



Impact of natural resource extraction on thermal properties of wood turtle (*Glyptemys insculpta*) habitat

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ABSTRACT

One of the main threats to freshwater turtle populations is habitat destruction, which occurs as a result of human activities such as infrastructure development, forestry, aggregate extraction, and agriculture. However, the impacts of these activities on thermoregulatory opportunities for turtles are not well understood. We examined the impacts of forestry and aggregate extraction on thermal characteristics of wood turtle (*Glyptemys insculpta*) habitat in the Sudbury District, Ontario, by measuring the differences in absolute temperature, thermal landscape structure, and habitat thermal quality among relatively undisturbed sites ($N = 2$), harvested forestry sites ($N = 2$), and aggregate pits ($N = 2$) in 2015. We also tested the potential use of the thermal landscape concept as a predictor of habitat thermal quality. Undisturbed habitats were of higher thermal quality than impacted sites in terms of temperatures experienced *in situ* by wild wood turtles in their natural home ranges, and never reached temperatures that would be injurious to turtles (i.e., below CT_{MIN} or above CT_{MAX}). The undisturbed sites were of lower quality in terms of optimal temperatures (i.e., T_{set}), and were generally cooler and their temperatures less variable than those in impacted habitats. The thermal landscape concept provided a useful predictor of habitat thermal quality when the influence of time of day was factored into the predictive model. Our data are important to the conservation and management of wood turtles because they provide a preliminary quantification of the thermal impacts of natural resource extraction on the habitat of an endangered species, and can guide the development of mitigation and rehabilitation plans by providing measures of, and targets for, thermal habitat quality.

1. Introduction

Landscapes vary spatially and temporally, and the animals that inhabit them must alter their behavior to accommodate these changes in order to survive (Berthold, 1988). Compared to endotherms, ectotherms have comparatively low material resource needs (food, water, oxygen, etc.) because their metabolic rates can be 20 times lower than those of endotherms (Cowles and Bogert, 1944), but ectotherms must thermoregulate behaviorally, which an endotherm only needs to do in extreme conditions (Gordon, 1985; Nagy, 2005; Nelson et al., 1984; Parlin et al., 2018). Sites suitable for thermoregulation are not distributed evenly across the landscape of an ectotherm's home range, and individuals must assess and navigate this thermal landscape to maintain appropriate body temperatures (Greenwald and Kanter, 1979; Stevenson et al., 1985; Arnold and Peterson, 1989). The thermal landscape concept, defined as spatial and temporal variations in temperature across the landscape, has been applied to studies of insects (McGeoch and

Samways, 1991), fish (Schultz et al., 2016), and rattlesnakes (Harvey, 2015), but has not been studied in relation to turtles. Like the tangible landscape, the thermal landscape varies spatially and temporally, but is far more dynamic. Animals can be sensitive to changes in the thermal regimes of their habitats (Lehmkuhl, 1972; Sweeney et al., 2018). For example, western rattlesnakes (*Crotalus oreganus*) in British Columbia, Canada, used upland forest habitats (higher foraging quality) when the thermal qualities of the forest were sufficient for them to function there, but used lower-quality arid grasslands when the forests were too cool (Harvey, 2015). Human activities can exacerbate natural thermal variability, and have been correlated with increased environmental temperatures at the local scale (e.g., urban heat islands; Kim, 1992; Estoque et al., 2017) and at the global scale in the form of climate change (IPCC, 2014).

In Ontario, Canada, habitat of the endangered wood turtle (*Glyptemys insculpta*) is commonly subject to intensive human activity, including forestry (Kittrede, 1996), gravel/aggregate extraction

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(Arvais et al., 2004; Walde et al., 2007), and agriculture (Saumure et al., 2007). All of these activities present conservation concerns for wood turtles through habitat loss (Kaufmann, 1992), injuries or fatalities from encounters with machinery (Kaufmann, 1992; Saumure et al., 2007), increases in populations of subsidized predators such as red foxes (*Vulpes vulpes*), raccoons (*Procyon lotor*), skunks (*Mephitis mephitis*), and corvids (Klemens, 2000; Buhlmann and Osborn, 2011), and increased exposure to illegal collection (i.e., poaching; COSEWIC, 2007). However, human development does not necessarily have a negative impact on wood turtle habitat. Wood turtles are an edge species (Kaufmann, 1992; Compton et al., 2002), and it is possible that forest harvesting can be beneficial to wood turtles if employed conscientiously as a forest management strategy, by opening up closed-canopy forest habitat (i.e., creating a habitat mosaic with more “edge”). Additionally, wood turtles have been observed nesting in aggregate pits, which resemble the elevated sandy beaches of their natural nesting sites (Harding and Bloomer, 1979; Walde et al., 2007; Hughes et al., 2009). These seemingly-contradictory findings illustrate the importance of studying the effects of natural resource extraction on wood turtle habitat before setting habitat management policies and best practices.

In this study, we assessed the thermal impacts (absolute differences in temperature) and consequences (differences in habitat thermal quality) of resource extraction on wood turtle terrestrial habitat. Our study population is located near the northern periphery of the wood turtle's range, where habitat thermal quality is at its greatest importance for ectotherms (Magnuson et al., 1979; Tracey and Christian, 1986; Greaves, 2007; Dubois et al., 2009). Our objective was to compare the thermal properties and qualities of sites with (relatively) undisturbed wood turtle habitat to habitats impacted by resource extraction. We predicted that sites impacted by resource extraction would be hotter and more variable in temperature than undisturbed sites, as greater canopy cover at the undisturbed sites would provide a thermal buffer (Zhou et al., 2007). We also predicted that habitat thermal quality would be lower in the resource extraction sites than in the undisturbed sites. Finally, to assess the usefulness of the thermal landscape concept as a conservation tool, we tested how well measures of the thermal landscape predicted habitat thermal quality. We predicted that more variable thermal landscapes (analogous to “rougher terrain”) would provide superior thermal habitats by increasing the variety of thermal microsites available for wood turtles. Concern for the future integrity of wood turtle populations requires a close look at natural resource extraction within wood turtle habitat to determine its impact on the quality of the local environment.

2. Methods

2.1. Study species

The wood turtle is a freshwater turtle, endemic to eastern North America, where it inhabits forest-edged rivers and streams (Harding and Bloomer, 1979; Ernst and Lovich, 2009). In Canada, where the species is listed as Threatened, wood turtles are distributed in spatially-disjunct populations in Ontario, Quebec, New Brunswick, and Nova Scotia (COSEWIC, 2007). Habitat destruction, road mortality, and collection for the pet trade are the main threats to the species (COSEWIC, 2007). Wood turtles are semi-aquatic, and frequently move between aquatic and terrestrial habitats during the active season (late spring through early autumn; Harding and Bloomer, 1979; Ernst and Lovich, 2009). Wood turtles, especially females, spend long periods of time in forested upland habitats, away from their home river (Arvais et al., 2002; Tuttle and Carroll, 2003; Greaves, 2007). Thus, the wood turtle is a model ectotherm for studying the effects of resource extraction on habitat thermal quality because it is seasonally terrestrial and occurs in areas impacted by forestry and aggregate extraction.

2.2. Study sites

We conducted field work from May to October 2015. The study area is located in the Sudbury District of Ontario; to protect the populations, exact locations will be kept confidential. This area is typical of wood turtle habitat in central Ontario: mixed coniferous/deciduous forest on glacial moraine soils, cool, clear rivers with sand/gravel/cobble substrates, and little human habitation. The primary natural resource industries near the study site are forestry and aggregate extraction. A subset of the wood turtle population within a ~3.5 km section of the river has been studied since 2003; we refer to this area as the primary study site. We selected six sites in or near this primary study site: two relatively undisturbed sites, two sites within previously-harvested forestry blocks, and two sites within aggregate (gravel) pits. All study sites are within 10 km of each other and within 300 m of the river used by the wood turtles; each site was 1.8 ha in area (200 m × 90 m). Surveys in 2007, 2009, and 2015 found wood turtles or evidence of wood turtle presence within 1 km of each of the study sites (Greaves, 2007; pers. obs.).

The relatively undisturbed sites were located within the primary study site, and were chosen for their limited amounts of recent human activity. Both sites include 45-year old jack pine (*Pinus banksiana*) plantation, and some evidence of camping and ATV trails, but have no recent large-scale disturbances comparable to those of the impact sites. The first undisturbed site (W_1) was chosen for its high incidence of wood turtles captures in previous studies (Greaves, 2007; Greaves et al. unpubl. data, Hughes, 2016). W_1 abuts the river, and includes natural riparian forest within the floodplain (274 m elevation) and 45-year-old jack pine plantation further inland/upland (281 m elevation). Given the proximity to the river, structural complexity and high incidence of observed use by the turtles, we made the assumption that this site represents “good” wood turtle habitat. W_1 has a closed canopy, except directly at the river's edge, around one large vernal pool in the floodplain, and in some parts of the plantation forest where jack pine trees have fallen and opened the canopy. The second undisturbed site (W_2) is located ~200 m from the river, abutting a black spruce (*Picea mariana*) bog to the north, and is composed entirely of upland (281 m elevation) jack pine plantation of the same age as in W_1 . The canopy is closed, but with patches opened by fallen pine trees. Although wood turtles have been encountered nearby (within 100 m; Hughes, pers. obs.) and observed using similar habitat, no wood turtles were captured directly within W_2 in 2015; this site was chosen as an example of potential wood turtle habitat.

Both of the sites within previously-harvested forestry blocks were red pine (*Pinus resinosa*) plantations. These sites were harvested in 4–7 m wide forced rows, rather than clear-cutting. The first forestry site (F_1 , 283 m elevation) was located within the primary study site, and was harvested in 2012; it was located 300 m from the river and 800 m from W_2 . The second site (F_2 , 295 m elevation) was harvested in 2014 and located 250 m from the river; it was ~3 km from the periphery of the primary study site, and ~350 m from one of the aggregate sites (G_1 - see below). F_2 was also within 500 m of a tributary of the primary river known to have wood turtles (Litzgus, pers. obs.). Both forestry sites had alternating rows of canopy and open ground, and were completely surrounded by similarly-harvested and unharvested red pine plantation.

The first aggregate (gravel) pit (G_1 , 291 m elevation) was located 80 m from the river and 3.5 km from the primary study site. G_1 was located within an area of the pit which had not been extracted since 2012, and had begun to show signs of early succession; sweet fern (*Comptonia peregrina*), balsam poplar (*Populus balsamea*), and white birch (*Betula papyrifera*) were returning to the open pit area, with stands of white birch and white spruce (*Picea glauca*) on elevated patches that had never been removed. The pit owners had placed a ~50 cm high fence around the pit's boundaries to prevent wood turtles from entering the active areas of the pit; nevertheless, we found a depredated turtle nest within G_1 in 2015 (species unknown, but suspected to have been a

wood turtle or Blanding's turtle (*Emydoidea blandingii*). G_1 was surrounded by an open, un-vegetated gravel pit to the north and east, and a red pine plantation forest to the south and west. The second pit (G_2 , 291 m elevation) was located within 50 m of the river, and 7.8 km from the primary study area. G_2 was located in a section of the pit which had been deliberately rehabilitated by the owners starting after 1996: the site is mostly open grassy field, with scattered stands of young jack pine, white birch, and balsam poplar. Both sites were largely open, with only some thin canopy cover in patches of G_1 where no excavations had occurred. G_2 was surrounded by open, un-vegetated gravel pit to the south and east, jack pine plantation to the west, and natural riparian forest to the north.

2.3. Thermal landscape mapping

We laid an array of thermal monitoring stations at each of the six sites (W_1 , W_2 , F_1 , F_2 , G_1 , and G_2); each station consisted of a thermal model, constructed to simulate the thermal profile of an adult wood turtle (adapted from Yagi and Litzgus, 2013). We constructed these models from plastic food containers (30 cm long x 18 cm wide x 5 cm tall; volume of 1.4 L) filled with water balloons (totalling ~1 kg of water) contained in a mesh bag to simulate turtle organs and mesentery. We spray-painted the “dorsal” surfaces of the containers brown to simulate a wood turtle's carapace coloration. To measure environmental temperature (T_e), we coated iButton dataloggers (DS1922L or DS1921G, Maxim Integrated, San Jose, CA, USA) in silicone caulking for waterproofing, and secured one each to the top of the thermal models with marine epoxy; these dataloggers recorded the model's “carapace” temperature every 2 h. Each array covered the entirety of the site, and consisted of 20 thermal models in a 5×4 grid, 50 m \times 30 m apart, covering an area of 1.8 ha. All six arrays were fully deployed by 15 May 2015, and we retrieved all data loggers and thermal models from the field by 30 September 2015. Additionally, we collected all dataloggers in late June, retrieved the recorded data, re-launched and returned them to the field in early July (maximum of 6 days with no monitoring coverage), to minimize data loss from potential equipment failure.

Approximately 17% of the temperature data points were irretrievable, either due to datalogger failure, or because the thermal models were destroyed by wildlife. Both aggregate pits were commonly visited by recreational ATV users, but we observed no obvious damage to the thermal models from human interference; the exception being a single model in G_2 which was crushed by the pit operators piling timber over it.

2.4. General analyses

We divided the temperature readings from each site into seasonal time periods that corresponded to wood turtle activity periods (adapted from Arvais et al., 2004) observed in 2015: Pre-Nesting (1 May to 1 June), Nesting (2 June to 20 June), Summer (21 June to 10 September), and Pre-Hibernation (11 September to 30 September). We further divided these into four 6-h diel periods for analysis: Early Morning (0000 h–0600 h), Late Morning (0601 h–1200 h), Afternoon (1201 h–1800 h), and Evening (1801 h–2400 h), to compensate for asynchronous temperature readings and short-term stochastic temperature events. The temperature readings of these diel periods served as our data points for analysis.

Due to the issues with lost data, the six sites had differing numbers of thermal models that could be successfully retrieved at the end of field studies. We conducted linear regressions on all temperature data to determine if the number of thermal models in a treatment had an effect on temperature readings, independent of treatment. We compared the number of thermal models to mean diel temperature across the arrays, and the number of thermal models to diel temperature variance across the arrays. The number of thermal models did not have an effect on

mean temperature ($R^2 = 0.001$, $F(1, 2782) = 3.58$, $P = 0.06$); there was also no effect on temperature variance ($R^2 < 0.001$, $F(1, 2782) = 0.22$, $P = 0.64$). Thus, we concluded that the missing thermal models had no practical effect on the temperature readings, and conducted our analyses accordingly.

All statistical analyses were performed with R (R version 3.1.2; R Core Team, 2013). Kruskal-Wallis tests with Multiple Comparisons were performed with the “agricolae” package (de Mendiburu, 2015); linear mixed models were performed and analysed with the “lme4” (Bates et al., 2015) and “car” (Fox and Weisberg, 2011) packages. In all post-hoc tests, we used the Bonferroni correction for multiple comparisons ($\alpha = 0.006$).

2.5. Absolute temperature analysis

We compiled temperature readings for each activity period-diel period to compare temperatures among treatments; for example, we compared all of the Early Morning data points from the Pre-nesting period among all six treatments. We compared absolute temperatures among treatments using ANOVAs with post-hoc Tukey's HSD test, between W_1 and W_2 , and between the undisturbed sites and impact sites (9 comparisons total); we did not perform post-hoc comparisons among the impact sites (F_1 , F_2 , G_1 , and G_2).

2.6. Thermal landscape relief analysis

We calculated the coefficient of variation (CV) across each thermal model grid for each activity period-diel period to estimate the thermal landscape's “roughness” (hereafter referred to as thermal landscape relief), analogous to the topographic relief of the physical landscape. Higher values of CV indicate a rougher thermal landscape (more thermal variation), and lower values of CV indicate a smoother thermal landscape (less thermal variation; Fig. 1). As the values of CV were not normally distributed, we compared thermal landscape relief among treatments for each activity period-diel period using Kruskal-Wallis tests with post-hoc Multiple Comparisons between W_1 and W_2 , and between the undisturbed sites and impact sites (9 comparisons total); we did not perform post-hoc comparisons among the impact sites.

2.7. Habitat thermal quality analysis

We selected five temperature ranges that have biological significance to wood turtles for comparisons of habitat thermal quality among the sites. Hertz et al. (1993) devised the variable T_{set} , which identifies the preferred temperature range of a given ectothermic species in ideal conditions. T_{set} is measured *ex situ* by placing an animal in an enclosure with a thermal gradient, and tabulating the range of temperatures that it selects most frequently (e.g., between the 25th to 75th percentiles), when other survival considerations (e.g., foraging, predator avoidance, etc.) are not factors (e.g., Rummery et al., 1995; Yagi and Litzgus, 2013). Dubois et al. (2008) measured T_{set} for a population of wood turtles in Québec; we assumed that the Sudbury and Québec populations have similar values of T_{set} , as they occur at similar latitudes. Dubois et al. (2008) used a novel criterion for T_{set} , taking the selected temperatures at the 95th percentile (30.0 °C, hereafter referred to as Metabolic T_{set}), rather than in the range of the 25th and 75th percentiles, as is more commonly done (e.g., Yagi and Litzgus, 2013). We also derived a conventional T_{set} range (23.0 °C–27.0 °C; hereafter referred to as General T_{set}) after the method of Yagi and Litzgus (2013) from the Dubois et al. (2008) data (Y. Dubois, pers. comm., 2017). Third, we estimated the range of temperatures used by turtles in the Sudbury population. Thermal usage was defined as the interquartile range of body temperatures (25th to 75th percentiles; 15.7 °C–22.0 °C; hereafter referred to as Usage) recorded from turtles in 2015 (adapted from Tucker et al., 2015). These temperature data were collected as part of another project (Hughes, 2016) by applying iButton dataloggers

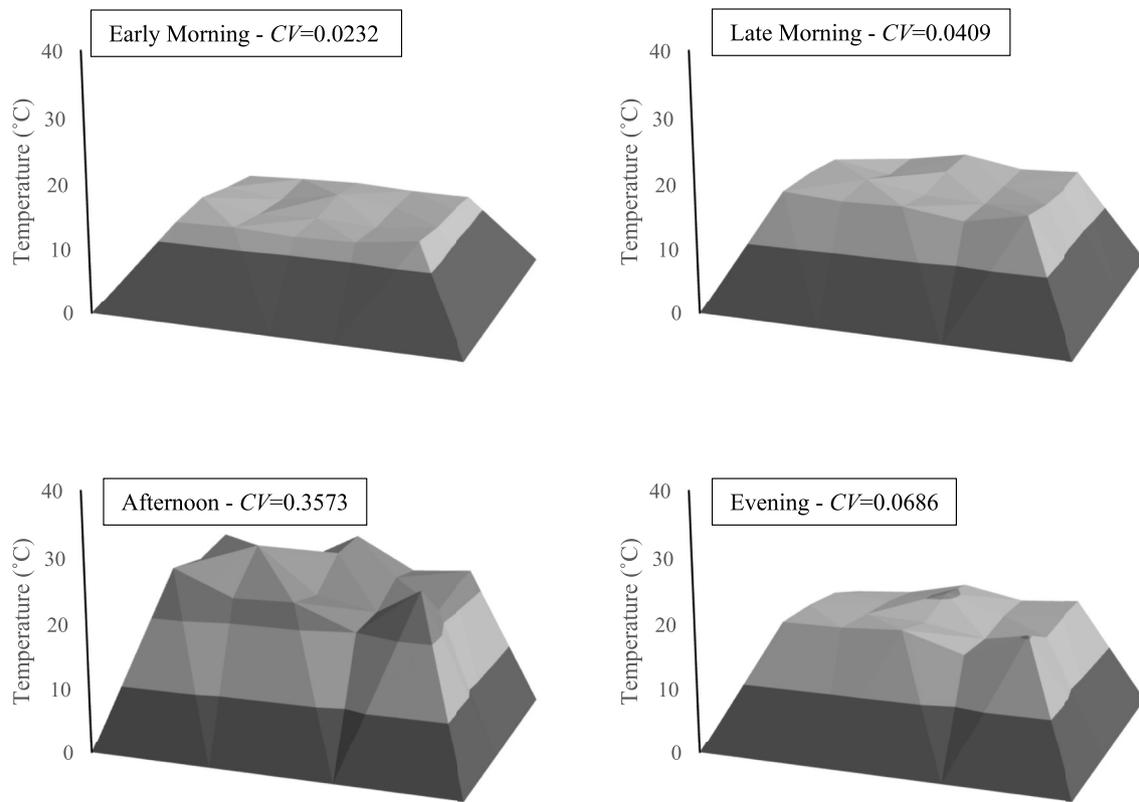


Fig. 1. Example of thermal landscape variation over a day (21 June 2015) at an aggregate site (G_1). Thermal data are generalized into 6 h diel periods: Early Morning (a - 0000 to 0600), Late Morning (b - 0601 to 1200), Afternoon (c - 1201 to 1800), and Evening (d - 1801 to 2400). CV shows the coefficient of variation across this thermal landscape, used as an estimator of thermal landscape relief.

to the carapaces of free-ranging wood turtles ($N = 15$) within the primary study site, which measured carapace temperature every 2 h. These temperature readings were generalized into the same 6 h diel periods as the readings from the thermal models. Finally, we considered temperatures below approximated CT_{MIN} as “Lethal Cold”, and temperatures above approximated CT_{MAX} as “Lethal Hot”. To our knowledge, these CT values have not been measured for wood turtles, and we were unable to measure them ourselves; a survey of the literature on other turtle species showed a consistent CT_{MIN} of 1–3 °C, and a consistent CT_{MAX} of 39–41 °C across several turtle families (e.g., Plummer et al., 2003; Ernst and Lovich, 2009; Xu et al., 2015). Based on these findings by other authors, we selected conservative estimates of < 1 °C and > 39 °C for our Lethal Cold and Lethal Hot categories, respectively.

We calculated habitat thermal quality for each site by comparing the number of diel periods that fell within each of the above categories (Lethal Cold, Usage, General T_{set} , Metabolic T_{set} and Lethal Hot). We created a weighted temperature value (T_{wgt}) by multiplying each temperature data point by the proportion of data points for that treatment for each temperature category. For example, if treatment W_1 had 20 data points that fell in the Usage temperature range out of a total of 500 data points ($20/500 = 0.04$), then each temperature data point from W_1 that fell within the Usage category would be multiplied by 0.04. A high T_{wgt} in the Usage, General T_{set} or Metabolic T_{set} categories indicates a high quality thermal environment, while a high T_{wgt} in the Lethal Cold or Lethal Hot categories indicates a low-quality thermal environment.

As these data were not normally distributed, we used Kruskal-Wallis tests with post-hoc Multiple Comparisons between W_1 and W_2 , and between the undisturbed sites and impact sites for each temperature category (Lethal Cold, Usage, General T_{set} , Metabolic T_{set} , and Lethal

Hot); we did not perform post-hoc comparisons among the impact sites. Note that for Metabolic T_{set} , we counted data points within a range of 28.5 °C to 31.5 °C (i.e., within 5 percentiles of 30 °C), as the other categories were ranges rather than single values.

2.8. Thermal landscape as a predictor of habitat thermal quality analysis

To determine if measuring the thermal landscape could predict thermal quality of wood turtle terrestrial habitat, we formulated a number of linear mixed effects models predicting D_e (defined as a measure of deviation of *in situ* environmental temperatures from T_{set} ; Hertz et al., 1993), using D_e based on three standards of quality (Usage, General T_{set} , and Metabolic T_{set}) as the response variables. The fixed predictive variables were mean diel temperature, thermal landscape relief, diel period (Early Morning, Late Morning, Afternoon, Evening), and season (Pre-nesting, Nesting, Summer, Pre-hibernation), while site was used as a random variable. We performed Akaike's Information Criterion tests on these models to determine which model was the most predictive of habitat thermal quality, for all three standards of quality.

3. Results

3.1. Absolute temperatures

Temperatures differed among sites across much of the seasonal and diel periods (Fig. 2). In the Pre-Nesting period, treatments did not differ in the early mornings ($F(5,99) = 0.12$, $P = 0.99$) and evenings ($F(5,99) = 1.31$, $P = 0.27$), but differed in the late mornings ($F(5,99) = 2.87$, $P = 0.02$), and afternoons ($F(5,99) = 10.37$, $P < 0.01$). In the Nesting period, treatments did not differ in the early mornings (F

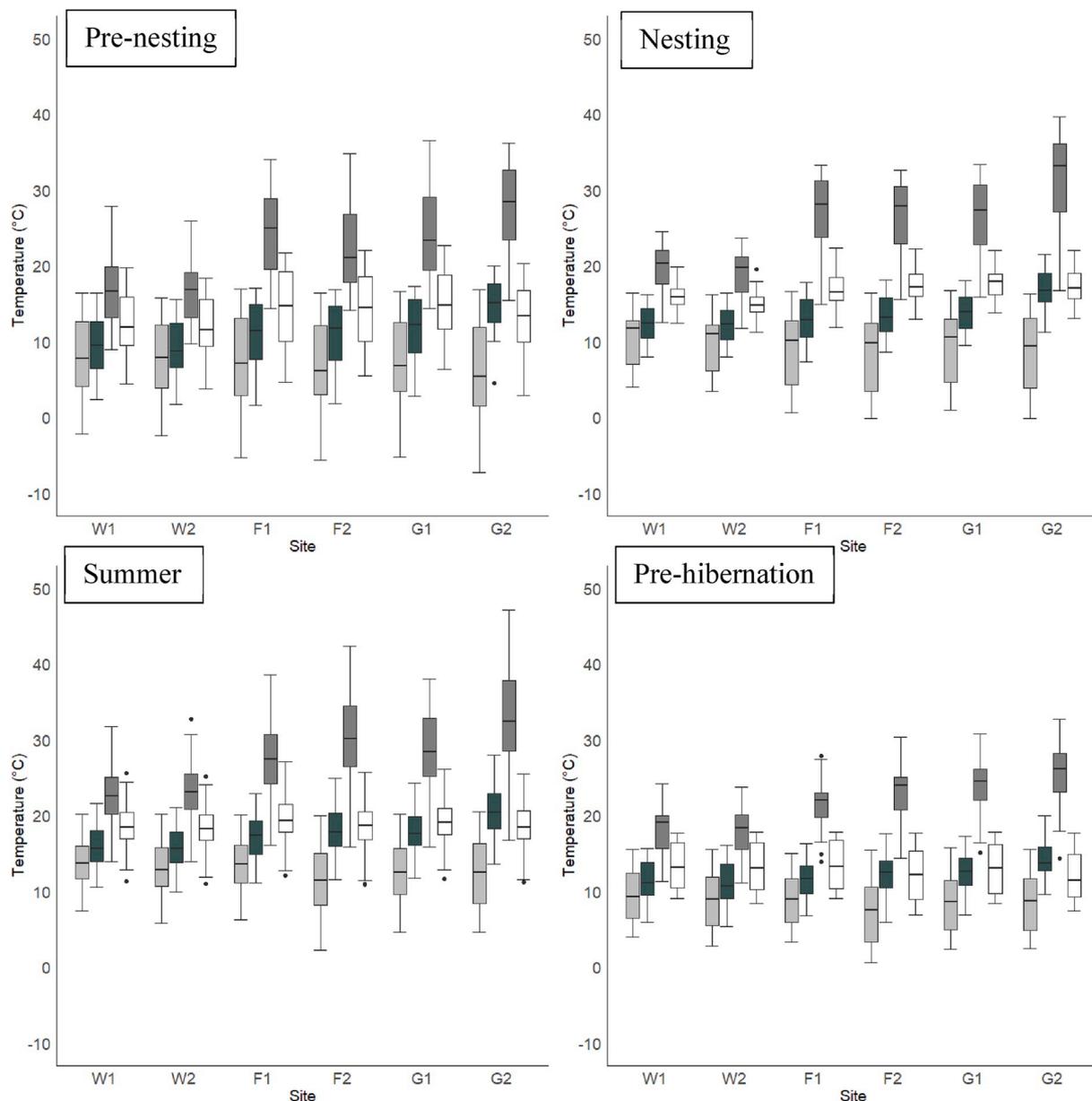


Fig. 2. Mean absolute temperature measurements for six experimental sites in Sudbury District, Ontario, in 2015. Mid-line shows median temperature, the boxes show 25th–75th percentiles, whiskers show 1.5 * IQR, and points show outliers. Light grey boxes show the Early Morning period (0000h–0600h), dark grey boxes show Late Morning (0601 h–1200 h), medium grey boxes show Afternoon (1201 h–1800 h), and white boxes show Evening (1801 h–2400 h).

(5,108) = 0.57, $P = 0.72$), but did in the late mornings ($F(5,108) = 7.75$, $P < 0.01$), afternoons ($F(5,108) = 14.05$, $P < 0.01$) and evenings ($F(5,108) = 4.09$, $P < 0.01$). In the Summer period, the treatments did not differ in the evenings ($F(5,448) = 1.62$, $P = 0.15$), but differed in the early mornings ($F(5,448) = 3.83$, $P < 0.01$), late mornings ($F(5,448) = 26.67$, $P < 0.01$), and afternoons ($F(5,448) = 41.99$, $P < 0.01$). In the Pre-Hibernation period, treatments did not differ in the early mornings ($F(5,102) = 0.48$, $P = 0.79$) and evenings ($F(5,102) = 0.72$, $P = 0.61$), but differed in the late mornings ($F(5,102) = 3.47$, $P < 0.01$) and afternoons ($F(5,102) = 14.69$, $P < 0.01$).

In general, undisturbed sites were cooler than impacted sites, with aggregate sites typically being much hotter, and forestry sites being intermediate between aggregate and undisturbed (Fig. 2). Temperature differences became most apparent in the afternoons, with impact sites being consistently hotter than undisturbed sites, and there was little difference across sites in early mornings (Fig. 2). Undisturbed sites also

showed the least variability within and across diel periods, having narrower ranges, higher temperatures in the early mornings and evenings, and cooler temperatures in the afternoons; G₂ was typically the coldest in the early mornings and evenings, and the hottest in the afternoons (Fig. 2).

3.2. Thermal landscape relief

Thermal landscape relief differed across diel and seasonal periods (Fig. 3). In the Pre-Nesting period, treatments did not differ in the early mornings ($X^2(5) = 7.16$, $P = 0.21$), but differed in the late mornings ($X^2(5) = 22.02$, $P < 0.01$), afternoons ($X^2(5) = 14.07$, $P = 0.02$) and evenings ($X^2(5) = 31.50$, $P < 0.01$). In the Nesting period, treatments differed in all diel periods: early mornings ($X^2(5) = 24.92$, $P < 0.01$), late mornings ($X^2(5) = 34.66$, $P < 0.01$), afternoons ($X^2(5) = 19.37$, $P < 0.01$) and evenings ($X^2(5) = 47.69$, $P < 0.01$). In the Summer period, treatments differed in all diel periods: early mornings

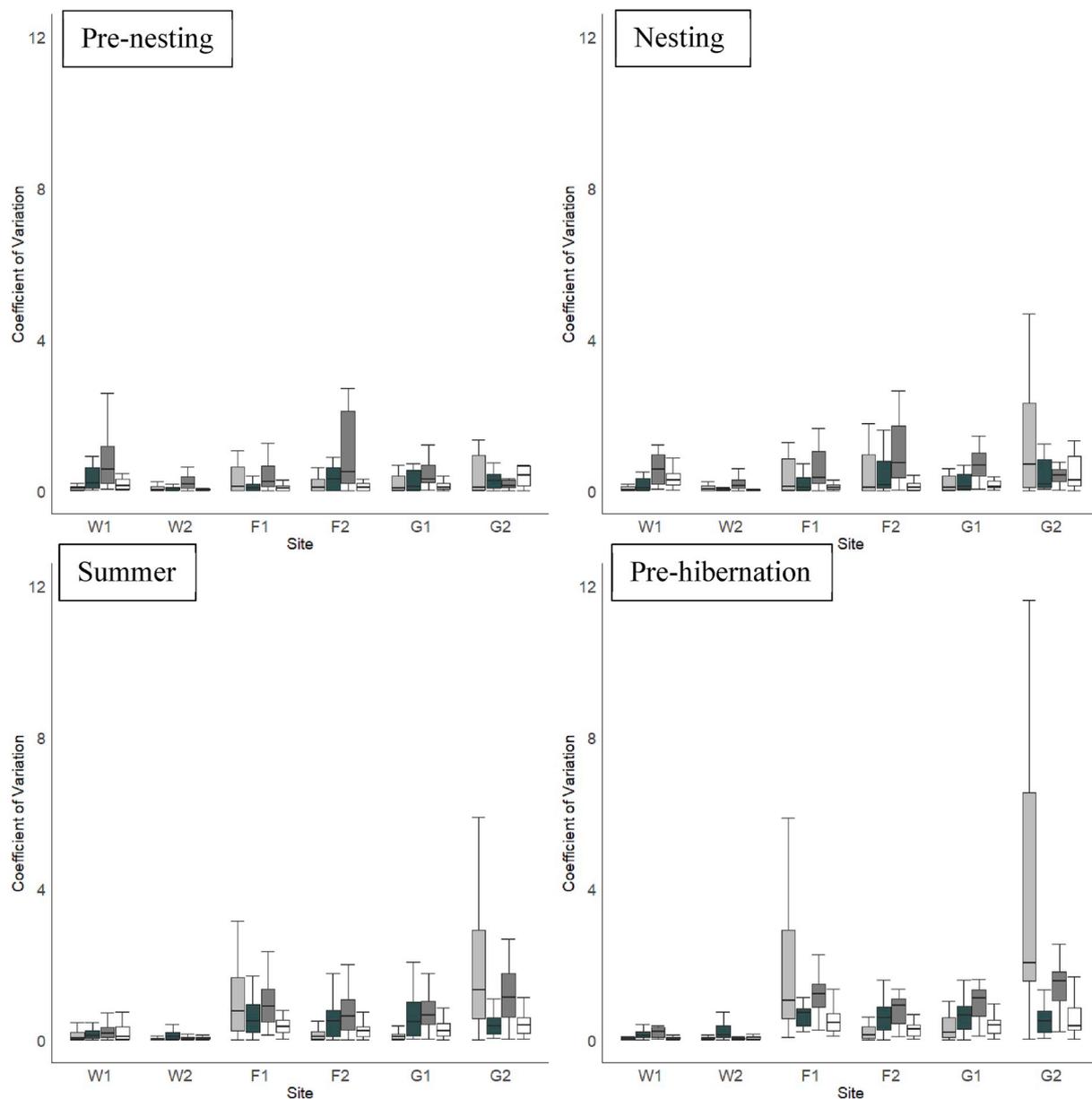


Fig. 3. Diel coefficients of variation (CV) estimating thermal landscape structure measured at six sites in Sudbury District, Ontario, in 2015. Mid-line shows median temperature, the boxes show 25th–75th percentiles, whiskers show $1.5 \times \text{IQR}$, and points show outliers. Light grey boxes show the Early Morning period (0000 h–0600 h), dark grey boxes show Late Morning (0601 h–1200 h), medium grey boxes show Afternoon (1201 h–1800 h), and white boxes show Evening (1801 h–2400 h).

($X^2(5) = 250.76$, $P < 0.01$), late mornings ($X^2(5) = 123.91$, $P < 0.01$), afternoons ($X^2(5) = 242.12$, $P < 0.01$) and evenings ($X^2(5) = 151.34$, $P < 0.01$). In the Pre-Hibernation period, treatments differed in all diel periods: early mornings ($X^2(5) = 77.33$, $P < 0.01$), late mornings ($X^2(5) = 41.42$, $P < 0.01$), afternoons ($X^2(5) = 70.26$, $P < 0.01$) and evenings ($X^2(5) = 64.16$, $P < 0.01$).

In every period that showed differences, W_2 had the smoothest thermal landscape, except during the Pre-Hibernation period when W_1 and W_2 never differed (Fig. 3); otherwise, W_1 was often rough in the afternoons (Fig. 3). Forestry sites and aggregate sites were usually rougher than the undisturbed sites, particularly in the afternoons, and in the Summer and Pre-Hibernation periods (Fig. 3).

3.3. Habitat thermal quality

The T_{wgt} for the Lethal Cold category did not differ among treatments ($X^2(5) = 1.2$, $P = 0.95$), but T_{wgt} did differ among treatments in

all other temperature categories (Usage: ($X^2(5) = 99.26$, $P < 0.01$), General T_{set} : ($X^2(5) = 99.38$, $P < 0.01$), Metabolic T_{set} : ($X^2(5) = 68.71$, $P < 0.01$), and Lethal Hot: ($X^2(5) = 18.54$, $P < 0.01$)). Both undisturbed sites (W_1 and W_2) had higher T_{wgt} ratings for the Usage category than the impact sites (F_1 , F_2 , G_1 , and G_2), indicating that these sites were more frequently within that range of temperatures. The impact sites typically had higher T_{wgt} ratings in the General T_{set} and Metabolic T_{set} categories, indicating that impact sites were more frequently within optimal temperature ranges for wood turtles than the undisturbed sites (Fig. 4). However, F_2 and G_2 both reached Lethal Hot temperatures (Fig. 4); F_2 reached lethal temperatures ($> 39^\circ\text{C}$) during 6 diel periods and G_2 during 15 diel periods, always during Summer afternoons.

3.4. Thermal landscape as a predictor of habitat thermal quality

The model that included mean temperature, thermal landscape

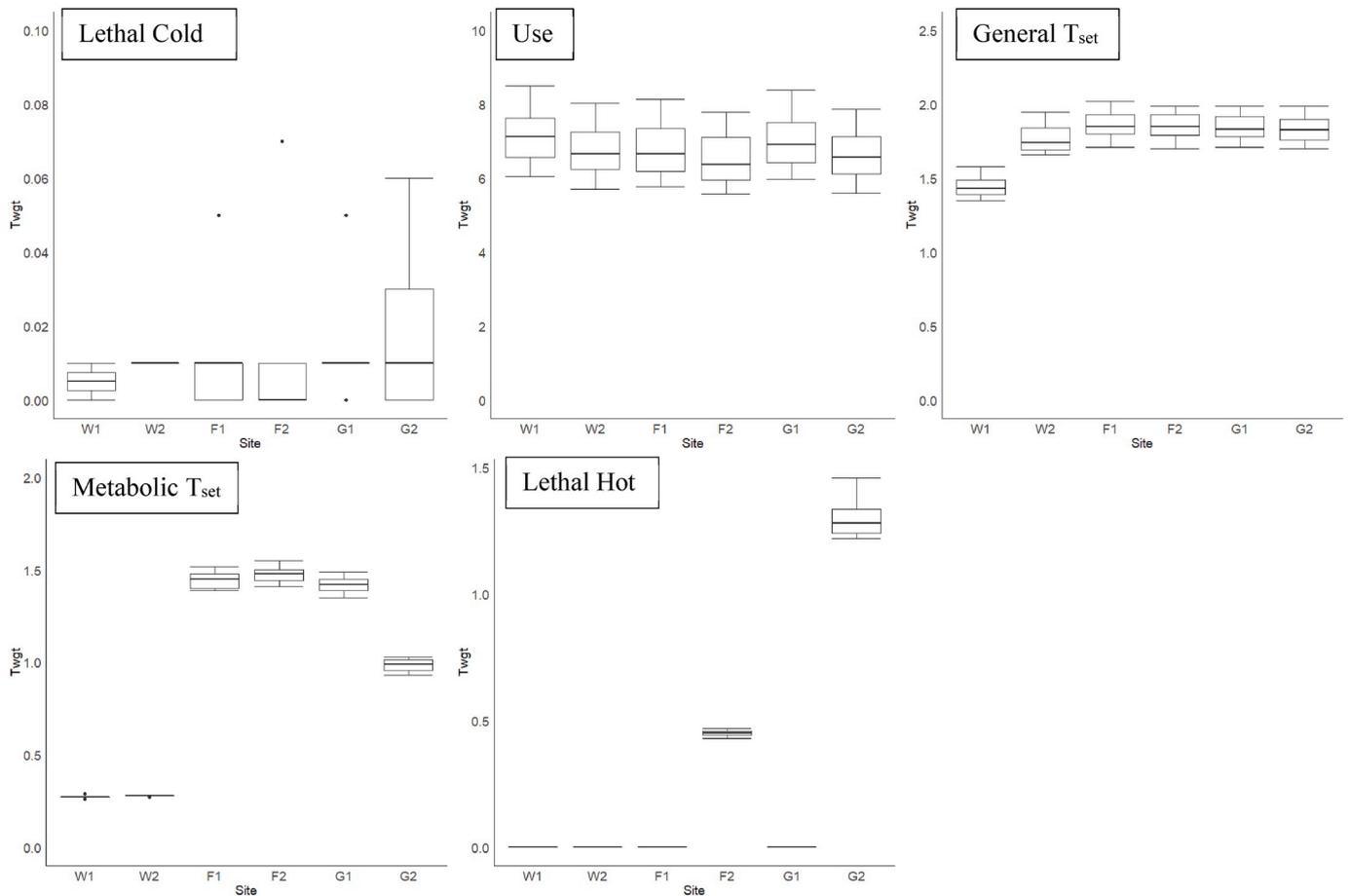


Fig. 4. Values of T_{wgt} (temperature weighted by frequency of those temperatures occurring) for all treatments in each temperature category. Lethal Cold ($< 1^{\circ}\text{C}$), Usage ($15.7^{\circ}\text{C} - 22^{\circ}\text{C}$), General T_{set} ($23^{\circ}\text{C} - 27^{\circ}\text{C}$), Metabolic T_{set} ($28.5^{\circ}\text{C} - 31.5^{\circ}\text{C}$), and Lethal Hot ($> 39^{\circ}\text{C}$). Mid-line shows median temperature, the boxes show 25th-75th percentiles, whiskers show $1.5 * \text{IQR}$, and points show outliers. Note that some categories/treatments have such a narrow range that they may be barely visible on the figures.

Table 1

Predictive utility of linear mixed-effects models used to predict thermal quality of wood turtle (*Glyptemys insculpta*) habitat in the Sudbury District, Ontario. The Site variable was used as a random effect. See text for descriptions of model variables.

Model	AIC	df	ΔAIC
General $T_{set} \sim \text{Temperature} + \text{Relief} + [\text{Site}]$	15951.6	5	194.9
General $T_{set} \sim \text{Temperature} + \text{Relief} + \text{Diel} + [\text{Site}]$	15756.7	8	0.0
General $T_{set} \sim \text{Temperature} + \text{Relief} + \text{Season} + [\text{Site}]$	15844.9	8	88.2
Metabolic $T_{set} \sim \text{Temperature} + \text{Relief} + [\text{Site}]$	13412.2	5	79.9
Metabolic $T_{set} \sim \text{Temperature} + \text{Relief} + \text{Diel} + [\text{Site}]$	13332.3	8	0.0
Metabolic $T_{set} \sim \text{Temperature} + \text{Relief} + \text{Season} + [\text{Site}]$	13391.4	8	59.1
Usage $\sim \text{Temperature} + \text{Relief} + [\text{Site}]$	16246.8	5	363.8
Usage $\sim \text{Temperature} + \text{Relief} + \text{Diel} + [\text{Site}]$	15883.0	8	0.0
Usage $\sim \text{Temperature} + \text{Relief} + \text{Season} + [\text{Site}]$	16096.8	8	213.8

General $T_{set} = 23^{\circ}\text{C}$ to 27°C
 Metabolic $T_{set} = 30^{\circ}\text{C}$
 Usage = 16°C to 22°C

relief, and diel period was most predictive against all three standards of habitat thermal quality (Table 1). Mean temperature emerged as the most predictive factor for General T_{set} and Metabolic T_{set} , while thermal landscape relief was the most predictive factor for Usage (Table 2).

4. Discussion

Natural resource extraction had an impact on the thermal landscape of wood turtle habitat. A clear pattern in overall temperatures emerged over the course of the field season, such that all treatments experienced

similar temperatures in the early mornings, heated up at different rates during the late mornings and afternoons, and cooled back down to similar temperatures in the evenings. The undisturbed sites were generally cooler and less variable than the impact sites, particularly W_2 . W_2 also had the least variable thermal landscape structure in nearly all cases, or was at least in the cluster of treatments with the smoothest structure (Fig. 3). W_2 had a more homogeneous physical landscape than the other sites, being solely flat jack pine plantation with a high degree of canopy cover, which may have contributed to this smooth thermal landscape. In contrast, W_1 was a mix of lowland riparian forest and

Table 2

Relative predictive utility of fixed effects in the strongest linear mixed-effects models used to predict thermal quality of wood turtle (*Glyptemys insculpta*) habitat in the Sudbury District, Ontario. See text for descriptions of variables.

Model	Variable	χ^2	df	P
General	Temperature	2893.8	1	< 0.01
$T_{set} \sim$ Temperature + Relief + Diel	Relief	837.4	1	< 0.01
+ [Site]	Diel	213.4	3	< 0.01
Metabolic	Temperature	11775.7	1	< 0.01
$T_{set} \sim$ Temperature + Relief + Diel	Relief	610.9	1	< 0.01
+ [Site]	Diel	95.4	3	< 0.01
Usage \sim Temperature + Relief + Diel	Temperature	109.0	1	< 0.01
+ [Site]	Relief	742.0	1	< 0.01
	Diel	398.5	3	< 0.01

General $T_{set} = 23^\circ\text{C}$ to 27°C

Metabolic $T_{set} = 30^\circ\text{C}$

Usage = 16°C to 22°C

upland jack pine plantation, F_1 and F_2 were alternating strips of red pine plantation and logged open ground, G_1 was a mix of early successional forest and open sand/gravel pit, and G_2 was a rehabilitated gravel pit (which was effectively grassland). The physical landscape mosaics of the treatments other than W_2 likely contributed to their rougher thermal landscapes; however, the impact sites were still typically rougher than W_1 (Fig. 3). These findings largely support our prediction of cooler and less variable temperatures at the undisturbed sites compared to the impact sites. However, our predictions were not supported for all diel periods, as the undisturbed sites were sometimes warmer than, or not different from, the impact sites, particularly in the early mornings or evenings, and W_1 was occasionally rougher than the impact sites, particularly in the Pre-Nesting period.

Habitat selection by wood turtles has been well-studied (Harding and Bloomer, 1979; Compton et al., 2002; Arvisais et al., 2004; Dubois et al., 2009). Compton et al. (2002) found that at home range scales, wood turtles prefer open habitat near water, but at watershed scales, they preferred forested areas with moderate canopy cover; they postulated that this reflected a trade-off between thermoregulatory vs. feeding needs for the species. Kaufmann (1992), and Arvisais et al. (2004) showed that wood turtles do not randomly select habitat based on availability, but actively seek out preferred habitats. Dubois et al. (2009) showed the link between habitat selection and thermoregulation, and suggested that heterogeneous habitats provided greater opportunities for thermoregulation, particularly in the northern limit of the species' range. An open or mosaic habitat provides more opportunities for both basking and feeding, and wood turtles are known as an edge species (Kaufmann, 1992; Compton et al., 2002); this may explain why we typically found more wood turtles in and around W_1 than W_2 during radio telemetry studies in the area (Greaves, 2007; Hughes, 2016). Other factors, such as proximity to the river and researcher search effort, may complicate this conclusion. Wood turtles are known to use water bodies as thermal refuges in cooler conditions (Dubois et al., 2009), and in particular, males rarely move away from their home streams (Kaufmann, 1992; Greaves, 2007); W_1 was closer to the river than any of the other treatments. Nevertheless, even without such assumptions of relative quality, the two undisturbed habitat sites showed clear differences in absolute temperature and in thermal landscape relief compared to the impacted sites.

Resource extraction had consequences for the thermal quality of wood turtle habitat. Our data support the conclusion that forestry and aggregate activities have the potential to degrade thermal habitat quality by resulting in lethal temperatures (i.e., F_2 and G_2), but it may also be possible for these resource extraction activities to maintain, or even improve, thermal quality of habitat for wood turtles (i.e., F_1 and G_1). Additionally, the habitats surrounding F_2 and G_2 could provide refuge for wood turtles as both of these sites had natural riparian forest and/or unharvested red pine plantation < 1 km away from them.

Although the impact sites showed higher frequencies of optimal temperatures (General T_{set} and Metabolic T_{set}), they also showed higher frequencies of temperatures that could pose health risks to the turtles (Fig. 4). Further, the undisturbed sites showed higher instances of temperatures in the Usage range (i.e. the temperatures used by wood turtles *in situ*; Fig. 4). From a thermal perspective, our findings suggest that retaining natural forest cover provides the highest quality habitat, at least in the summer months, and studies on other turtle species corroborate our findings. Quesnell et al. (2013) found that forest cover surrounding wetlands was the strongest predictor of presence/absence in Blanding's turtles and musk turtles (*Sternotherus odoratus*); as wood turtles are more terrestrial than either species, it is reasonable to hypothesize that available forest cover is even more important to wood turtles. For three-toed box turtles (*Terrapene carolina triunguis*), which are more terrestrial than wood turtles, vegetative cover was second only to thermal habitat characteristics in importance for habitat selection (Reagan, 1974); however, box turtles also use logged areas, indicating that with proper care, forced-row silviculture may not completely destroy the thermal complexity of terrestrial habitat (Agha et al., 2017). The two resource extraction forms that we studied removed vegetation from the landscape, both in the canopy and the understory, which has clear and well-studied thermal consequences to habitat (Liddle and Moore, 1974; Zhou et al., 2007). For wood turtles, these consequences potentially translate into degradation of habitat.

The rehabilitated gravel pit, G_2 , generally provided the least suitable thermal habitat (Fig. 4). This may appear to be an argument against rehabilitation efforts; however, the rehabilitation plan was drafted and implemented starting in 1996, the same year that the wood turtle was designated as Special Concern in Canada by COSEWIC (2007), and five years before wood turtles were first officially recorded in this watershed (C. Blomme, pers. comm., 2016). The rehabilitation plan was thus not obligated to consider wood turtles in its initial development or implementation, and a grandfather clause may have absolved the aggregate company from needing to update the plan once wood turtles were up-listed to Threatened in 2007 (COSEWIC, 2007), or when wood turtle habitat was officially protected by the government of Ontario in 2010 (OMNRF, 2010). Based on our findings, and those of Compton et al. (2002) and Dubois et al. (2009), a rehabilitation effort that would be more beneficial to wood turtles would be one that fostered natural forest regrowth resembling W_1 .

In general, the forestry sites differed less from the undisturbed sites than the aggregate sites, thermally-speaking, and it is less clear what our results would mean for forestry operations and/or regeneration objectives. The difference may be a result of the dominant tree species; we never observed wood turtles in red pine plantations (like F_1 and F_2) during field work, but we located several individuals in jack pine plantations (similar to W_2 and parts of W_1) incidentally and during the radio-telemetry studies (Hughes, pers. obs). Anecdotally, the red pine plantations were noticeably drier than the jack pine plantations, with less understory or mossy ground cover; this includes areas that had not been harvested. Further studies on the thermal and physical characteristics of different forest conditions would be instructive in providing operational guidance on the maintenance and/or enhancement of wood turtle habitat. Investigations on suitable ranges of stocking density and canopy closure, thinning practices, vegetation species composition, and the maximal patch sizes of clearings, are a few research ideas that could better inform forest management planning and practices regarding wood turtle conservation.

The thermal landscape concept can be used to predict the thermal quality of wood turtle habitat; however, our prediction was not fully supported, as habitat thermal quality generally decreased with increasing thermal landscape roughness. Our results suggest that a smoother thermal landscape indicates higher thermal quality, seemingly contradicting Dubois et al. (2009)'s conclusion that heterogeneous habitats are of higher quality for wood turtles. This can potentially be reconciled by considering the different scales at which our

studies investigated habitat. According to Dubois et al. (2009), heterogeneity improves habitat quality at the home range scale, but wood turtles in the Sudbury District have home ranges of ~60 ha (Greaves, 2007); our arrays covered less than 2 ha. As such, it is possible that at the smaller habitat patch scale that we were measuring, a smoother thermal landscape indicates higher quality. The model with the highest predictive utility included mean temperature, thermal landscape relief, and diel period (Table 1). For the two measures of T_{set} that we used as standards of quality (General T_{set} and Metabolic T_{set}), mean temperature was the most predictive single variable within the model; for Usage, however, the most predictive variable was thermal landscape relief (Table 2). To draw an analogy with physical landscape topography, evaluations of habitat thermal quality must account for both landscape “relief” (structure) and “elevation” (mean temperature). Additionally, as the thermal landscape is highly dynamic over short periods of time, the habitat thermal quality varies with time of day; this may force wood turtles to shift micro-habitats as the thermal quality of the available habitat increases and decreases over the course of the day.

5. Conclusions

Resource extraction has thermal impacts and consequences for wood turtle habitat, both in absolute terms (temperature, thermal landscape) and in terms of habitat thermal quality. Our first and second predictions were supported: temperatures and thermal landscape relief differed among the undisturbed sites and the impact sites, and the undisturbed sites differed from impact sites in thermal quality. In addition, the undisturbed sites were typically cooler and less variable than the impact sites, and showed greater similarity to the temperatures used by wood turtles in the wild. The impact sites also showed higher frequencies of temperatures optimal to wood turtle biology, but two of the sites reached temperatures that could be injurious to the turtles. This creates a complex picture of the effects of resource extraction on wood turtle habitat. Wood turtle populations in northern Ontario and Quebec have been studied intensively for their thermally-limiting environments, and the consequences of limited thermal resources on habitat selection (Dubois et al., 2009), nesting (Walde et al., 2007; Hughes et al., 2009), overwintering (Greaves and Litzgus, 2007), and energetics (Dubois et al., 2008). These studies highlight the importance of environmental thermal properties to the viability of the species in the north, and its potentially precarious situation as global climate continues to destabilize (IPCC, 2014). Our study shows the potential hazards of human tampering with wood turtle habitat, but also the potential benefits of a conscientious resource extraction plan that could increase habitat thermal quality for the species. These benefits and hazards should be taken into consideration, along with all of the other issues faced by the species that are contributing to its decline (COSEWIC, 2007), when deciding management policies and best practices.

Our study attempted to determine the effects of resource extraction on thermal properties of terrestrial habitats, but because of logistical constraints, our replicates for each treatment were not perfectly similar, and use of sites by wood turtles was not confirmed in all cases. Future studies should seek to map the thermal landscapes of replicated undisturbed and impact types that we were unable to sample, such as agricultural fields, clear-cut forestry sites, and more-recently active aggregate pits with less early-successional vegetation, and should confirm habitat use by turtles at all sites. Larger arrays of thermal models would also allow for more extensive and representative thermal landscape mapping; our arrays (1.8 ha) were smaller than the mean home range of adult wood turtles in our study population (~60 ha; Greaves, 2007). We showed that the thermal landscape concept can be used as a predictor of habitat thermal quality, and could serve as a new tool in assessing general habitat quality for terrestrial ectothermic species. Future studies should experiment with different array sizes and resolutions, to determine the most optimal and efficient mapping

techniques, and in exploring additional environmental variables that could affect thermal habitat quality.

Author contributions

GNH and JDL conceived the ideas; GNH performed the experiment, collected and analysed the data; GNH and JDL interpreted the data analyses and drafted the manuscript. Both authors approved the final version of the manuscript.

Declarations of interest

The authors declare no conflicts of interest.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.jtherbio.2019.07.031>.

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