (Esri Inc., Redlands, CA, USA, 2019), we developed thermal habitat maps of the study area using existing habitat shapefiles (City of Ottawa, Scholars GeoPortal), satellite images, and ground-truthing. We calculated mean daily environmental temperature available to turtles depending on the scale of analysis: 1) by averaging habitat temperatures within the entire study area (when analysing thermal selection of home ranges), 2) and within a radius of 75 m surrounding daily centroid turtle locations ("home ranges") determined from GPS telemetry (when analysing thermal selection of locations within home ranges). A radius of 75 m represents 10% of the mean home range of both species (~18 ha) in our study populations, and was the smallest relevant spatial scale corresponding to the temporal scale of one day (mean daily linear movement distance = $68.4 \pm (SD) 39.2 \text{ m}$) that included enough habitat types to estimate meaningful temperature means and variation. Within the same areas (study area, home range), we calculated available thermal variability as the coefficient of variation (C.V.) of hourly temperatures of all habitats during a day.

We validated the assumption that temperatures recorded by shellmounted dataloggers were representative of environmental temperatures experienced by turtles (as opposed to measuring operative environmental temperatures; see also Vickers and Schwarzkopf 2016; Parlin et al., 2017) by assessing temperature correspondence between AxyTrek units mounted on a turtle model (Blanding's turtle carapace attached to a water-filled container) and iButton dataloggers. The model was moved between a variety of sunny and shaded locations within habitats in the study area and showed that both temperature loggers responded similarly to temperature changes in the environment (average difference between readings: 0.32 °C \pm 0.40 °C; n = 506) and had comparable heat-up and cool-down patterns across the range of temperatures and habitat types.

To compare selected vs. available absolute temperatures or temperature variability within and across home ranges, we first averaged recorded 1 Hz AxyTrek temperatures over each hour per individual. Note that AxyTrek temperature data could span any habitat used by the animal during the 1-h period, and all recorded data within one day were included in the analysis. We then calculated daily temperature means and C.V. as a measure of thermal variability, both in AxyTrek (selected) and iButton (available) temperatures, for each turtle. Selected aquatic vs. terrestrial habitat was determined using a water sensor threshold of 500 V (aquatic, sensor in water: <500 V; terrestrial, sensor out of water: <500 V), determined by separate trials with transmitters in $(234 \pm 5.4 \text{ V} (n = 13.7 \text{ million}))$ and out $(979.9 \pm 13.5 \text{ V} (n = 13.2 \text{ million}))$ of water (Auge et al., 2022). We note that when the sensor was out of water, turtles were mostly motionless on land $(91.5 \pm 5.4\%)$ of the time), and near ponds (Auge et al., 2022), suggesting most of the time spent out of water was spent basking.

2.3. Data analyses

We assessed selection of the thermal environment at two spatial scales: 1) thermal home range selection (temperatures of selected home ranges vs. available temperatures within the study area), and 2) temperature selection within home range. At the latter spatial scale, we assessed a) selection of thermal locations across habitats (aquatic and terrestrial) vs. available temperatures within the home range, and b) selection of thermal locations in and out of water vs. available temperatures in aquatic and terrestrial habitats within the home range. respectively. We used linear mixed effect models and compared selected mean temperature or temperature variability to those available at each spatial scale. For these analyses, daily mean temperature or daily temperature C.V. was the response variable, and location (selected vs. available), species, and season were fixed effects. We ran models both with a 3-way interaction (location x species x season) and with two 2way interactions (location x species, location x season), and selected the top model using AIC. Each mixed effect model included turtle ID and location (selected vs. available) as random intercept and slope, and turtle ID and season as random intercept and slope, assuming random variation in temperature selection between individuals (Zuur et al., 2009). Mixed effect models were analysed using the R package lme4 (Bates et al., 2015). Marginal and conditional R² values were computed using the R package piecewiseSEM (Lefcheck, 2016). We identified discrete seasons as pre-nesting (April 28-May 31), nesting (June 1-July 21), and post-nesting (July 22-August 23) based on our field observations of both species. We note that in this case linear mixed effect models are superior to other habitat analysis methods (e.g., resource selection functions, step selection functions), because of the low spatial resolution of our environmental temperature data (Hebblewhite and Haydon 2010; Street et al., 2021), and because our analysis considered time-varying temperature profiles (i.e., adjusted daily) that were difficult to model using conventional approaches (Lortie et al., 2020; Northrup et al., 2022). All data were analysed using R version 4.0.2 (R Development Core Team, Vienna, Austria, 2020).

3. Results

In 2019 and 2020, we captured 23 Blanding's and 25 painted turtles. We obtained temperature data from 17 Blanding's and 24 painted turtles, and each species was monitored on average 61.7 days (range: 8–121 days) and 74.6 days (range: 20–117 days), respectively. Our incomplete GPS fix dataset meant that we considered a restricted sample of days with corresponding environmental temperature (Blanding's, mean days per individual: 32.6 days (range: 3–81); painted, mean days per individual: 45.9 days (range: 6–97 days)). On average, monitored Blanding's turtles' body mass was 1627 ± 250 g (n = 17) compared to 457 ± 118 g (n = 24) for painted turtles. Thus, on average, painted turtles in our sample had 28% of the body mass of Blanding's turtles.

3.1. Selection of thermal home ranges

There was no evidence that animals selected home ranges with mean temperatures that differed from the available environment in the study area, with the exception of post-nesting season when turtles selected home ranges that were a negligible 0.4 °C warmer (95% CI: 0.1–0.7) (Fig. 1, Table 1, Supplementary Table 1). Despite this, on average, temperature variation in turtle home ranges was 4.4% (2.6–6.2) less than in the environment (Fig. 1, Table 1). Furthermore, at the scale of the home range, variation in temperature between selected and available locations varied seasonally and was strongest during pre-nesting, when animals selected home ranges that were 7.1% (4.8–9.4) less variable than available. In contrast, later in the year home ranges were \leq 3.5% less variable than the environment (Fig. 1; Supplementary Table 1). Contrary to prediction, both species occupied home ranges with apparently similar thermal profiles, in terms of both the mean and the variability in temperature (Table 1).

3.2. Selection of thermal locations within home ranges

At the scale of location within the home range, turtles selected locations that were 4.0 °C (3.7–4.3) warmer overall, compared to the surrounding environment within their home range, across all habitat types (Fig. 2, Table 2). Strength of temperature selection varied seasonally and was greatest during pre-nesting, when selected locations averaged 4.4 °C (4.0–4.8) warmer than overall for the home range, and this disparity declined to \leq 3.9 °C through the nesting and post-nesting seasons (Fig. 2, Table 2, Supplementary Table 1).

On average, turtles selected thermal locations that were 5.3% (2.0–8.7) less variable during the day than their home range, but selection strength depended on season (Table 2, Fig. 2). Turtles buffered temperature variation in the environment most strongly during prenesting, when selected locations were 8.1% (4.5–11.8) less variable in temperature, followed by nesting and post-nesting seasons (\leq 3.6% less variable; Fig. 2, Supplementary Table 1). Thermal habitat patch selection patterns did not appear to differ between species (Table 2).

3.3. Selection of thermal locations in and out of water

Overall, within habitats, turtles selected areas that were warmer than available, but this selection was less pronounced when they were in water (Fig. 3, Table 3). Turtles that were in water selected environments that were 3.1 °C (2.8–3.4) warmer than the surrounding aquatic habitat, whereas when on land selected locations were 8.2 °C (7.6–8.8) warmer compared to surrounding terrestrial habitat (Fig. 3). Again, the magnitude of temperature selection both in and out of water differed by season, but not by species (Table 3). In water, the difference between selected and available temperature was greatest during pre-nesting and nesting season (\geq 3.2 °C) compared to post-nesting season, when selected locations were 2.6 °C (2.2–3.1) warmer than available water

temperatures (Fig. 3, Supplementary Table 1). Out of water, selection for warmer locations was strongest during the pre-nesting season (8.9 °C warmer, 8.1–9.7) compared to nesting and post-nesting season (\leq 8.1 °C, Supplementary Table 1).

When turtles were under water, there was no evidence that they experienced temperature variability that differed from available aquatic habitat (Fig. 3, Table 3), except during post-nesting when they selected locations that were 1.7% (0.2–3.2) less variable (Fig. 3, Supplementary Table 1). On land, temperature was generally more variable through the day, and turtles appeared to buffer this temperature variation by selecting locations that were overall 21.2% (17.0–25.4) less variable compared to their surroundings (Fig. 3, Supplementary Table 1). Turtles demonstrated seasonal variation in their buffering temperature on land, with the greatest variation occurring during pre-nesting (26.3% (21.7–31.0)) compared to nesting and post-nesting season (\leq 17.7% less variable; Fig. 3, Supplementary Table 1).

4. Discussion

Our study revealed that, near the northern range limit for Blanding's and painted turtles, thermal landscapes can influence patterns of turtle habitat selection. Turtles of both species were consistently located in areas that were warmer than average when compared to sites within their home ranges, but this pattern was not detected when compared to sites outside their home range. Further, turtles selected areas that experienced less temperature variability than the surrounding environment at all spatial scales except within aquatic habitat. As predicted, temperature selection was stronger during the pre-nesting season compared to nesting and post-nesting seasons, but these patterns were surprisingly consistent between species. Our study illustrates microhabitat selection for ectotherms that is contingent on spatial scale and season. Therefore, this study highlights how ectotherms navigate the thermal landscape by being sensitive to small-scale differences in both mean temperature and temperature variation.

Our finding that turtles did not select home ranges according to mean environmental temperature likely reflects that at the home range scale, the spatial extent was too large for animals to perceive and respond rapidly to variation in ambient temperature (see also Hughes 2016). This low sensitivity probably relates to relatively low mobility of both turtle species, and their inability to respond to large scale temperature variation at the relatively short temporal scale at which this behaviour was assessed (Mayor et al., 2009; Miguet et al., 2016). However, there is evidence that animals can use a variety of spatial scales when responding to environmental heterogeneity, depending on their resource requirements. For example, while ectotherms may traverse



Fig. 1. Thermal home range selection for Blanding's and painted turtles in eastern Ontario, Canada: a) Mean temperatures and b) temperature variability (C.V.) in home ranges selected by turtles compared to the available environment in the study area during each season. Displayed are marginal means as predicted by mixed effect models and 95% confidence intervals (95% CI). Species did not differ in their patterns of thermal selection and therefore are pooled for display.

Table 1

Thermal home range selection for Blanding's and painted turtles in eastern Ontario, Canada. ANOVA results and R² values from mixed effect model comparing mean environmental temperature and mean temperature coefficient of variation (C.V.) within turtle home ranges vs. available environment in the study area ('location').

Response variable	Fixed effect	Num. DF	Den. DF	F-value	p-value	Marginal R ²	Conditional \mathbb{R}^2
Mean temperature	Location	1	39.002	1.021	0.318	0.645	0.983
	Species	1	30.643	0.813	0.374		
	Season	2	28.962	182.069	< 0.001		
	Location x species	1	38.386	1.657	0.206		
	Location x season	2	57.004	8.790	< 0.001		
Mean temperature C.V.	Location	1	29.215	24.544	< 0.001	0.402	0.911
	Species	1	26.319	0.018	0.895		
	Season	2	42.298	39.521	< 0.001		
	Location x species	1	28.634	1.129	0.297		
	Location x season	2	76.412	6.941	0.002		



- Available - Selected

Fig. 2. Temperature selection within home ranges for Blanding's and painted turtles in eastern Ontario, Canada: a) Mean temperatures and b) temperature variability (C.V.) selected by turtles compared to those available in their home ranges during each season. Displayed are marginal means as predicted by mixed effect models and 95% confidence intervals (95% CI). Species did not differ in their patterns of thermal selection and therefore are pooled for display.

Table 2

Temperature selection within home ranges for Blanding's and painted turtles in eastern Ontario, Canada. ANOVA results and R² values from mixed effect model comparing mean environmental temperature and mean temperature coefficient of variation (C.V.) selected by turtles vs. available within home ranges ('location').

Response variable	Fixed effect	Num. DF	Den. DF	F-value	p-value	Marginal R ²	Conditional R ²
Mean temperature	Location	1	34.483	741.699	< 0.001	0.734	0.967
	Species	1	27.621	1.645	0.210		
	Season	2	27.265	141.486	< 0.001		
	Location x species	1	33.752	0.002	0.961		
	Location x season	2	55.426	4.416	0.017		
Mean temperature C.V.	Location	1	36.261	10.431	0.003	0.368	0.877
	Species	1	15.365	0.318	0.581		
	Season	2	30.209	42.242	< 0.001		
	Location x species	1	35.953	1.639	0.209		
	Location x season	2	72.374	5.939	0.004		

larger spatial scales in search of food, ambient temperature is usually perceived at a finer spatial scale (e.g. Compton et al., 2002). Indeed, microhabitats can be important thermal refugia, effectively buffering animals from temperature extremes and sometimes reducing temperature-related mortality (Scheffers et al., 2014). Despite acknowledging the importance of analysing ecological and behavioural data at multiple scales, in reality many studies still fail to do so (McGarigal et al., 2016), and our results demonstrate that without a multi-scale approach that is relevant to the target species, temperature-based habitat selection processes may be overlooked (see also Mayor et al., 2009).

The observation that turtles experienced markedly warmer and less variable temperatures relative to the environment when they were out of water is most likely related to the high temperatures that they experience when basking (e.g. Millar et al., 2012). Indeed, many ectotherms

bask on sun-exposed sites with little to no shade (e.g. Vicenzi et al., 2019). These sites experience high temperature with limited thermal variation throughout the day, while most other terrestrial habitats, including forests, experience considerable daily temperature variation. Open and sun-exposed environments can provide high thermal quality for a variety of ectotherms (e.g. Row and Blouin-Demers 2006; Elzer et al., 2013), and can improve thermoregulatory effectiveness and maximise net energy gain (e.g. Stellatelli et al., 2013; Valenzuela-Ce-ballos et al., 2015). We interpret the observed weaker thermal site selection under water as a reflection of higher heat retention and efficient temperature transfer properties in water (Turner 1987). Thus, we surmise that the more thermally homogeneous aquatic habitat provided turtles with fewer opportunities (or necessity) to seek warmer and less thermally variable sites (Sears et al., 2016). Generally, our results are consistent with the notion that temperature is an important driver of



Fig. 3. Temperature selection within habitats for Blanding's and painted turtles in eastern Ontario, Canada: Mean temperatures selected by turtles when a) in and c) out of water and temperature variability (C.V.) selected by turtles when b) in and d) out of water compared to those available in aquatic and terrestrial habitat, respectively, during each season. Displayed are marginal means as predicted by mixed effect models and 95% confidence intervals (95% CI). Species did not differ in their patterns of thermal selection and therefore are pooled for display.

Table 3

Temperature selection in and out of water for Blanding's and painted turtles in eastern Ontario, Canada. ANOVA results and R^2 values from mixed effect models comparing mean environmental temperature and mean temperature coefficient of variation (C.V.) selected by turtles vs. available within aquatic and terrestrial habitat types ('location').

Habitat	Response variable	Fixed effect	Num. DF	Den. DF	F-value	p-value	Marg. R ²	Cond. R ²
In water	Mean temperature	Location	1	40.970	390.866	< 0.001	0.717	0.963
		Species	1	32.092	2.185	0.148		
		Season	2	27.292	135.248	< 0.001		
		Location x species	1	40.268	0.343	0.561		
		Location x season	2	65.847	5.246	0.008		
	Temperature C.V.	Location	1	35.582	0.056	0.814	0.193	0.821
		Species	1	32.594	0.312	0.580		
		Season	2	33.846	16.336	< 0.001		
		Location x species	1	35.209	1.210	0.279		
		Location x season	2	85.655	7.117	0.001		
Out of water	Mean temperature	Location	1	36.496	780.390	< 0.001	0.821	0.931
		Species	1	29.495	0.469	0.499		
		Season	2	26.501	56.574	< 0.001		
		Location x species	1	35.786	0.113	0.739		
		Location x season	2	59.586	4.704	0.013		
	Temperature C.V.	Location	1	36.439	104.198	< 0.001	0.612	0.900
		Species	1	27.387	0.0001	0.991		
		Season	2	41.428	37.080	< 0.001		
		Location x species	1	35.899	0.030	0.865		
		Location x season	2	75.317	10.892	< 0.001		

habitat selection in ectotherms at their northern range limit, which ultimately should maximise their physiological performance and fitness under extreme conditions (Huey 1982, 1991).

Our results suggest that, despite their body mass differences, thermal site selection was consistent across the two species. In theory, the >3-fold mass advantage of Blanding's turtles would conceivably lead to lower thermal sensitivity due to their larger body size being able to retain heat longer (e.g. Fitzgerald and Nelson 2011; Blake et al., 2021). Given that the 2 species were entirely syntopic in our study area (A. Auge, pers. obs.) and therefore exposed to the same thermal landscape, their comparable thermal responses could indicate that this resource was not sufficiently limiting during our study to elicit mass-related differences in response. Further, we acknowledge that other differential traits may contribute to temperature selection behaviour in the two species (e.g., similarities in feeding or basking sites), and could have compensated for any body-size-related behavioural differences.

The observed difference in turtle responses to the thermal environment across seasons is a phenomenon reported in other ectotherms (e.g. Bouazza et al., 2016; Cote et al., 2019; Rowe et al., 2020, 2022), and is likely related to variation in ambient temperature depending on time of year. Reptiles generally may be more sensitive to variation in temperature early in the year, when average temperatures are usually coldest, because they require relatively high body temperature to accelerate metabolic activity to support growth and reproduction (Kingsolver et al., 2015; Bouazza et al., 2016). For example, turtles use up to \sim 50% of their total yearly energy to engage in reproductive activities (Congdon and Tinkle 1982; Krawchuk and Brooks 1998), and species in temperate environments need to keep their body temperature between 24 and 28 °C to assimilate this energy (Picard 2008). Further, higher spatio-temporal heterogeneity in ambient temperature in the spring may force ectotherms to exploit relatively warmer thermal locations more efficiently (Sears and Angilletta 2015; Sears et al., 2016). In northern climates, animals experience shorter active seasons with ambient temperatures that are particularly cold and variable through space and time, compared to species or populations at lower latitudes (Tuttle and Gregory 2012). It follows that northern ectotherms have limited time to assimilate sufficient energy for growth, foraging, and reproductive activities, and thus invest more effort into selecting higher temperature early during the active season (Tuttle and Gregory 2012, 2014; Rowe et al., 2017).

Overall, our results imply that reptiles near their northern range limit exploit thermally heterogeneous landscapes, which advances our understanding of ectotherm ability to select thermal habitats. We surmise that turtles used a combination of actively moving between microclimates to stay within favourable temperature ranges, and selecting locations that are inherently warmer and/or that buffer temperature variation (see Woods et al., 2015). To better understand the intricate relationship between environmental temperature, thermoregulation, and habitat selection, we recommend that future studies incorporate animal activity or energetic data as well as animal body temperature in the analysis. Through the advent of new technologies like miniaturized bio-logging devices, it is now possible to obtain precise acceleration or body temperature measurements which then can be related to ambient temperature (Wilson et al., 2015). Collectively, these research efforts will provide a better understanding of how ectotherms navigate a heterogeneous landscape, and thus help predict how they will respond to future temperature variation in rapidly-changing environments.

Data availability

The datasets used and/or analysed during the current study are available from the corresponding author upon reasonable request.

Author contribution

AA, GBM, and DM conceived the study and designed methodology.

AA conducted fieldwork, analysed the data, and led the writing. All authors contributed critically to the ideas and drafts and gave final approval for publication.

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Declaration of competing interest

The authors declare there are no conflicts of interests.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jtherbio.2023.103725.

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