

Navigating the Thermal Landscape: Thermo-Spatial Ecology of Wood Turtles (*Glyptemys insculpta*) in the North

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ABSTRACT

Thermal ecology studies of ectotherms, like turtles, have typically focused on a species' thermal preferences and tolerances, or on thermoregulation site selections; only recently have landscape-scale thermal ecology studies been performed. I examined the spatial and nesting ecology of wood turtles in Sudbury District of Ontario, Canada, in a thermal context. I also measured the thermal impacts of natural resource extraction on wood turtle habitat. Wood turtles (*Glyptemys insculpta*) cover a wide variety of terrestrial and aquatic habitats during their annual cycle, making them ideal for thermo-spatial studies. I tracked movements and thermal use of 15 radio-tagged adult turtles during the active season, comparing their selections to temperature monitoring stations spread in an array across the study area, to determine if the turtles are navigating a thermal landscape. Temperature had minimal influence on home range-scale movements, but possibly influenced movements at a smaller spatial scale. I compared the thermal landscape (using thermal imagery), soil moisture, and grain size distribution of 3 nesting beaches to determine the strongest predictor of nest-searching behaviour. Temperature range appeared to be an important cue, but females were apparently using a suite of cues to select their nest sites. I mapped the thermal landscapes of six sites: two relatively undisturbed wood turtle habitat sites, two recently-harvested forestry sites, and two active gravel pits, to find the effects of resource harvesting on wood turtle habitat. The undisturbed sites were cooler and less variable than the disturbed sites, and provided higher-quality thermal habitat. My results support the findings of previous studies: that temperature is a stronger driver of turtle behaviour at the micro-habitat scale than the home range scale, and that soil temperature co-varies with soil structural variables at the micro-habitat scale. The data from the habitat mapping provide useful information for conservation efforts when mitigating or rehabilitating wood turtle habitat.

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"Though we abuse and exploit them, we remain irresistibly drawn to our fellow creatures... But our best hope lies in the education of a new generation, and a growing reverence for life in all its forms. Let us celebrate our kinship with all the wild things, and spare ourselves the unbearable loneliness of their vanishing."

-Richard Kiley (1995)

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GENERAL INTRODUCTION

THE THERMAL LANDSCAPE

When considering an animal species' resource requirements, research often focuses on the material needs of the species, such as food, water, and oxygen (Ayres *et al.*, 2010; Ganesh *et al.*, 2010; Wheatley *et al.*, 2012). Animals must navigate the landscape of their home ranges in order to acquire these resources; this landscape varies spatially and temporally, and animals must alter their behaviour to accommodate these changes in order to survive (Berthold, 1988). Endotherms have high material resource requirements, as they generate body heat metabolically; in contrast, ectotherms have comparatively low material resource needs (metabolic rates can be up to 20 times lower than an endotherm's), but they must thermoregulate behaviourally, which an endotherm only needs to do in extreme conditions (Cowles and Bogart, 1944; Gordon, 1985; Nagy, 2005; Nelson *et al.*, 1984). Ectotherms are not wholly at the mercy of their environments; variations in blood-flow, posture, and colour allow individuals to better exploit their thermal environments (Nelson *et al.*, 1984). Some species can raise or maintain their body temperatures in other ways: for example, some python species will shiver while brooding their eggs, generating heat with their musculature (Harlow and Grigg, 1984), while leatherback sea turtles (*Dermochelys coriacea*) can use their sheer mass to retain heat generated from their activity, in a process known as thermal kinesis (Frair *et al.*, 1972). Tattersall *et al.*, 2004 have even shown metabolically-generated body heat in digesting rattlesnakes. Nonetheless, the majority of an ectotherm's body heat comes from its environment.

Environmental temperatures affect an ectotherm's ability to metabolize (Greenwald and Kanter, 1979), move (Stevenson *et al.*, 1985), and grow (Arnold and Peterson, 1989). This makes ectotherms, such as turtles, dependent on 'thermal resources': sites where they may bask to

gain body heat, and utilize shelter to retain body heat in cool conditions or to cool off in hot conditions. As these thermal resources are scattered across the landscape, ectotherms must shuttle from site to site to maintain their preferred body temperatures as much as possible (Berk and Heath, 1975); this requirement creates a conceptual 'thermal landscape', which an ectotherm must navigate to acquire these thermal resources in the same way that they navigate the physical landscape to acquire food or water. The thermal landscape has been studied extensively in urban engineering (Song *et al.*, 2014) and urban ecosystems, such as the interrelation of temperature and green spaces (Gang and Dong-sheng, 2012; Xie *et al.*, 2013), air pollution (Weng and Yang, 2006), and climate change (Sears *et al.*, 2011), but it has been less well-studied with respect to habitat and thermal resource selection by animals despite its clear importance for the fitness of ectotherms. The thermal landscape has been examined for insects (McGeoch and Samways, 1991), and more recently in fish (Schultz *et al.*, 2016), and snakes (Harvey, 2015) but has not been studied in relation to habitat and resource selection by turtles.

As reptiles must behaviourally thermoregulate (Nelson *et al.*, 1984), I posited that this thermal landscape is at least as important a governor of reptile behaviour as the more tangible characteristics of the landscape. The objective of my study was to explore this position, to determine whether the thermal landscape is a useful concept in spatial ecology. To do this, I studied wood turtle (*Glyptemys insculpta*) behaviour near the northern limit of the species' range in Ontario, Canada, where optimal temperature selection is putatively the most critical factor for survival (Greaves and Litzgus, 2008; Dubois *et al.*, 2009). The study describes different aspects of the thermal landscape and its effect on reptile behaviour: 1) a macro-habitat study that explores how the thermal landscape concept can be used to predict turtle spatial selection within a home range, 2) a micro-habitat study that explores how the thermal landscape concept can be

used to predict nest-site selection by female turtles, and 3) a study on the thermal consequences of natural resource extraction on turtle habitat.

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). In Canada, the species is found in spatially-disjunct populations in Ontario, Quebec, New Brunswick, and Nova Scotia (COSEWIC 2007). It has one congener, the bog turtle (*G. muhlenbergii*) of the eastern United States, and no recognized subspecies. The wood turtle was once included in the genus *Clemmys*, along with the spotted turtle (*C. guttata*) and the Pacific pond turtle (*C. marmorata*, now *Actinemys marmorata*), but Holman and Fritz (2001) placed the wood turtle and bog turtle in their own genus. The wood turtle is a medium-sized species (adults 1 kg to 1.5 kg in mass), with a highly-sculpted brown carapace that has the appearance of rough wood or tree bark; the plastron is yellow with regular black blotches. The head, tail, and feet are brown or black, while the skin on the legs, neck, throat, and in the leg sockets is red, orange, or yellow; colour varies across the species' range and possibly seasonally (Harding and Bloomer, 1979). Males are generally larger than females, and can be distinguished visually by their longer and thicker tails, broader heads, and concave plastrons (Harding and Bloomer, 1979). Individuals from northern populations tend to be larger than those from southern populations, and individuals from central populations are smaller than those on the range extremes (Greaves and Litzgus, 2009).

I chose the wood turtle as a model ectothermic species to study the effect of the thermal landscape on reptile behaviour in the north. Turtles in general make excellent model organisms for ecology studies; adult turtles are long-lived and protected by their bony shells, which reduces

the likelihood of losing study animals to old age or predation. I was also able to attach monitoring equipment to my study animals (i.e., radio transmitters and temperature data loggers glued to the carapace surface) in a far less invasive manner than similar studies would require for members of other reptile taxa (e.g., surgical implantation of radio transmitters into snakes). Wood turtles are semi-aquatic, and frequently move between aquatic and terrestrial habitats in the active season (Harding and Bloomer, 1979). Wood turtles, especially females, are noted to spend long periods of time in the forest and away from their home river (Ernst, 1968; Arvisais et al., 2002; Tuttle and Carroll, 2003; Greaves, 2007).

Ontario has eight species of turtle, seven of which are listed as Species at Risk by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC; www.cosewic.gc.ca/eng/sct1/index_e.cfm) and by the Committee on the Status of Species at Risk in Ontario (COSSARO; ontario.ca/environment-and-energy/species-risk-ontario-list). Habitat loss, road mortality, and illegal collection for food or the pet trade are primary threats faced by the taxon; subsidized predators such as red foxes (*Vulpes vulpes*), raccoons (*Procyon lotor*), and striped skunks (*Mephitis mephitis*) are also a concern (Klemens, 2000). Wood turtles are declining throughout their range (Arvisais et al., 2002; Daigle and Jutras, 2005; Walde et al., 2007; van Dijk and Harding, 2013), and Ontario is no exception. The species is listed as Endangered in Ontario (OMNRF, 2010) and as Threatened federally (COSEWIC, 2007). Habitat loss and degradation are concerns throughout much of the species' range; in southern Ontario, the loss is primarily due to agriculture and human development (Tessier et al., 2003; Saumure et al., 2007), whereas further north the loss is due to natural resource extraction from forestry and aggregates (Arvisais et al., 2002, 2004). Wood turtles are also especially vulnerable to collection for the pet trade; they remain relatively small (16 - 23 cm carapace length as adults),

and are typically gentle and inquisitive, making them engaging pets (Harding and Bloomer, 1979; Brooks *et al.*, 1992; Levell, 2000). Due to this vulnerability, every effort will be made to keep the location of the study site confidential.

STUDY AREA

The study site is located within the Sudbury District in Northeastern Ontario; it is a confluence of two shallow rivers, both of which are utilized by wood turtles (Greaves, 2007). The primary river (hereafter referred to as the 'River' to protect the population's location) is sandy-bottomed and meandering, in which the local wood turtles overwinter (Greaves and Litzgus, 2007; Greaves and Litzgus, 2008), and nest on its high, sandy beaches (Hughes *et al.*, 2009). The secondary river (hereafter referred to as the 'Tributary') is gravel- and cobble-bottomed and has a braided channel pattern; the Tributary is utilized by some wood turtles in summer but they are not known to overwinter or nest there (Greaves and Litzgus, 2008). Both rivers are clear, cold, and fast-running, which are considered key habitat features for wood turtles (Harding and Bloomer, 1979; Ultsch, 2006). Oxbow lakes and ephemeral pools are common along the River in spring, but most are partially or completely dry by mid-summer. Human habitation is prevalent both upriver and downriver of the study site, but there is little human inhabitation at the site. Human recreational activity in the area is generally limited to fishing in the Tributary or ATV-ing along old logging roads.

The surrounding terrestrial habitat is a mix of natural forest (characteristic of the Great Lakes St. Lawrence Lowlands/Boreal Forest intergrade) and artificial plantation, all based on sand and gravel moraine soils. Common tree species include trembling aspen (*Populus tremuloides*), white birch (*Betula papyrifera*), white spruce (*Picea glauca*), eastern white cedar

(*Thuja occidentalis*), and balsam fir (*Abies balsamea*). Red pine (*Pinus resinosa*) and jack pine (*Pinus banksiana*) occur both naturally and in artificial plantations. A series of shallow wetlands are located north of the River, which the wood turtles sometimes use in spring and summer; alder (*Alnus* spp.), beaked hazel (*Corylus cornuta*), willow (*Salix* spp.), and ash (*Fraxinus* spp.) are common shrub and tree species along the edges of the wetlands and the riverbanks. The southern bank of the River intersects a ridge line of rocky cliffs, which limits the movements of turtles south of the River.

This study site gives a wide selection of the habitats chosen by wood turtles near the northern limit of their range, allowing for a broad sampling of the thermal and physical landscapes that wood turtles may encounter.

PROJECT OVERVIEW

The purpose of this M.Sc. project was to study the thermal landscape as it relates to reptile spatial ecology and conservation. The wide variety of habitats that wood turtles use makes them an ideal study species for my project. By studying turtle movements, habitat selection, and nest-site selection in terms of temperature, I was able to map the thermal landscape of the study site, investigate the wood turtles' use of it, and compare that use to their use of the non-thermal components of the landscape, such as soil composition. In addition, I examined the thermal landscape of harvested forestry and pit aggregate sites near the primary study site to determine the thermal effects of resource extraction on wood turtle habitat. The objectives of the study were to: 1) describe large-scale wood turtle movements and determine the effect of thermal landscape on said movements, 2) describe wood turtle nest-site selection and determine the thermal or non-thermal cues that best predict said selection, and 3) determine the

thermal effects and consequences of natural resource extraction on wood turtle habitat. I predicted that the thermal landscape will be a useful predictor of wood turtle movements at the home range scale, of wood turtle nest-site selection, and provide a useful way to describe the effects of resource extraction on wood turtle habitat. These studies can provide insight into the spatial ecology of an Endangered species of turtle, and provide conservation initiatives with new tools to identify and map the general and key habitats of wood turtles.

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CHAPTER 1

The thermal landscape as a predictor of wood turtle (*Glyptemys insculpta*) movements at the home range scale

ABSTRACT

Northern turtles have limited thermal resources during certain times of the year, which may force them to navigate a thermal landscape to acquire the thermal resources required for activity. I examined wood turtle spatial selection at the home range scale to determine if and how much temperature influences this selection. I radio-tracked wood turtles (*Glyptemys insculpta*, n = 15) through their home ranges in the active season of 2015 in the Sudbury District of Ontario and measured the temperatures used by them. I deployed an array of thermal models (n = 48) to record temperatures around the study site. I examined the turtle's carapace temperature and thermoregulation efficiency (D_b), and compared them to the temperatures in their available surroundings at the home range scale, recorded by the thermal models. Wood turtles did not show strong thermal landscape navigation at the home range scale. Some evidence emerged that wood turtles do navigate a thermal landscape at a smaller habitat scale. These findings corroborate the findings of previous authors.

INTRODUCTION

In regions that experience long, harsh winters, turtles are forced into inactivity for as much as eight months of the year (Ultsch, 1989; Greaves and Litzgus, 2007, 2008); this makes the short summers especially important, as it is only during this time that turtles can feed, grow, and reproduce (Dubois *et al.*, 2009). As ectotherms, turtles must acquire sufficient thermal resources before they can begin to disperse from their overwintering sites to forage, digest, and mate. All of these vital activities must be performed in a four to six-month period before dropping temperatures force them back into their overwintering sites (Ultsch, 1989). Wood turtles (*Glyptemys insculpta*) have larger home ranges and make longer daily forays than other semi-aquatic Emydid species like bog turtles (*Glyptemys muhlenbergii*), spotted turtles

(*Clemmys guttata*) and Eastern box turtles (*Terrapene carolina*), which are known to have small home ranges, short daily movements, and periods of inactivity in summer (Strang, 1983; Ernst, 1986; Litzgus and Brooks, 2000; Arvisais *et al.*, 2002; Rasmussen and Litzgus, 2010). Wood turtles also tend toward larger home range sizes in the northern parts of the species' range due to the relatively lower productivity of the habitat (Smith, 2000; Greaves, 2007; Curtis and Vila, 2015). Previous studies on habitat selection by wood turtles have noted purposeful selection in their habitat choices. Compton *et al.* (2002) studied movements with respect to distances to water, canopy cover, and nearby food sources, and found that wood turtles split their time between foraging in forested environments and basking in open areas. Dubois *et al.* (2009) measured temperature directly and found that wood turtles prefer open habitat to bask, and use aquatic habitats as thermal refuges at night or in cool weather, a finding corroborated by Greaves (2007) for my study population in the Sudbury District. The findings of these authors suggest that wood turtles are capable of recognizing thermal resources, and exploiting their distribution across the landscape of their home ranges.

For wood turtles in the Sudbury District, spring emergence consists of moving from their overwintering sites in the River to the slightly warmer ephemeral pools, oxbow lakes, and wetlands adjacent to the River (Greaves, 2007; pers. obs.). Throughout the summer, wood turtles move around their nominal home ranges; males tend to remain near the River and Tributary while females often venture further afield into the surrounding upland forests (Greaves, 2007). Females also conduct long, energy-costly forays in the nesting season to lay their eggs (Walde *et al.*, 2007; Greaves, 2007; Hughes *et al.*, 2009). As autumn approaches, wood turtles retreat to the River and congregate in deeper pools, where they remain until spring (Greaves and Litzgus, 2008). I posit that this pattern of behaviour is highly dependent on the

ambient temperatures of the habitat, and that temperature will be predictive of wood turtle spatial selection.

Previous studies on the thermal aspects of reptile spatial selection focused on the micro-habitat (Reagan, 1974; Dubois *et al.*, 2008; Schofield *et al.*, 2008). The purpose of my study was to quantify spatial selection by wood turtles in the Sudbury District at the home range scale, with particular emphasis on how environmental thermal characteristics affect this selection. As the Sudbury District population is near the northern range limit of the wood turtle (Ernst and Lovich, 2009), temperature is a highly important factor to the species' ecology (Greaves, 2007; Dubois *et al.*, 2009). I mapped the thermal landscape of the ~125 ha of my study site, and radio-tracked wood turtles through their home ranges during the active season of 2015. I hypothesized that wood turtle spatial selection is driven by temperature, and that wood turtles navigate a thermal landscape at the home range scale. I predicted that, if wood turtles navigate a thermal landscape, then thermal habitat quality would generally decrease with distance from the wood turtle (Fig. 1.1); although there presumably is a limit to the turtle's ability to detect land surface temperatures as distance increases.

METHODS

Radiotelemetry - I radio-tracked wood turtles (n = 15, 9 females and 6 males) at my study site during the active season of 2015 (1 May to 30 September). When I captured a wood turtle that I wished to add to the study group, I attached a radio transmitter (R1850 or R1920 models, Advanced Telemetry Systems, Isanti, MN, USA) to its carapace using PC-7 paste epoxy and PC-Marine putty epoxy (Protective Coating Company, Allentown, PA, USA). Each turtle was tracked 2 to 3 times per week over the course of the study season using an ATS receiver Model R410 and 3-element Yagi antenna (Advanced Telemetry Systems, Isanti, MN, USA). I tracked

wood turtles that moved outside of the study area less frequently, only to ensure that I knew when they returned to the study site. Each time a turtle was radio-located, I recorded date and time, GPS location (Universal Transverse Mercator, NAD83) with a Garmin GPSMap 64 series handheld GPS receiver (Garmin, Schaffhausen, Switzerland), along with habitat type and behaviour.

Thermal Data Collection - I attached iButton dataloggers (DS1922L or DS1921G - Maxim Integrated, San Jose, CA, USA) to each wood turtle in the study group; these dataloggers recorded carapace temperature every 2 hours. Grayson and Dorcas (2004) found that carapace temperature predicted body temperature (T_b) in painted turtles (*Chrysemys picta*), and Pittman and Dorcas (2009) assumed that this held true for bog turtles (*Glyptemys muhlenbergii*) which are smaller than painted turtles; Brown (1992) found a similar relationship between body and carapace temperatures in snapping turtles (*Chelydra serpentina*), and as wood turtles are smaller than snapping turtles, I made the same assumption as Pittman and Dorcas (2009). I coated all dataloggers in General Electric Premium Waterproof silicone caulking (General Electric, Fairfield, CT, USA) for waterproofing and secured them to the wood turtles' carapaces with PC-7 and PC-Marine epoxy; waterproofing of dataloggers does not impact temperature readings (Roznik and Alford, 2012; Riley *et al.*, 2014).

Thermal Landscape Mapping - To map the thermal landscape of the study site, I built an array of temperature monitoring stations across the site; all stations were in place by 11 May 2015. The monitoring stations ($n = 48$) were distributed across the study site in a systematic 8 x 6, 300 m x 100 m grid pattern totalling 2100 m x 500 m in size (Fig. 1.2). Additionally, I placed monitoring

stations (adapted for underwater operation) within the River ($n = 1$) and the Tributary ($n = 1$). Each station consisted of a thermal model, constructed to simulate the thermal profile of an adult wood turtle (adapted from Yagi and Litzgus, 2013); I constructed them from plastic food containers (30 cm long x 18 cm wide x 5 cm tall; volume of 1390 mL) filled with water balloons (totalling ~1 kg of water) contained in a mesh bag to simulate turtle organs and mesentery (Fig. 1.2). I spray-painted the 'dorsal' surface of the container brown to simulate a wood turtle's carapace colouration. If the model was placed underwater, I secured it to a cinderblock to hold it in place. To measure operative environmental temperature (T_e), I coated an iButton datalogger in silicone caulking for waterproofing and secured it to the top of the thermal model with marine epoxy; these dataloggers recorded the model's "carapace" temperature every 2 hours. I collected the dataloggers from the thermal models in late June and returned them to the field in early July (maximum of 6 days with no monitoring coverage), to minimize data loss due to potential equipment failure. Another retrieval was planned for mid-August, but I decided a visual inspection of the wood turtles and thermal models was sufficient. I retrieved all data loggers and thermal models from the field by 10 October 2015.

Prior to the commencement of the 2015 field season, I validated the effectiveness of the thermal models by comparing their thermal profiles under controlled conditions (indoors, in a temperature-controlled room) with those of captive wood turtles supplied by Scales Nature Park in Orillia, Ontario. I placed captive wood turtles ($n = 2$, both adult females) in large plastic tubs with iButton dataloggers duct-taped to their carapaces; I provided each wood turtle with a dish of water for the duration of the test. I placed thermal models ($n = 2$) in identical tubs with iButtons duct-taped to their 'dorsal' surfaces, with water dishes in the tubs in case the water acted as a heat sink. The containers with wood turtles and thermal models were placed in an alternating row

and the iButtons recorded temperature once per hour for 24 hours. I also placed an iButton nearby to monitor air temperature. At the end of the test, I returned the wood turtles to their enclosures. I compared the temperatures recorded among the turtles and models using an ANOVA followed by a post-hoc Tukey's Honest Significant Difference test; I used the Bonferroni correction for multiple comparisons ($\alpha = 0.005$).

Analyses - I divided all temperature readings into 6-hour diel periods, and calculated the mean temperature from all temperature readings within each diel period to compensate for asynchronous readings and stochastic thermal events. Means for each diel period were used in statistical analyses. The diel periods were: early morning (00h to 06h), late morning (06h to 12h), afternoon (12h to 18h), and evening (18h to 24 h). Due to the nature of field work, all turtle location track points used in the analysis were either in the late morning or afternoon.

I randomly selected 4 male and 4 female wood turtles from the study group for analysis. Greaves (2007) reported that the mean home range size of adult wood turtles in this population was 59.2 ha (MCP), so for each wood turtle track point I created a circular zone with a 300 m radius (covering ~50% of the mean home range) for analysis. I identified all thermal models within this zone for each turtle track point for comparison to the turtle's carapace temperature. I calculated the mean diel temperature (concurrent with the track point) from each of these thermal models and derived habitat thermal quality (D_e) from them by measuring the absolute deviation from the wood turtle's preferred temperature range (T_{set} ; Hertz *et al.*, 1993); a higher D_e indicates a lower-quality thermal environment. Dubois *et al.*, 2009 calculated T_{set} for a Quebec population of wood turtles at a similar latitude to my study population, so I used their calculated T_{set} value for my analyses (30°C). I measured distance between the thermal models and track points using

Pythagorean Theorem with the GPS points. If the River or Tributary fell within 300 m of the track point, I measured distance using the 'ruler' tool in Google Earth (Google Inc., 2015) between the turtle and the nearest point on the water body. I performed a linear regression between distance (independent variable) and D_e (dependent variable) for each model within range of each wood turtle track point; I performed multiple tests at different maximum ranges, from 300 m to 10 m. If D_e and distance showed a positive slope, I considered my prediction supported, as this would show that habitat thermal quality is higher at closer ranges to the wood turtle.

I also constructed a series of linear models to determine what drives wood turtle thermoregulation efficiency (D_b , the deviation of T_b from T_{set} ; Hertz *et al.*, 1993); as with D_e , a higher D_b indicates lower thermoregulation efficiency. These linear models included the variables distance between the thermal model and turtle track point ('d'), habitat thermal quality (' D_e '), day and diel period of the turtle track point (e.g. 1 May - early morning = 1, 1 May late morning = 2; 'diel'), individual wood turtle ('turt'), and the individual thermal model ('loc'). I performed model selection using Akaike's Information Criterion (AIC) to determine which of these linear models best predicted D_b .

All statistical analyses were performed with R (R version 3.1.2; R Core Team 2013).

RESULTS

Thermal Model Validation - The thermal model temperature readings (Table 1.1) did not differ from those of captive wood turtles in the early morning ($F_{(4, 25)} = 1.61$, $p = 0.20$) and evening ($F_{(4, 25)} = 1.34$, $p = 0.28$), but differed in the late morning ($F_{(4, 25)} = 13.69$, $p < 0.01$) and afternoon ($F_{(4, 25)} = 5.78$, $p < 0.01$). Post-hoc analysis showed that one wood turtle was significantly cooler

than air temperature and both thermal models ($p < 0.001$ in all cases) in the late mornings; the afternoon period showed no differences after the Bonferroni correction.

The wood turtle that had cooler T_b than the thermal models knocked over her water dish during testing, which may have reduced her body temperature via evaporative cooling. The other wood turtle did not knock over her water dish, and her T_b did not differ from that of air or the models in all time periods. Thus, I concluded that the thermal models sufficiently mimicked the thermal profile of an adult wood turtle, and proceeded accordingly.

Thermal Landscape Navigation - Wood turtles in the Sudbury District did not strongly select their locations based on temperature at the home range scale. At a 300 m radius around the wood turtle track point, distance from the turtle explained less than 1% of the variance in D_e (Table 1.2). I also tested the relationship between D_e and distance at varying maximum ranges and found that a 50 m radius had the greatest explanatory power, although only 9% of the variation in D_e was explained by distance at that maximum radius (Table 1.2; Fig. 1.4).

Akaike's Information Criterion selected one model out of nine possibilities to explain D_b of wood turtles in the Sudbury District. The model which showed the relationship between D_e and distance, and accounted for the interaction of individual wood turtle with those variables, showed the strongest predictive utility for D_b ($R^2 = 0.46$; Table 1.3).

DISCUSSION

Wood turtles in the Sudbury district do not appear to navigate a thermal landscape at the home range scale; my findings (Fig. 1.3) did not match my predictions (Fig. 1.1). Although distance between wood turtle track points and thermal models provided some explanatory power

for D_e , the explanatory value was weak at all maximum distances tested ($R^2 < 10\%$; Table 1.2). I interpret this to mean that wood turtles are able to largely ignore ambient temperatures in large-scale spatial selection, and that engaging in periodic basking is sufficient to give them the thermal resources required to engage in their daily activities. This is supported by Compton *et al.*, (2002), whose findings showed that large-scale movements in wood turtles were largely driven by foraging needs, with smaller-scale spatial selection more focused on thermoregulation. As the greatest support for thermal landscape navigation was within 50 m of the wood turtle (Table 1.2), I would suggest that my findings show weak support for Compton *et al.*, (2002)'s hypothesis. Other literature supports this conclusion for other chelonian species. Reagan (1974) found that three-toed box turtles (*Terrapene carolina triunguis*) selected habitat most strongly for temperature, but this was for a very specific behaviour (form digging) that was strongly tied to micro-habitat. Pittman and Dorcas (2009) showed that bog turtle thermoregulation was tied to the microhabitat, particularly mud temperature and depth, while burrow microhabitat was extremely important to desert tortoises (*Gopherus agassizii*; Zimmerman *et al.*, 1994). Wood turtles show different activity patterns in the active season (larger home ranges, less frequent basking events, no aestivation periods, etc.) than Eastern box turtles, bog turtles, and spotted turtles (Strang, 1983; Ernst, 1986; Rasmussen and Litzgus, 2010); Ernst (1986) posited that this was due to the wood turtle's greater body sizes, which may grant them greater resistance to extreme temperature. Wood turtles also have larger home ranges and more daily activity than desert tortoises, despite having smaller body sizes (O'Connor *et al.*, 1994; Zimmerman *et al.*, 1994), likely a result of the extreme temperatures and low productivity of the tortoise habitat. Despite these differences, wood turtles appear to show the same pattern of thermal utilization as these chelonian species.

The single predictor variable that provided the greatest explanatory power for D_b was D_e , while distance had no significant effect on its own (Table 1.3). If D_e and D_b vary together, regardless of distance, it would suggest that a wood turtle's T_b is largely dependent on daily ambient temperatures, and that the turtle is thermoconforming to its surroundings. The linear model that best explained D_b incorporated the D_e and distance, and also considered the individual wood turtle (Table 1.2); this supports the idea that ectotherms can take action to regulate their T_b by exploiting their micro-habitats (Dubois *et al.*, 2009), but distance's low utility as a covariate suggests that the thermal landscape concept does not strongly affect D_b at the home range scale. Curtis and Vila (2015) found that wood turtle T_b in terrestrial habitats was always within 8°C of air temperature, and wood turtle T_b in aquatic habitats as always within 5°C of water temperature; this pattern of non-random body temperature is also widely known from other reptile studies. Schofield *et al.* (2008) showed that loggerhead sea turtles (*Caretta caretta*) in Greece had non-random temperature selection, a difference that became less distinct as the field season progressed and ambient sea temperatures warmed; the sea turtles used warm surface water patches to keep their T_b above ambient water temperatures. The lizard *Psammodromus algirus* showed that T_b was predictive of when the animal was basking in the open vs. in shade, from the correlations between body, air, and ground temperatures (Carrascal and Diaz, 1989). Milksnakes (*Lampropeltis triangulum*) in Ontario and Western rattlesnakes (*Crotalus oreganus*) in British Columbia showed non-random habitat selection, which was heavily temperature-based (Row and Blouin-Demers, 2006; Harvey, 2015).

In conclusion, my findings suggest that temperature is more important to wood turtle spatial selection at a smaller habitat scale than the home range; they must use the thermal resources around them to survive, but appear to do so by exploiting their micro-habitat.

Compton *et al.*, (2002) suggested that the common description of wood turtles as an edge species (Kaufmann, 1992) allows them to bask in open habitat, before moving into cooler, forested habitat to forage. Future studies that seek to explore the thermal landscape concept with wood turtles or other species would be better served to focus on the micro-habitat scale. However, my methods for measuring the thermal landscape may have limited the effectiveness of data collection; Row and Blouin-Demers (2006) and Harvey (2015) showed thermal influence in snake spatial selection at the home range scale, and their methods differed from mine. The array of thermal models may have been too coarse to adequately measure the thermal landscape in a biologically-significant way, and if future studies pursue this line of research, I would recommend using a finer-resolution grid (no more than 20 m between models), perhaps with a staggered or offset grid pattern for superior coverage of the landscape. Dubois *et al.* (2009) also used an unusual criterion for T_{set} (digestion temperature), which provides a preferred temperature considerably higher than those of other Emydid species studied using the methods devised by Hertz *et al.* (1993), such as for spotted turtles (20°C to 26°C; Yagi and Litzgus, 2013). Future studies should perform a standard thermal gradient study on wood turtles to better estimate T_{set} .

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CHAPTER 1 TABLES

TABLE 1.1 - Mean environmental temperatures (\pm standard deviation) measured to test the validity of thermal models for comparison to the thermal profile of adult wood turtles (*Glyptemys insculpta*) prior to the 2015 field season. 'Turtle 1' and 'Turtle 2' were captive adult females supplied by Scales Nature Park (Orillia, ON), 'Model 1' and 'Model 2' were thermal models compared to the wood turtles, and 'Air' was air temperature. Temperatures were divided into four six-hour diel periods. Superscript letters represent post-hoc groupings ($\alpha = 0.005$).

Treatment	Mass (g)	Early Morning (°C)	Late Morning (°C)	Afternoon (°C)	Evening (°C)
Turtle 1	739	^A 25.4 \pm 0.4	22.8 \pm 0.5	^A 23.2 \pm 0.9	^A 22.8 \pm 1.0
Turtle 2	780	^A 24.6 \pm 0.4	^A 23.5 \pm 0.3	^A 23.3 \pm 1.1	^A 23.3 \pm 0.7
Model 1	1053	^A 25.1 \pm 0.1	^A 23.9 \pm 0.2	^A 24.8 \pm 0.5	^A 23.8 \pm 1.0
Model 2	993	^A 24.8 \pm 0.4	^A 23.9 \pm 0.2	^A 24.5 \pm 0.5	^A 23.7 \pm 0.6
Air	---	^A 24.8 \pm 0.4	^A 23.9 \pm 0.2	^A 24.5 \pm 0.1	^A 23.7 \pm 0.6

TABLE 1.2 - Regression results for habitat thermal quality (D_e) of thermal models (independent variable) and distance between wood turtle (*Glyptemys insculpta*) track points and thermal models (dependent variable), in Sudbury, Ontario, in 2015.

Maximum Range (m)	R ²	F-value	df	p-value
300	<0.01	2.06	1, 719	0.15
250	<0.01	3.67	1, 552	0.06
200	0.02	7.50	1, 387	<0.01
150	0.04	11.90	1, 276	<0.01
100	0.05	8.83	1, 168	<0.01
50	0.09	10.58	1, 107	<0.01
25	0.01	0.09	1, 69	0.77
20	0.02	2.17	1, 62	0.15
15	0.01	0.28	1, 50	0.60
10	0.04	1.57	1, 37	0.22

TABLE 1.3 - Model selection results using Akaike's Information Criterion (AIC) to select the strongest model predicting wood turtle (*Glyptemys insculpta*) thermoregulation efficiency (D_b). Variable short forms are 'De' (habitat thermal quality), 'd' (distance between wood turtle track point and thermal model), 'diel' (diel period), 'loc' (individual thermal model), and 'turt' (individual wood turtle). The model with the most support is highlighted in grey.

Model	AIC (df)	ΔAIC	R²	F-value	df	p-value
De	3987 (03)	17	0.44	556.1	1, 719	<0.01
d	4399 (03)	429	<0.01	0.4	1, 719	0.52
diel	4374 (03)	404	0.03	26.2	1, 719	<0.01
loc	4417 (34)	447	0.02	1.38	32, 688	0.08
turt	4349 (09)	379	0.08	9.28	7, 713	<0.01
De + d	3989 (04)	19	0.44	277.8	2, 718	<0.01
(De + d) * diel	3990 (07)	20	0.44	112.1	5, 715	<0.01
(De + d) * loc	4009 (98)	39	0.48	8.0	96, 624	<0.01
(De + d) * turt	3970 (25)	0	0.46	28.1	23, 697	<0.01

CHAPTER 1 FIGURES

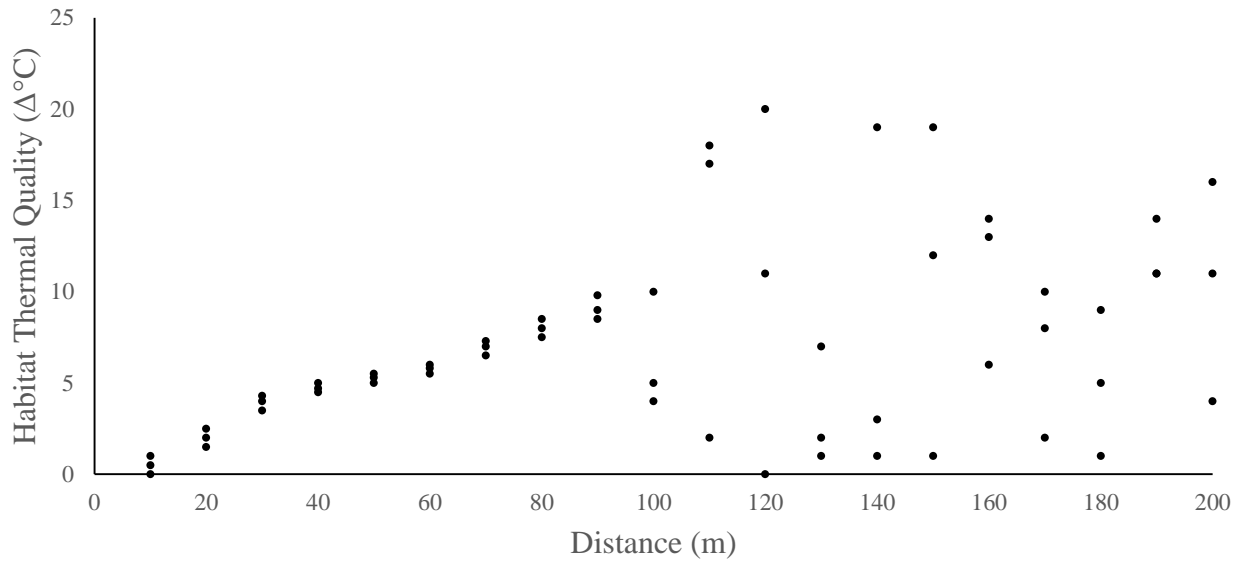


FIGURE 1.1 - Predicted relationship between distance from a wood turtle (*Glyptemys insculpta*) track point and a thermal model, and the habitat thermal quality (D_e) of the thermal model. This figure is constructed with dummy data to visually represent my prediction; this figure assumes that wood turtles can detect land surface temperatures up to 100 m away.



FIGURE 1.2 - Deployment map of thermal models to map the thermal landscape of a wood turtle (*Glyptemys insculpta*) population in the Sudbury District, ON, in 2015. Inset picture shows the appearance of a thermal model. The black line in the bottom right corner scales to 100 metres. Models 2.2, 3.1, and 4.2 were damaged or destroyed, making them irretrievable; they are thus absent from this map.

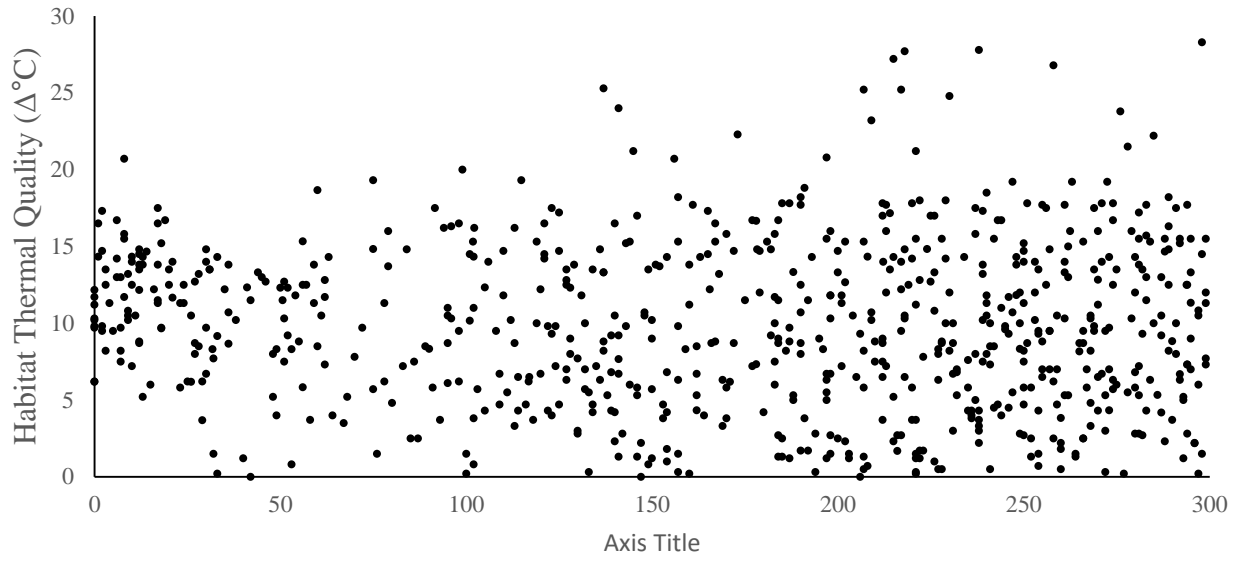


FIGURE 1.3 - Distance between wood turtle (*Glyptemys insculpta*) track points and thermal models, compared to habitat thermal quality (D_e) measured at that thermal model, in the Sudbury District, ON, in 2015. Compare to the predicted relationship displayed in Fig. 1.1.

CHAPTER 2

The thermal landscape as a predictor of wood turtle (*Glyptemys insculpta*) nest-site selection

ABSTRACT

Wood turtle (*Glyptemys insculpta*) females are noted for their intensive and extensive nest-searching activities, often spending days probing their nesting beaches before laying their eggs. Presumably, these behaviours are indicative of a highly-choosy nest-selection regime, the benefit of which is increased female fitness. I examined wood turtle nest-site selection to determine if and how much temperature drives this selection process (i.e. is temperature a strong cue in determining nest-site selection). I selected three known nesting beaches and collected thermal imagery, soil moisture content, and soil texture (grain size distribution), to determine the strongest driver of female attention to different areas of the beaches. Temperature range was generally the strongest predictor of female nest-searching attention, but soil moisture and mean temperature also showed varying degrees of importance. Wood turtle females either selected their nesting sites based on a mix of covarying environmental cues, or a single cue that my statistical models were not sensitive enough to distinguish. Thermal imagery did not prove to be a cost-effective method of thermal mapping nesting beaches; more traditional methods of nest surveying, such as looking for the distinctive wood turtle trackways, may be more useful and cost-effective than thermal imagery.

INTRODUCTION

For oviparous species with no parental care, such as turtles, nest-site selection represents the only point at which a mother may behaviourally invest in her offspring; a poor nest environment cannot be compensated for post-nesting, so females are motivated to select high-quality nest sites to increase their fitness (Shine and Harlow, 1996; Kolbe and Janzen, 2002; Kamel and Mrosovsky, 2005). The definition of a 'high-quality' nest environment changes for different chelonian taxa; most turtle species have temperature-based sex determination, and so

must target a range of temperatures that ensure a balanced sex ratio for their offspring (Ewert and Nelson, 1991). Wood turtles (*Glyptemys insculpta*) are genetically sex-determined (Ewert and Nelson, 1991), and are instead able to select nest conditions that maximize successful embryonic development (Compton, 1999; Hughes *et al.*, 2009). Previous studies on the Sudbury District wood turtle population determined that wood turtle females select nest sites for high-but-variable nest temperatures; nest temperatures were consistently higher than non-nests, except in the early mornings when nest temperatures dropped below those of non-nest sites (Hughes *et al.*, 2009). Lab studies have shown that variable nest temperatures speed development of wood turtle embryos (Compton, 1999), suggesting that wild wood turtle females are deliberately selecting for variable temperatures to increase their fitness (Hughes *et al.*, 2009).

For wood turtles in the Sudbury District, nesting season typically begins in late May and ends in early June (Greaves, 2007; Hughes *et al.*, 2009); wood turtles are not known to have multiple clutches in a given year (Powell, 1967). Wood turtle females often spend several days searching sandy beaches in the early mornings and late evenings (Harding and Bloomer, 1979; Walde *et al.*, 2007; Hughes *et al.*, 2009). They may begin digging at various locations, only to abandon the effort and continue searching (Hughes and Brooks, 2006), and will often appear to sniff, nuzzle, or lick the soil as they move (Harding and Bloomer, 1979). These behaviours suggest that wood turtle females are highly selective of their nest sites, and previous studies show that temperature plays a large role in their nest-site selection and embryonic development (Compton, 1999; Hughes *et al.*, 2009). Additionally, these nesting behaviours resemble those reported for several species of sea turtles, which use a mix of cues in their nest-site selection. For example, the loggerhead sea turtle (*Caretta caretta*) uses temperature variation to identify nesting sites (Stoneburner and Richardson, 1981), while green sea turtles (*Chelonia mydas*)

select based on sand texture (Mortimer, 1990). Elsewhere, wood turtles nest in agricultural fields, gravel pits, or artificial nesting mounds (Harding and Bloomer, 1979; Castellano *et al.*, 2008; Buhlmann and Osborn, 2011), but the Sudbury District population has sufficient natural nesting habitat so that the females can apparently afford to be more discriminatory.

The purpose of this project was to quantify nest-site selection by female wood turtles in the Sudbury District, with the intention of identifying the cues that females use to identify good nesting sites. By studying both the thermal and soil properties (moisture and grain size distribution, as in Hughes *et al.*, 2009) of known nesting beaches at the study site, and comparing them to the general thermal and soil selections made by nesting wood turtle females, I will determine whether wood turtles navigate a thermal landscape, and if this thermal landscape is more important in determining their behaviour than the non-thermal aspects of the landscape. I hypothesized that wood turtle nest-site selection is driven by temperature, and that wood turtles navigate a thermal landscape at the micro-habitat scale while nest-searching. Here I assume that female nest-searching attention is indicative of nest-site selection. I predict that, if wood turtles navigate a thermal landscape, then the thermal properties of a nesting beach will be a stronger predictor in nesting female attention than the non-thermal properties of a nesting beach. I also wanted to test the efficacy of thermal imagery as a surveying tool for wood turtle nesting beaches; if the thermal cameras could distinguish nesting areas from non-nesting areas, then I would consider them a useful tool for future studies.

METHODS

Site Selection - Based on previous studies on the Sudbury District wood turtle population (Greaves, 2007; Hughes *et al.*, 2009), I selected three beaches in 2016 along the River that wood

turtle females were known to nest on (labelled as M-beach, W-beach, and B-beach). I divided each of these nesting beaches into 2 m x 2 m grids with stake wire flags (Fig. 2.1), which conformed to the shape of the beaches; I gave each plot an identifying number (Fig. 2.2). I did not include heavily vegetated areas of the beaches, as females were not known to nest in these locations in previous studies (Hughes *et al.*, 2009). M-beach and W-beach were very similar in appearance, being north-facing beaches formed by the meandering of the River. Both had a slight slope, and were primarily sand with some gravel; M-beach had 44 plots, while W-beach had 54 plots (Fig. 2.2). B-beach was a steep, south-facing, sandy bluff close to the River, with a narrow vertical strip of open sand where the females nested (Fig. 2.1), and the rest covered in vegetation (primarily sweet fern, *Comptonia peregrina*); B-beach had 12 plots (Fig. 2.2).

Data Collection - To determine nesting preferences for the female wood turtles, I made daily observations of the number, direction, and density of trackways left in the soil of the beaches by nest-searching females. I categorized each plot into a usage class based on my observations of female attention: no use, low use (straight trackways, low-density of tracks, suggesting that the females were simply crossing the plot), and high use (high density of winding tracks or observed nest digging, suggesting that females found the plot favourable). My decisions about the final usage zones were partially subjective, based on observations of female usage over the entire nesting period. For example, a plot with a single straight trackway in the beginning of the nesting period that saw no activity later in the season would be considered a no use zone. Based on these observations, I combined contiguous clusters of plots with similar levels of female attention into 'usage zones', which served as my response variables for modelling.

To measure the thermal landscape of the nesting beaches, I placed a Fluke TI-55 FT thermal imaging camera (Fluke Electronics, Everett, WA, USA) ~40 m from the base of each nesting beach, pointed toward the beaches. The cameras were deployed from 3 June until 12 June, when I had not observed fresh nest-searching behaviour for three consecutive days. I placed each camera in a custom-made waterproof container to protect them from the elements, and mounted these on posts to elevate them enough to capture as much of the beaches as possible. The thermal cameras were connected to a MotoMaster 300W inverter (Canadian Tire, Toronto, ON), which I then connected in parallel to two MotoMaster 35 amp-hour deep cycle batteries (Canadian Tire, Toronto, ON) to power them through the day; the thermal cameras also came with integral lithium-ion power cells, and I swapped in fresh deep cycle batteries and power cells every day that the thermal cameras were deployed. I programmed the cameras to record a thermal image every 30 minutes; emissivity was set to 0.95, and background temperature was set to 20°C. I analysed the thermal images using Fluke SmartView 3.9 (Fluke Thermography, Plymouth, MN, USA); I used the software's 'draw polygon' function to draw polygons covering the usage zones on each image, which measured the mean temperature, maximum temperature, and minimum temperature readings within the polygon. I did this for each thermal image for each nesting beach, starting at 17h00 until dusk (~22h00), when I could no longer see the stake wire flags on the visible light versions of the thermal images; the batteries did not provide enough power to last through the night, and I was unable to sample the early morning nesting foray periods.

To measure the soil characteristics of the nesting beaches, I collected soil samples (~300 g) from the surface (>5 cm deep) of four haphazardly-selected plots within each usage zone on each nesting beach after the end of nesting activity (26 June). I dried the samples in a drying

oven at 80 °C for at least 12 hours prior to analysis. I weighed each representative sample with a Mettler PM6000 electronic scale (Mettler-Toledo LLC, Columbus, OH, USA), and poured the sample into a stack of laboratory test sieve pans (#8, #16, #30, #50, #100, and #200; Fisher Scientific, Ottawa, ON). I placed the sieve stack into a Ro-Tap testing sieve shaker (W.S Tyler Company of Canada, St. Catharines, ON) for 10 minutes, after which I re-weighed the soil within each sieve pan. I divided these grain sizes into categories based on the United States Department of Agriculture soil classification system (Soil Survey Division Staff, 1993): fines (all grains ≤ 0.074 mm grain size diameter), very fine sand (0.074 - 0.15 mm), fine sand (0.15 - 0.25 mm), medium sand (0.25 - 0.5 mm), coarse sand (0.5 - 1 mm), very coarse sand (1 - 2 mm), and gravel (≥ 2 mm).

During the nesting season, I daily measured the soil moisture content of each plot with an ML3 ThetaProbe Soil Moisture Sensor (Delta-T Devices Ltd, Cambridge, UK) by inserting the probe into the soil at the centre of each plot, at an angle to measure moisture content as close to the surface as possible.

Analysis - To analyse the thermal characteristics of the nesting beaches, I took the daily median of the mean temperatures and range of temperatures from each polygon/usage zone. I compared these daily medians of mean temperatures and range of temperatures among usage ones within nesting beaches, for each day that temperature data were available. I also compared the daily medians of mean temperatures and range of temperature of the high use zones among nesting beaches, to determine if females were showing individual preferences for nesting cues.

To analyse the moisture characteristics of the nesting beaches, I calculated the daily median soil moisture for each usage zone by taking the median of all soil moisture readings from

the plots within the usage zone. I compared these daily medians of soil moisture among usage ones within nesting beaches. I also compared the daily medians of soil moisture of the high use zones among nesting beaches, to determine if females were showing individual preferences for nesting cues.

To analyse the texture characteristics of the nesting beaches, I calculated the median proportions of each soil class for each usage zone by taking the median of all sample's soil proportions within the usage zone. I compared these medians of proportional soil sizes among usage ones within nesting beaches. I also compared the medians of proportional soil sizes of the high use zones among nesting beaches, to determine if females were showing individual preferences for nesting cues.

As some of these data were not normally distributed, I used a Kruskal-Wallis test with post-hoc Multiple Comparisons to compare these thermal and soil variables.

To determine the strongest predictor of female attention, I constructed a series of multinomial logistic models with mean temperature ('m.temp'), temperature range ('r.temp'), soil moisture ('water'), and all soil grain sizes ('gravel', 'vcsand', 'csand', 'msand', 'fsand', 'vfsand', and 'fines') as predictor variables, and the usage zone classification ('zone') as the response variable (Table 2.1). I constructed separate models for each nesting beach for each day that thermal imagery data were available. As the different predictive variables had different sample sizes, I used a random number generator to select from the larger data sets so that all variables had equal sample sizes, and performed five iterations with randomized sub-sampling per nesting beach per day. I compared each day's logistic models from each nesting beach using Akaike's Information Criterion (AIC) to select the strongest predictive model, and plotted the AIC scores of all iterations for all days for each nesting beach. I used a line of best fit for each predictive variable

to determine the general consensus of AIC scores for each predictor variable, and selected the most-supported logistic model.

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). Multinomial logistic regressions were performed with the 'nnet' package (Venables and Ripley, 2002).

RESULTS

Nesting Female Attention - M-beach had two high-use zones, four low-use zones, and three no-use zones; W-beach had one large high-use zone, two low-use zones, and two no-use zones (Fig. 2.2). The majority of female nesting activity was on the lee of the beaches, relative to the River's current (Fig. 2.1). B-beach had a single high-use zone (B-HU), a single no-use zone (B-NU), and no low-use zones (Fig. 2.2); the high-use zone consisted of the bottom half of the open, sandy bluff, while the no-use zone was the top half.

Thermal Imagery - Thermal imagery only partially covered M-beach and W-beach (Fig. 2.2), so only the covered usage zones were used in my analyses (including soil data); each of these beaches had coverage of one of each type of usage zone. Additionally, the thermal camera apparatus would sometimes be shifted off-target by wind, so usable thermal imagery was only available for certain days. Usable thermal imagery was available for M-beach on 6 June, 9 June, and 10 June, for W-beach on 5 June, 6 June, 8 June, and 11 June, and for B-beach on 9 June, 10 June, and 11 June.

Thermal imagery could not consistently distinguish high use zones from low use and no use zones with mean temperatures, but they generally could distinguish with temperature ranges (Fig. 2.3 to 2.8; Table A.1, A.2). On M-beach, mean temperature could better distinguish the usage zones than temperature range, particularly later in the nesting period, where M-HU was hotter than M-NU but cooler than M-LU (Fig. 2.3, 2.4; Table A.1, A.2). On W-beach, temperature range always distinguished the usage zones, while mean temperature never did (Fig. 2.5, 2.6; Table A.1, A.2); W-HU was always less variable than W-LU or W-NU, except on 8 June when it was more variable. On B-beach, mean temperature never distinguished usage zones, and temperature range only distinguished usage zones on 6 June (Fig. 2.7, 2.8; Table A.1, A.2). Comparisons among high use zones from different beaches showed that W-beach was significantly hotter than M-beach and B-beach, while M-beach and B-beach did not differ (Table A.3). M-beach had significantly greater temperature ranges than W-beach and B-beach, while W-beach and B-beach did not differ in temperature variability (Table A.3).

Soil Moisture - Soil moisture content was not generally distinguishable among usage zones (Fig. 2.9 to 2.11; Table A.4). On M-beach, M-HU was generally drier than M-NU, and drained more rapidly than M-LU and M-NU after a period of rainfall on 5 June and 6 June (Fig. 2.9; Table A.4). On W-beach, W-HU differed from W-NU, but was sometimes wetter and sometimes drier, and only differed from W-LU on 9 June (Fig. 2.10; Table A.4). On B-beach, B-HU never differed from B-NU in soil moisture content (Fig. 2.11). Comparisons among high use zones from different beaches showed that B-beach was generally significantly wetter than M-beach and W-beach; when M-beach and W-beach differed, M-beach was drier than W-beach (Table A.5).

Soil Grain Size Distribution - Grain size distribution was generally distinguishable among usage zones; generally, the beaches consisted of coarse sand, medium sand, and fine sand (Fig. 2.12 to 2.14; Table A.6). On M-beach, M-HU had smaller proportions of gravel, very coarse sand, coarse sand than M-NU and M-LU, and less medium sand than M-NU; it had greater proportions of fine sand than M-NU and M-LU (Fig. 2.12; Table A.6). On W-beach, W-HU was indistinguishable from W-LU; both usage zones had smaller proportions of gravel and greater proportions of coarse sand and very fine sand than W-NU (Fig. 2.13; table A.6). On B-beach, B-HU and B-NU differed in all grain size classes except for fines; B-HU had smaller proportions of fine sand and very fine sand, and greater proportions of all other size classes than B-NU (Fig. 2.14; Table A.6). Comparisons among high use zones from different beaches showed some differences among the beaches, W-beach and B-beach did not differ in grain size classes except for medium sand and fines, which B-beach had more of (Table A.7). M-beach differed from the other two beaches, having smaller proportions of larger grain sizes (gravel, very coarse sand, and coarse sand) and greater proportions of fine sand (Table A.7).

Predictive Utility - Akaike's Information Criterion had difficulty isolating a strong predictor for some nesting beaches on some days, but generally temperature range was the strongest predictor (Fig. 2.15 to 2.17). Usage zones on M-beach were best explained by soil moisture at the beginning of the nesting season, but mean temperature and temperature range mean temperature converged with soil moisture as the season progressed (Fig. 2.15; Table A.8). For W-beach, temperature range was always the most explanatory variable (Fig. 2.16; Table A.9). For B-beach, temperature range was the most explanatory variable early in the season, but converged with mean temperature and soil moisture as the season progressed (Fig. 2.17; Table A.10).

DISCUSSION

Temperature range was generally the strongest explanatory variable for nest-site selection, although soil moisture showed high importance on M-beach (Fig. 2.15 to 2.17). However, the AIC scores are in some cases too close to arrive at a strong conclusion on preferred nesting cues (Fig. 2.15 to 2.17). Use of temperature range as a cue may be supported by reports of nest-searching female wood turtles extended periods of time on the nesting beaches, as they may be investigating changes in the soil's temperature over time while undertaking these behaviours (Harding and Bloomer, 1979). Previous studies show that soil temperature influences nest-site selection in wood turtles; Hughes *et al.* (2009) reported that wood turtles prefer variability in their nest chambers, which may speed development of the embryos, although the mechanism is unknown (Compton, 1999). Other reptile species show a wide variety of preferences in nesting cues. Loggerhead sea turtles may shift their nest-searching movements in response to as little as 1°C change in temperature from one patch of sand to the next (Stoneburner and Richardson, 1981). Brown and Shine (2004) found that keelback snakes (*Tropidinophis mairii*) selected their nest sites based on high substrate moisture, which produced larger and healthier offspring. Nesting jackie dragons (*Amphibolurus muricatus*) also selected for soil moisture, a limiting factor in their arid habitat (Warner and Shine, 2008). Snapping turtles (*Chelydra serpentina*) in Illinois showed selection based on vegetation cover, preferring minimal cover and high sun exposure (Kolbe and Janzen, 2002). Loggerhead sea turtles nesting in Florida show preference based on the size and slope of beaches, and the proportion of calcium carbonate in the soil (Garmestani *et al.*, 2000); however, this study did not measure surface temperature directly. These reported differences in nesting cues represent actual reptilian

reproductive ecology, or they may reflect differing study methodologies on the parts of the investigators.

Brown and Shine (2004) discussed how the thermal and structural properties of a substrate can strongly co-vary, which I believe is supported by the often-low ΔAIC scores among the different logistic models; the statistical models I used may not have been sensitive enough to distinguish among the co-variates in a reliable manner. A more sensitive statistical model may be beneficial when moving forward with this data set. It is also possible that nest-site selection takes place on a finer scale than what my sampling methods were capable of detecting; Stoneburner and Richardson (1981) found that temperature shifts of <1 °C could influence nest-searching movements of loggerhead sea turtles, whose nest-searching behaviours are reportedly similar to those of wood turtles. Wood turtles are known to be able to sense temperature differences of at least 3 °C, although these tests were conducted on juveniles in laboratory conditions and not nesting females, and older juveniles could better distinguish favourable temperatures than younger juveniles (Tamplin, 2006, 2009).

As a technique for field studies, thermal imagery proved to be challenging in ways that introduce some caveats to the results of this study. The imagers needed to be set up ~40 m from the nesting beaches to cover a sizeable portion of the beach; thermal imagers have a known data loss at such distances, which resulted in my temperature readings being likely underestimated by as much as 4°C (Faye *et al.*, 2015). Additionally, the emissivity of the sand (0.7) was lower than the 0.95 programmed into the cameras (Mira *et al.*, 2007), which could confound the readings of the thermal imagery, as can differences in atmospheric conditions such as humidity (Faye *et al.*, 2015). However, as I was examining comparisons among different parts of the beaches, rather than attempting to measure absolute temperatures, my data can still provide insights into the

relative temperature selections by nesting wood turtle females. Thermal imagery may require a stronger survey protocol and less-improvised support apparatus to be effective as a tool for nesting surveys. The posts I used to support the thermal cameras would sometimes shift in the wind, putting the camera off-target; sinking the posts deeper into the ground may be more effective. The deep-cycle batteries that I used to power the thermal cameras would last ~12 hours, and thus I missed capturing the female's early morning nesting forays; a different, stronger power source would be more effective in future studies. I also attempted to collect thermal imagery in 2015, and was unable to collect usable images due to misunderstanding that the thermal images and visible light images did not line up totally; the 2015 thermal images covered only a small fraction of the nesting beaches. The combined costs of thermal imager rental and shipping was considerable; more direct thermal sampling, such as an array of buried temperature dataloggers, may be more cost-effective and reliable at measuring temperature in future studies. My results suggest that a temperature-based nesting survey strategy may not be effective, anyway. The differing conditions of the high use zones suggest that wood turtle females show some degree of individual preference in their nest-searching attentions; despite their physical similarity (Fig. 2.1), M-beach and W-beach differed more in temperature than M-beach and B-beach (Table A.X). These results make it difficult to select a target range of temperatures for a thermographic survey protocol, and I would suggest continued use of nest-searching trackways, which are highly diagnostic of wood turtle presence/absence, in future studies. I made one observation of similarity between M-beach and W-beach; the greatest amount of female attention was on the lee of these beaches, relative to the River's current (Fig.2.1). The River's path opened up the forest to the south from these areas, allowing for more sunlight to reach the surface of the soil than other parts of the beaches.

In conclusion, my study did show evidence for thermal characteristics being the most important environmental cue for nest-site selection in wood turtles, but in all likelihood it is a mix of highly-covariant factors that govern female attention. Temperature is important in egg incubation, and the females may be mapping temperature shifts over time when selecting a nest site. A number of previous studies have been conducted on wood turtle intelligence, with the general consensus being that they are on the higher end of the reptile intelligence spectrum (Tinklepaugh, 1932; Harding and Bloomer, 1979). If the reports of their ability to learn and remember are accurate, it may provide an explanation for their intensive nesting behaviour; perhaps the females are constructing a mental map of the nesting beach, comparing their findings in the moment to previous nesting forays.

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CHAPTER 2 TABLES

TABLE 2.1 - Multinomial logistic regression models used to determine the variable that best predicted female wood turtle (*Glyptemys insculpta*) nest-searching attention. The response variable is usage zone ('zone'), and the predictor variables are mean temperature ('m.temp'), range of temperatures ('r.temp'), soil moisture ('water'), and soil texture. Soil texture is the combined proportions of soil grain sizes: gravel, very coarse sand ('vcsand'), coarse sand ('csand'), medium sand ('msand'), fine sand ('fsand'), very fine sand ('vfsand'), and fine particles ('fines').

Model Equation
zone ~ m.temp
zone ~ r.temp
zone ~ water
zone ~ (gravel + vcsand + csand + msand + fsand + vfsand + fines)

CHAPTER 2 FIGURES



FIGURE 2.1 - Images of wood turtle (*Glyptemys insculpta*) nesting beaches used in 2016: M-beach (top), W-beach (middle), and B-beach (bottom). The arrows indicate the direction of the River's current.

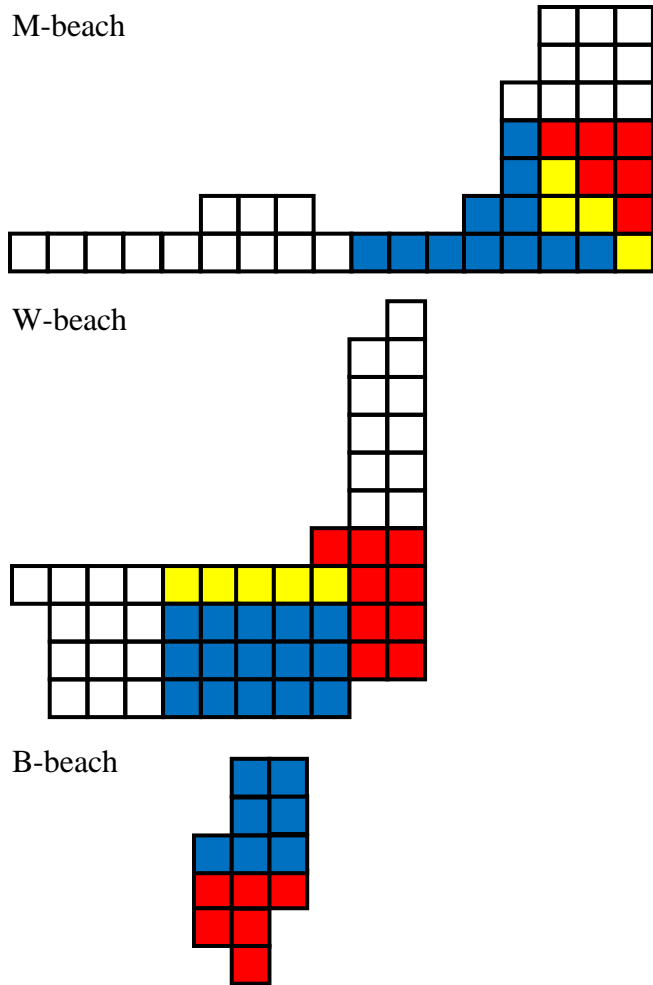


FIGURE 2.2 - Outline of plots used on wood turtle (*Glyptemys insculpta*) nesting beaches in 2016 in the Sudbury District, ON. Each square represents a 2 m x 2m plot on the un-vegetated parts of the beaches. Blue squares represent no-use zones (female avoidance), yellow squares represent low-use zones (minimal use by females), and red squares represent high-use zones (areas females were likely to nest in); empty squares represent areas not covered by thermal imagery.

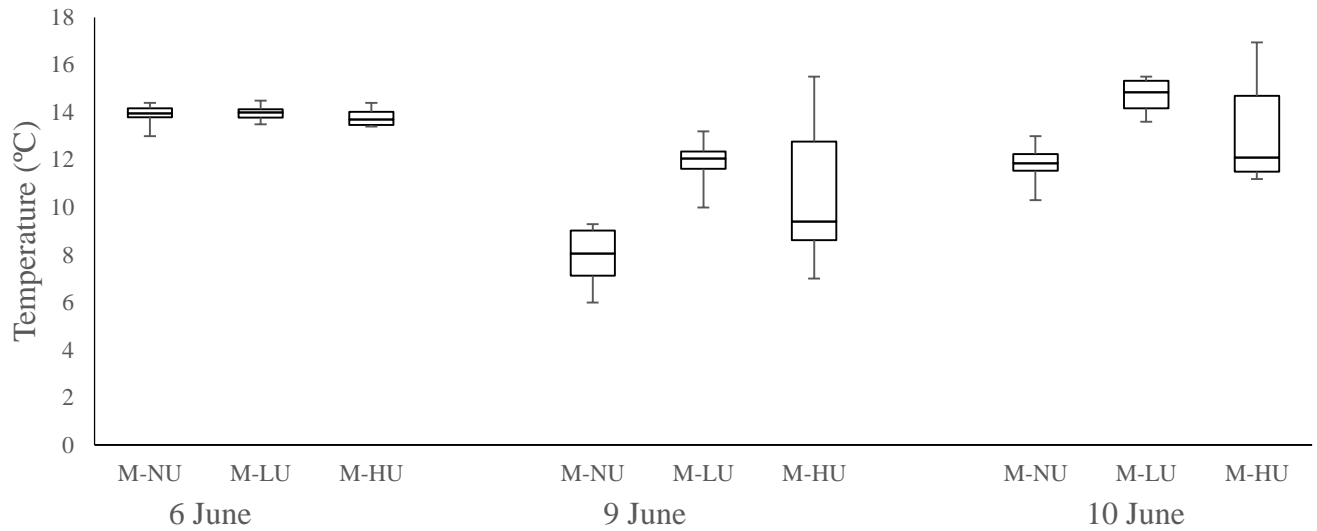


FIGURE 2.3 - Mean surface temperatures of usage zones on M-beach, a wood turtle (*Glyptemys insculpta*) nesting beach in the Sudbury District, ON, in 2016. M-NU is a 'no use zone' avoided by females; M-LU is a 'low use zone' with little female attention, M-HU is a 'high use zone' with considerable female attention. Middle line shows the median of all mean temperatures, boxes show interquartile range, and the whiskers show the total range.

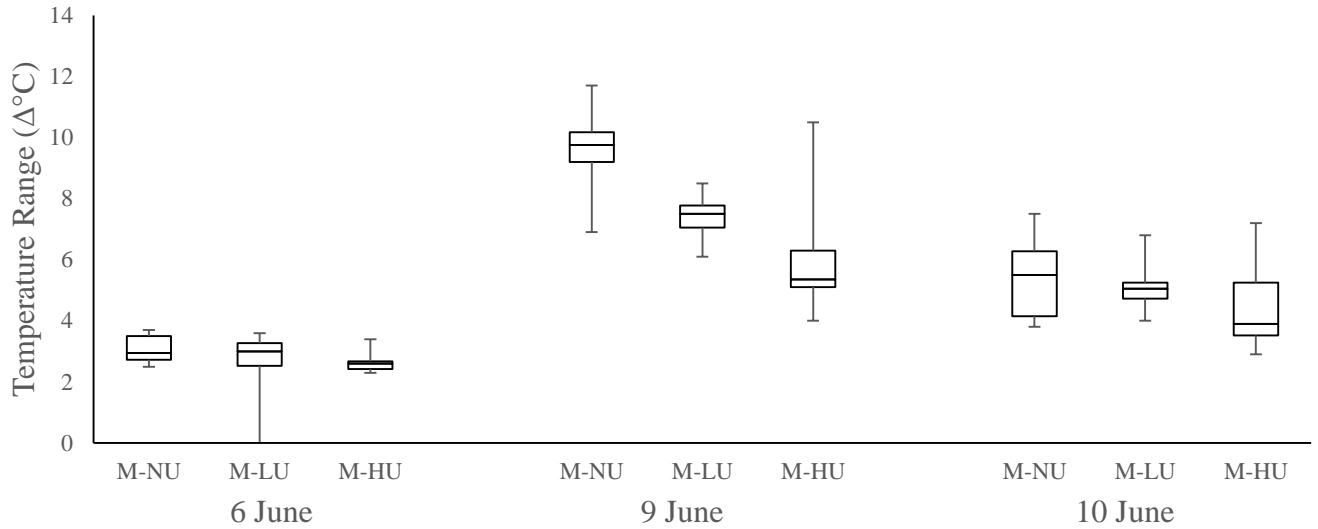


FIGURE 2.4 - Surface temperature ranges of usage zones on M-beach, a wood turtle (*Glyptemys insculpta*) nesting beach in the Sudbury District, ON, in 2016. M-NU is a 'no use zone' avoided by females; M-LU is a 'low use zone' with little female attention, M-HU is a 'high use zone' with considerable female attention. Middle line shows the median of all mean temperatures, boxes show interquartile range, and the whiskers show the total range.

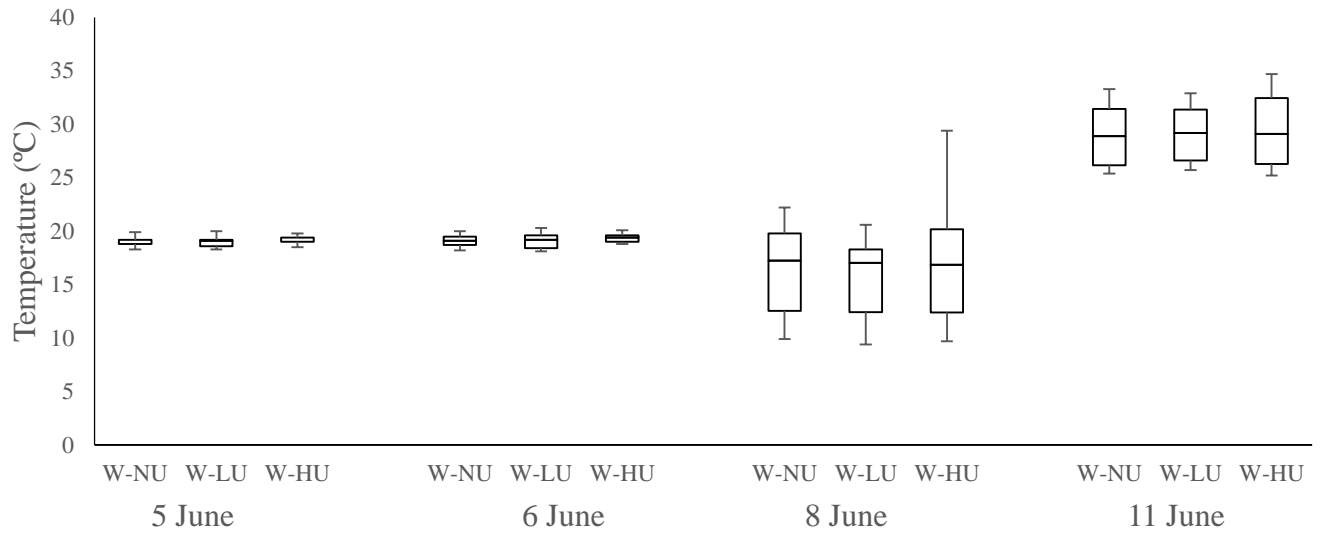


FIGURE 2.5 - Mean surface temperatures of usage zones on W-beach, a wood turtle (*Glyptemys insculpta*) nesting beach in the Sudbury District, ON, in 2016. W-NU is a 'no use zone' avoided by females; W-LU is a 'low use zone' with little female attention, W-HU is a 'high use zone' with considerable female attention. Middle line shows the median of all mean temperatures, boxes show interquartile range, and the whiskers show the total range.

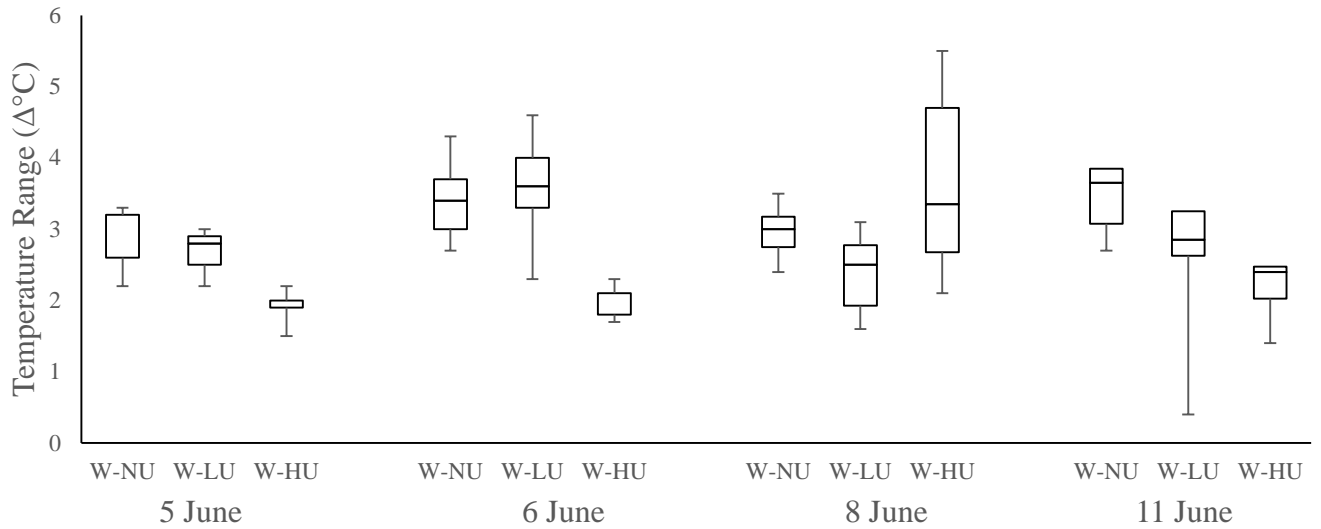


FIGURE 2.6 - Surface temperature ranges of usage zones on W-beach, a wood turtle (*Glyptemys insculpta*) nesting beach in the Sudbury District, ON, in 2016. W-NU is a 'no use zone' avoided by females; W-LU is a 'low use zone' with little female attention, W-HU is a 'high use zone' with considerable female attention. Middle line shows the median of all mean temperatures, boxes show interquartile range, and the whiskers show the total range.

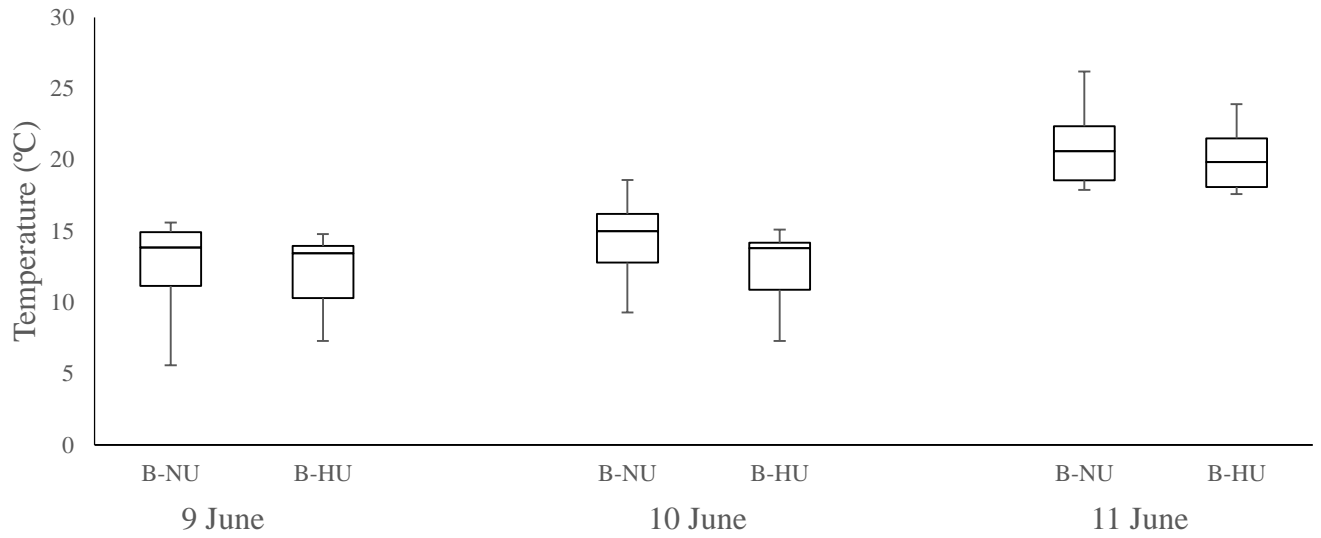


FIGURE 2.7 - Mean surface temperatures of usage zones on B-beach, a wood turtle (*Glyptemys insculpta*) nesting beach in the Sudbury District, ON, in 2016. B-NU is a 'no use zone' avoided by females; B-HU is a 'high use zone' with considerable female attention. Middle line shows the median of all mean temperatures, boxes show interquartile range, and the whiskers show the total range.

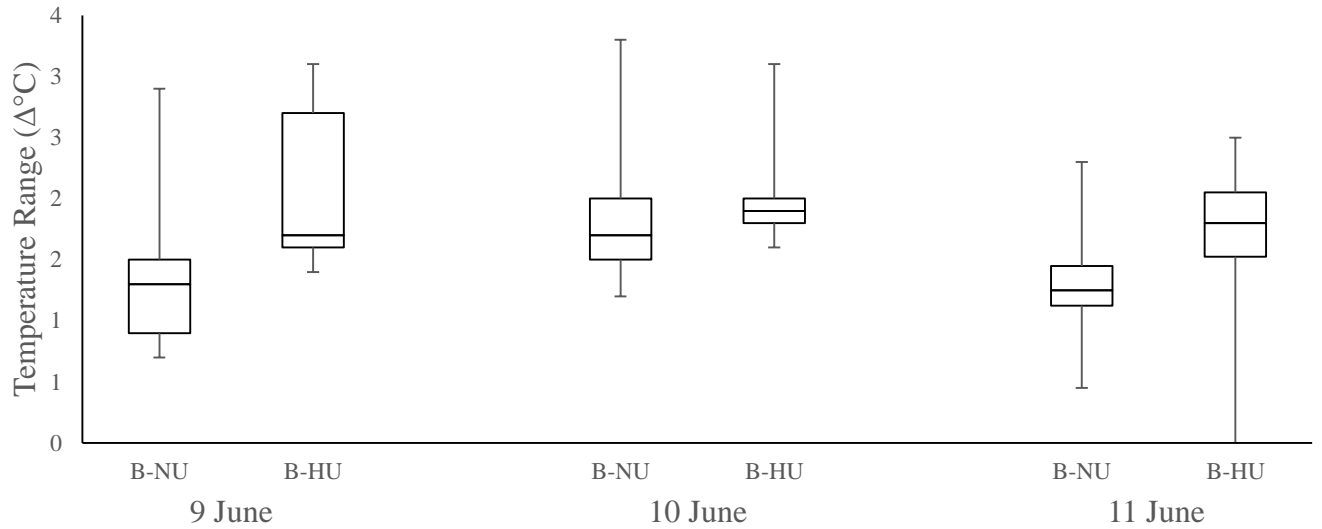


FIGURE 2.8 - Surface temperature ranges of usage zones on B-beach, a wood turtle (*Glyptemys insculpta*) nesting beach in the Sudbury District, ON, in 2016. B-NU is a 'no use zone' avoided by females; B-HU is a 'high use zone' with considerable female attention. Middle line shows the median of all mean temperatures, boxes show interquartile range, and the whiskers show the total range.

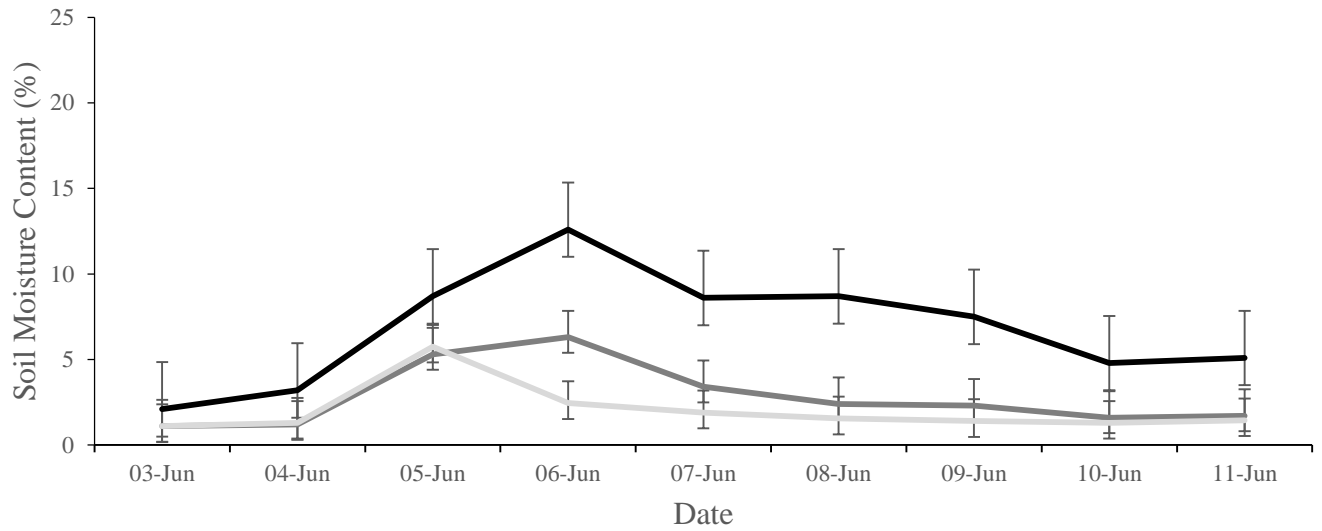


FIGURE 2.9 - Median soil moisture content of usage zones on M-beach, a wood turtle (*Glyptemys insculpta*) nesting beach in the Sudbury District, ON, in 2016. The black line is M-NU, the dark grey line is M-LU, and the light grey line is M-HU. Whiskers show interquartile range.

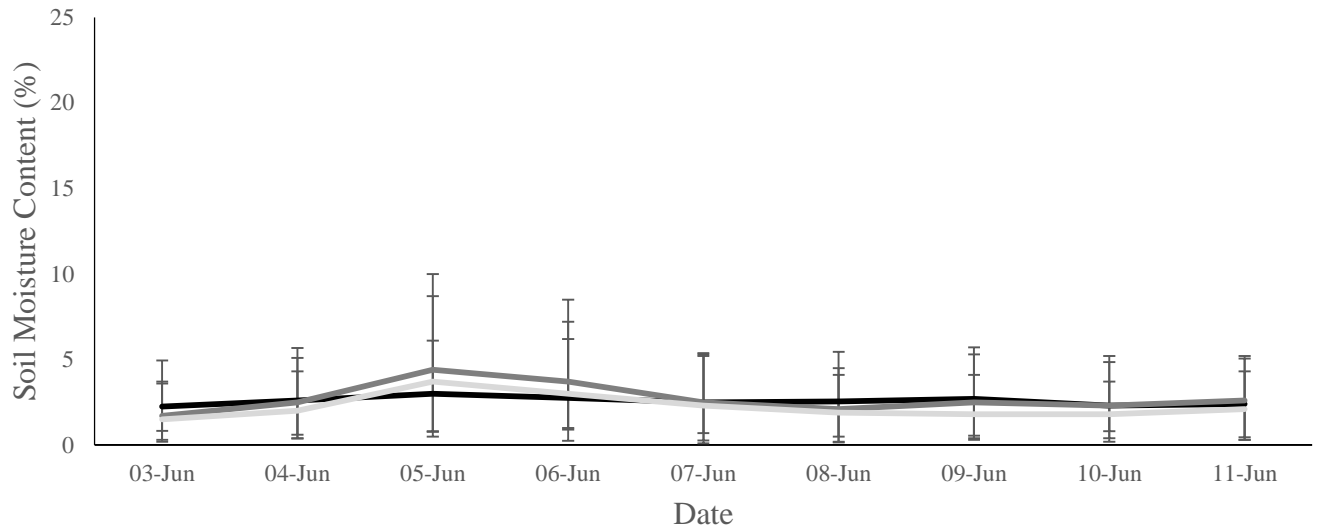


FIGURE 2.10 - Median soil moisture content of usage zones on W-beach, a wood turtle (*Glyptemys insculpta*) nesting beach in the Sudbury District, ON, in 2016. The black line is W-NU, the dark grey line is W-LU, and the light grey line is W-HU. Whiskers show interquartile range.

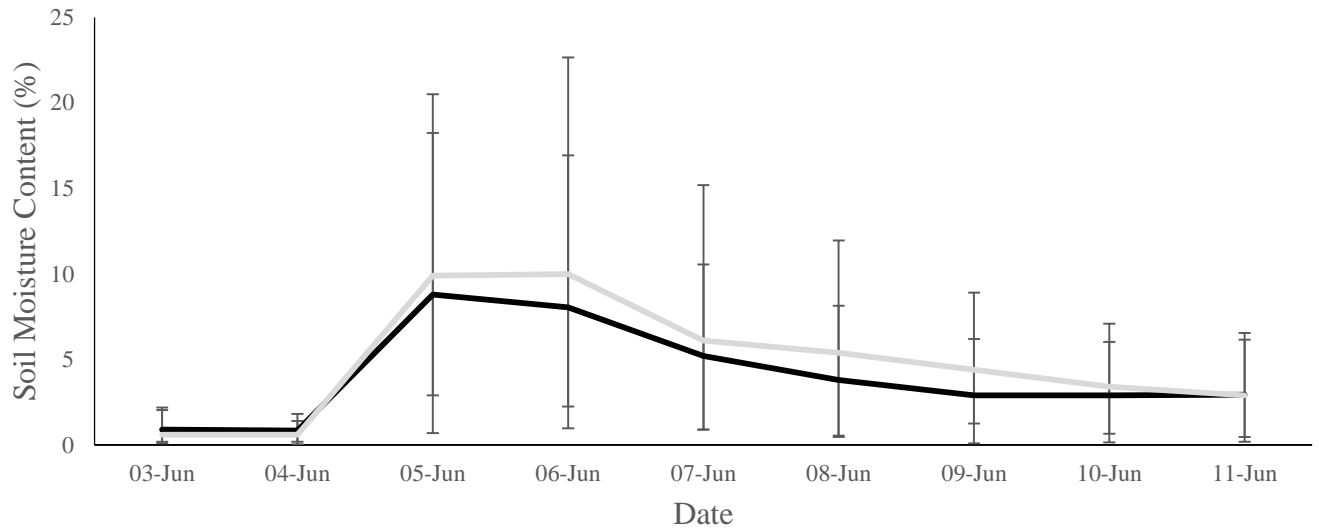


FIGURE 2.11 - Median soil moisture content of usage zones on B-beach, a wood turtle (*Glyptemys insculpta*) nesting beach in the Sudbury District, ON, in 2016. The black line is B-NU, and the light grey line is B-HU. Whiskers show interquartile range.

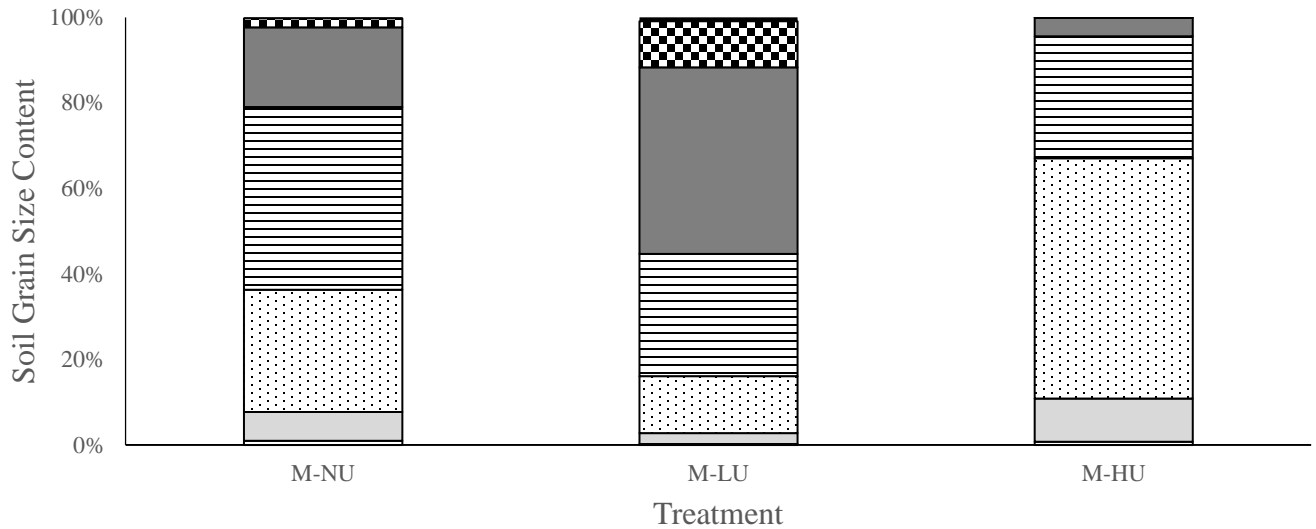


FIGURE 2.12 - Grain size distribution of usage zones on M-beach, a wood turtle (*Glyptemys insculpta*) nesting beach in the Sudbury District, ON, in 2016. Solid black represents gravel (>2 mm grain diameter), black checker pattern represents very coarse sand (1 to 2 mm), solid dark grey represents coarse sand (0.5 to 1 mm), horizontal bars represent medium sand (0.25 to 0.5 mm), dots represent fine sand (0.15 to 0.25 mm), solid light grey represents very fine sand (0.074 to 0.15 mm), and solid white represents fine grains (<0.074 mm).

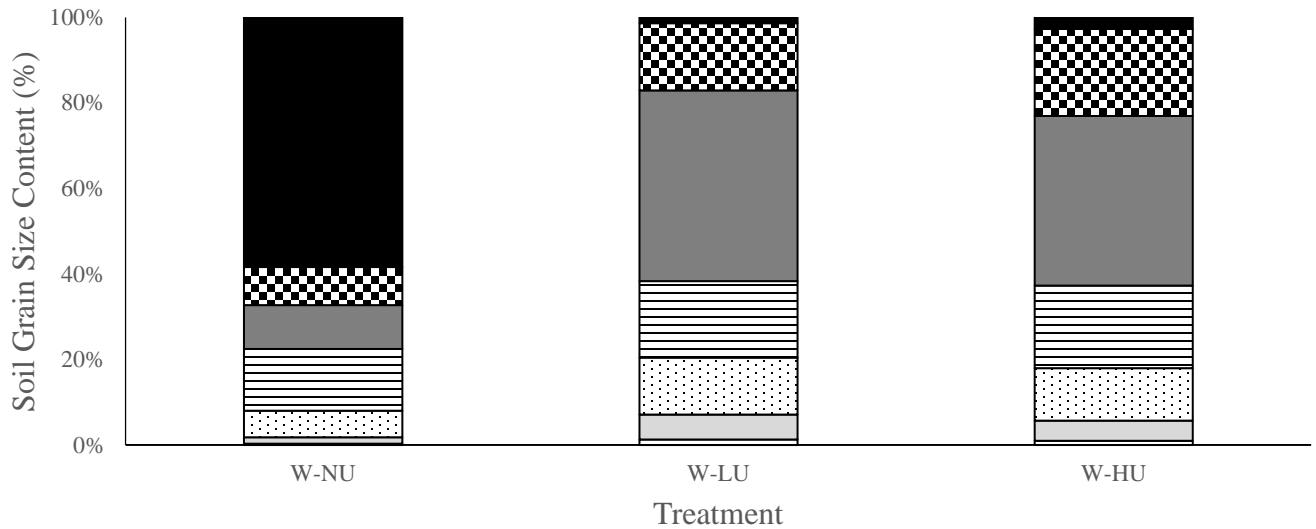


FIGURE 2.13 - Grain size distribution of usage zones on W-beach, a wood turtle (*Glyptemys insculpta*) nesting beach in the Sudbury District, ON, in 2016. Solid black represents gravel (>2 mm grain diameter), black checker pattern represents very coarse sand (1 to 2 mm), solid dark grey represents coarse sand (0.5 to 1 mm), horizontal bars represent medium sand (0.25 to 0.5 mm), dots represent fine sand (0.15 to 0.25 mm), solid light grey represents very fine sand (0.074 to 0.15 mm), and solid white represents fine grains (<0.074 mm).

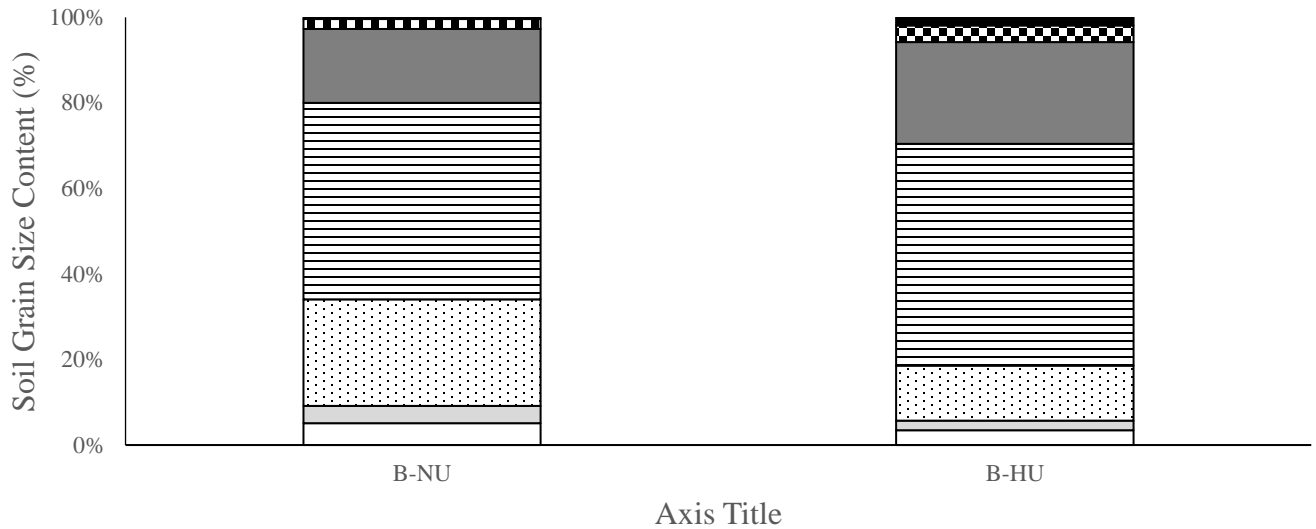


FIGURE 2.14 - Grain size distribution of usage zones on B-beach, a wood turtle (*Glyptemys insculpta*) nesting beach in the Sudbury District, ON, in 2016. Solid black represents gravel (>2 mm grain diameter), black checker pattern represents very coarse sand (1 to 2 mm), solid dark grey represents coarse sand (0.5 to 1 mm), horizontal bars represent medium sand (0.25 to 0.5 mm), dots represent fine sand (0.15 to 0.25 mm), solid light grey represents very fine sand (0.074 to 0.15 mm), and solid white represents fine grains (<0.074 mm).

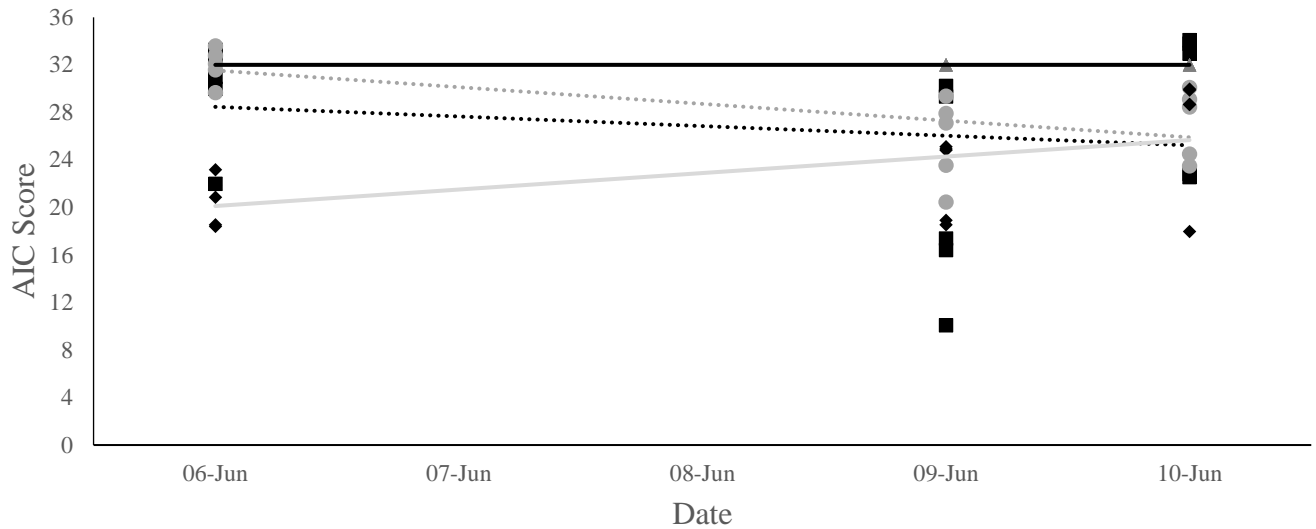


FIGURE 2.15 - AIC scores from multiple iterations of model selection to determine the strongest predictive variable for female nest-searching attention on M-beach, a wood turtle (*Glyptemys insculpta*) nesting beach in the Sudbury District, ON, in 2016. The lines of best fit represent the consensus of AIC scores from multiple iterations ($n = 5$) of randomized subsets of data. Grey circles and a dotted grey line represent mean temperature ($df = 4$), black squares and a dotted black line represent temperature range ($df = 4$), black diamonds and a solid grey line represent soil moisture content ($df = 4$), and grey triangles and a solid black line represent soil grain size distribution ($df = 16$).

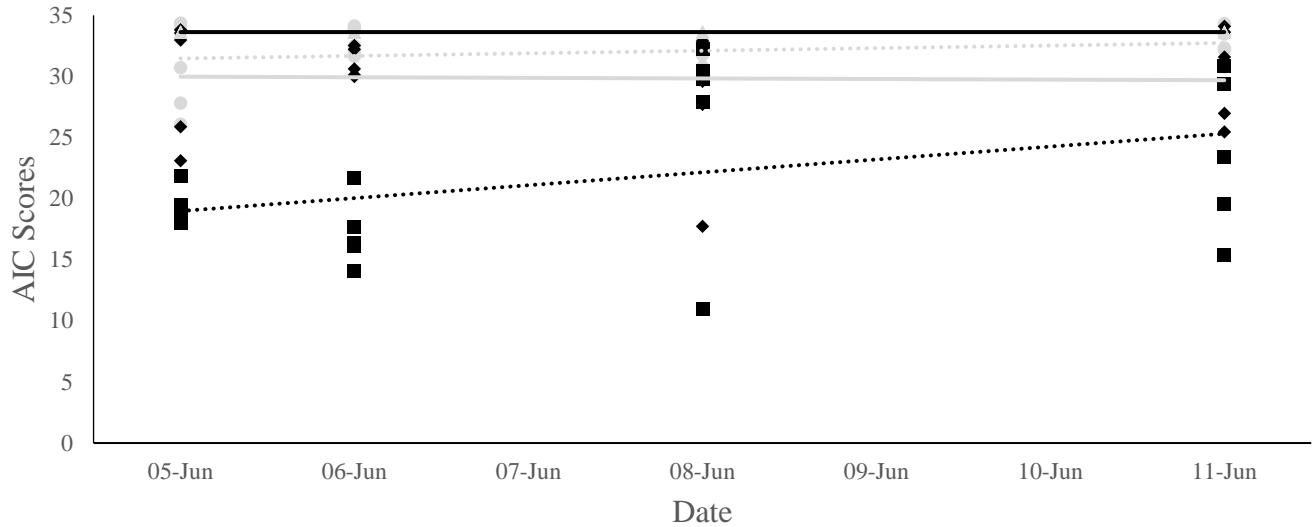


FIGURE 2.16 - AIC scores from multiple iterations of model selection to determine the strongest predictive variable for female nest-searching attention on W-beach, a wood turtle (*Glyptemys insculpta*) nesting beach in the Sudbury District, ON, in 2016. The lines of best fit represent the consensus of AIC scores from multiple iterations ($n = 5$) of randomized subsets of data. Grey circles and a dotted grey line represent mean temperature ($df = 4$), black squares and a dotted black line represent temperature range ($df = 4$), black diamonds and a solid grey line represent soil moisture content ($df = 4$), and grey triangles and a solid black line represent soil grain size distribution ($df = 16$).

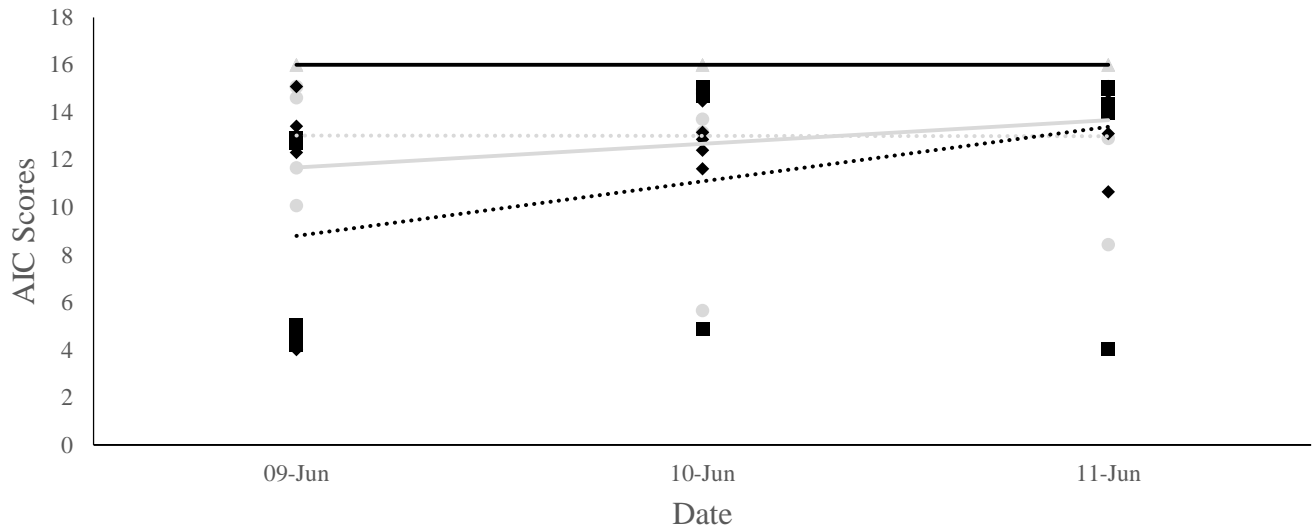


FIGURE 2.17 - AIC scores from multiple iterations of model selection to determine the strongest predictive variable for female nest-searching attention on B-beach, a wood turtle (*Glyptemys insculpta*) nesting beach in the Sudbury District, ON, in 2016. The lines of best fit represent the consensus of AIC scores from multiple iterations ($n = 5$) of randomized subsets of data. Grey circles and a dotted grey line represent mean temperature ($df = 2$), black squares and a dotted black line represent temperature range ($df = 2$), black diamonds and a solid grey line represent soil moisture content ($df = 2$), and grey triangles and a solid black line represent soil grain size distribution ($df = 8$).

CHAPTER 3

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

ABSTRACT

Wood turtle habitat is shrinking across the species' range, largely due to human activity (e.g., forestry, aggregate extraction, agriculture). I examined the thermal consequences of forestry and aggregate extraction on wood turtle habitat in the Sudbury District of Ontario by measuring the differences in temperature (overall temperature and min/max extreme temperatures), thermal landscape structure/topography, and habitat thermal quality among relatively undisturbed sites (n = 2), harvested forestry sites (n = 2), and aggregate pits (n = 2) in the 2015 field season. I also tested the potential use of the thermal landscape concept as a predictor of habitat thermal quality. Undisturbed habitats were generally cooler and their temperatures less variable than in impacted habitats, and were of higher thermal quality. The thermal landscape concept provided a useful predictor of habitat thermal quality, so long as the influence of time of day was factored into the predictive model. Data collected for my study are important in considering conservation and management for this species, by illuminating the thermal impacts of natural resource extraction on the habitat of an endangered species, and guiding the development of mitigation and rehabilitation plans, by providing measures of and targets for thermal habitat quality.

INTRODUCTION

Human land use and the harvesting of natural resources can have a profound impact on the environment, which in turn affects the organisms that live there. Examples of these impacts include pollution (Hayden *et al.*, 2015; Sasaki *et al.*, 2015, 2016), destruction and fragmentation of habitat (Tommeraaas, 1993; Mac Nally and Brown, 2001), and disruption of natural fire regimes (Platt *et al.*, 2010; Poulos *et al.*, 2013). These impacts affect the ecology and evolution

of the species that live in impacted regions through disruptions to gene-flow, gene pool size, physiology, and species diversity (Saunders *et al.*, 1991; Sasaki *et al.*, 2015, 2016). Species are also sensitive to changes in the thermal regimes of their habitats (Lehmkuhl, 1972); for example, marble trout (*Salmo marmoratus*) embryos and hatchlings show a chronic stress response to increased environmental temperatures (Simčič *et al.*, 2015). Human activity is correlated with increased environmental temperatures at the local scale (e.g., urban heat islands; Kim, 1992) and at the global scale in the form of climate change (IPCC, 2014).

In Ontario, habitat of the wood turtle (*Glyptemys insculpta*) is subject to human development, including forestry (Kittrede, 1996), aggregates (Arvisais *et al.*, 2004; Walde *et al.*, 2007), and agriculture (Foscarini, 1994; Saumure *et al.*, 2007). All of these impacts present conservation concerns for wood turtles through habitat loss (Kaufmann, 1992), injuries or fatalities from encounters with machinery (Kauffman, 1992; Saumure *et al.* 2007), subsidized predators such as red foxes (*Vulpes vulpes*), raccoons (*Procyon lotor*), skunks (*Mephitis mephitis*), and corvids (Klemens, 2000; Buhlmann and Osborn, 2011), or increased exposure to illegal human collection (Litzgus and Brooks, 1996). In general, increased human activity has a negative correlation with wood turtle populations (Garber and Burger, 1995). However, human development may not exclusively have a negative impact on wood turtle habitat; wood turtles are known as 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 forest habitat (i.e. creating a 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 how important it is to thoroughly

study the effects of natural resource extraction on wood turtle habitat when deciding management policies and best practices.

The purpose of my study was to describe the thermal impact of natural resource harvesting on wood turtle habitat. As the study population is located near the northern range limit of the wood turtle's distribution, temperature is a highly important factor to the species' ecology (Magnuson *et al.*, 1979; Tracey and Christian, 1986; Greaves, 2007; Dubois *et al.*, 2009). The primary natural resource industries near the study site are forestry and aggregate extraction, both of which are common in wood turtle habitat throughout the species' range (Kittrede, 1996; Arvisais *et al.*, 2004). One objective of my study was to compare the thermal properties of (relatively) undisturbed known wood turtle habitat to habitat impacted by natural resource extraction. To do this, I mapped and compared the thermal landscapes of sites with wood turtles and nearby sites (<10 km) that were recently logged or from where aggregates were extracted. I hypothesized that if resource extraction has a thermal impact on wood turtle habitat, then the thermal landscape of these developed sites (which were once presumably similar to the undeveloped sites) will be significantly different from that of the primary study site. I predicted that the impacted sites will be hotter and more variable than the undisturbed sites, due to greater canopy cover at the undisturbed sites providing a thermal buffer (Zhou *et al.*, 2007). Another objective of my study was to relate these thermal data to wood turtle biology; I compared the temperature readings of my undisturbed and impacted sites to wood turtle temperature selections measured in Chapter 1. I hypothesized that if resource extraction has a thermal impact on wood turtle habitat, then the impacted and non-impacted sites will differ in providing for the thermal needs of wood turtles such that the impacted sites will be of lower thermal quality. Finally, to assess the usefulness of the thermal landscape concept in conservation, I compared measures of

the thermal landscape to the thermal quality of the environment to test predictive utility. I hypothesized that if the thermal landscape concept can be used to predict the thermal quality of the landscape, then thermal landscape structure will show a relationship with thermal quality; I predicted that a 'rougher' thermal landscape will provide a superior thermal habitat, by providing a greater variety of microsites 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 environment.

METHODS

Study Sites - I mapped the thermal landscapes of six sites (3 treatments with 2 replicates each; see below) in or near the primary study site (Chapters 1 and 2). All study sites are within 10 km of each other and within 300 m of the River. 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 *et al.*, 2007; pers. obs.).

The two relatively undisturbed sites were located within the primary study site. The first, W₁, was chosen for the high incidence of wood turtles captured in or near it throughout the year; I make the assumption that this area represents "good" wood turtle habitat. W₁ abuts the River, covering natural riparian forest and dogwood thicket, and includes 45-year-old jack pine (*Pinus banksiana*) plantation further inland/upland. The second, W₂, is located ~200 m from the River, and is located entirely in upland jack pine plantation of the same age as in W₁, abutting a black spruce (*Picea mariana*)/tamarack (*Larix laricina*) bog to the north. Although wood turtles have been encountered nearby (within 100 m; pers. obs.) and observed using similar habitat, no wood

turtles were captured directly within W₂ in 2015; this site was chosen as an example of potential wood turtle habitat.

Two sites were located within harvested forestry blocks. Both sites were previously 45-year-old red pine (*Pinus resinosa*) plantations, harvested using 4 to 7 m wide forced rows with light selective harvesting in the standing rows. The first site, F₁, was harvested in 2012 and located 300 m from the River and 800 m from the eastern boundary of the primary study site. The second site, F₂, was harvested in 2014 and located 250 m from the River and 4500 m from the eastern boundary of the primary study site; F₂ was also within 500 m of a tributary of the River known to have wood turtles living in it (Litzgus, pers. comm.). No examples of clear-cut forestry or harvesting of natural stands were scheduled during the course of my field studies near the study site, so I was unable to sample these forestry techniques.

Two sites were located within active aggregate (gravel) pits. The first, G₁, was located 80 m from the River and 5000 m from the eastern boundary of the primary study site. G₁ 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 the predominant plant species returning to the open pit, 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, I found a depredated turtle nest within G₁ in 2015 (species unknown, but suspected to have been a wood turtle or Blanding's turtle (*Emydoidea blandingii*)). The second pit, G₂, was located within 50 m of the River, and 9000 m from the eastern boundary of the primary study site. G₂ 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. I was unable to acquire landowner permission to set up a third site within active parts of an aggregate pit.

Thermal Landscape Mapping - I laid an array of thermal models, at each of the six sites; the thermal models were identical to those used in Chapter 1. These arrays were smaller (1.8 ha) and had finer resolution than the array used in Chapter 1, consisting of 20 thermal models in a 5 x 4 grid, 50 m x 30 m apart. The dataloggers were set to record temperature every 2 hours; these readings were generalized into mean temperatures for 6-hour diel periods to compensate for asynchronous temperature readings and short-term stochastic temperature events. The six arrays were fully deployed by 15 May 2015. I collected the dataloggers in late June and returned them to the field in early July, to protect against data loss from equipment failure. Another retrieval was planned for mid-August, but I decided a visual inspection of the thermal models for damage was sufficient. I retrieved all thermal models from the field by 30 September 2015.

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 I observed no obvious damage to the thermal models from human interference; the exception being a single model which was crushed by the pit operators in G₂ piling timber over it (I assume unintentionally).

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. I 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; I compared the number of thermal models to mean diel temperature, and the number of thermal models to diel temperature variance.

I divided the temperature readings from each site into time periods that correspond to wood turtle activity periods (adapted from Arvisais *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). I further divided these into four 6-hour diel periods for analysis: Early Morning (00h to 06h), Late Morning (06h to 12h), Afternoon (12h to 18h), and Evening (18h to 24 h). I compiled overall temperatures, and temperature readings in the 10th and 90th percentiles (to represent minimum and maximum extremes), for each activity period-diel period, to compare temperatures among treatments. I compared overall temperatures among treatments using ANOVAs with post-hoc Tukey's Honest Significant Difference test. The upper and lower extreme temperatures did not show a normal distribution, so I used 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); I did not compare among the impact sites.

I calculated the coefficient of variation (V) across each thermal model grid for each activity period-diel period to estimate the thermal landscape's "roughness" (hereafter referred to as thermal landscape structure), analogous to the topographic relief of the physical landscape; higher values of V indicate a 'rougher' thermal landscape (more thermal variation), and lower values of V indicate a 'smoother' thermal landscape (less thermal variation; Fig. 3.1). As the values of V were not normally distributed, I compared thermal landscape structure 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); I did not compare among the impact sites.

I estimated the thermal usage range for the wood turtle study group in Chapter 1; thermal usage range is here defined as the interquartile range of body temperatures (25th to 75th percentiles) for the wood turtle study group in 2015 (adapted from Tucker *et al.*, 2015), and represents the majority of temperatures carapace temperatures experienced by the wood turtles. I calculated habitat thermal quality for each treatment by taking the absolute temperature differences of each environmental temperature data point (T_e) from the thermal use range, and then comparing median habitat thermal quality among treatments; as these data did not show a normal distribution, I used a Kruskal-Wallis test with post-hoc Multiple Comparisons between W_1 and W_2 , and between the undisturbed sites and impact sites (9 comparisons total); I did not compare among the impact sites.

To determine if thermal landscape structure could predict thermal quality of the habitat, I formulated a number of linear models predicting habitat thermal quality; the predictive variables were comprised of mean diel temperature ('mean.temp'), thermal landscape structure ('struc'), diel period ('diel'), and treatment ('site'). I performed an Akaike's Information Criterion test on these models to determine which model was the most predictive of habitat thermal quality.

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). In all post-hoc tests, I used the Bonferroni correction for multiple comparisons ($\alpha = 0.006$).

RESULTS

The number of thermal models had a near-significant effect on mean temperature ($R^2 = 0.001$, $F_{(1, 2782)} = 3.58$, $p = 0.06$), and no effect on temperature variance ($R^2 < 0.001$, $F_{(1, 2782)} = 0.22$, $p = 0.64$); thus, I concluded that the missing thermal models had no practical effect on the temperature readings, and conducted my analyses accordingly.

Overall Temperatures - In the Pre-Nesting period (Fig. 3.2), overall temperatures did not differ from each other among sites in the Early Mornings; in all other seasonal and diel periods, sites differed from each other (Fig. 3.2 to Fig. 3.5; Table A.11). In general, overall temperatures among the six sites were similar in the early mornings and evenings, and consistently different in the late mornings and afternoons (Fig. 3.2 to Fig. 3.5). The differences in temperature among treatments were most apparent in the afternoons, which also showed the most consistent pattern of significant temperature differences: W_1 and/or W_2 were always the coldest treatments in the afternoons, and G_2 was typically the hottest treatment (Fig. 3.2 to Fig. 3.5).

Maximum Temperatures - In all seasonal and diel periods, maximum temperatures differed amongst sites. (Fig. 3.6 to Fig. 3.9; Table A.12). Maximum temperatures showed a similar general pattern as the overall temperatures: cooler, less variable temperatures in the early mornings and evenings, and hotter, more variable temperatures in the late mornings and afternoons; exceptions were W_1 , F_1 , and G_2 , which showed high variability in early mornings in Summer (Fig. 3.8), which F_1 and G_2 also showed in Pre-Hibernation (Fig. 3.9). W_2 was nearly always the coolest and least variable site in all activity periods and diel periods, while G_2 was nearly always the hottest site (Fig. 3.6 to Fig. 3.9).

Minimum Temperatures - In all seasonal and diel periods, minimum temperatures different amongst sites. (Fig. 3.10 to Fig. 3.13; Table A.13). Minimum temperatures generally reflected those shown in the overall temperatures: cooler, less variable temperatures in the early mornings and evenings, and hotter, more variable temperatures in the late mornings and afternoons. The Pre-Nesting period was an exception, with the early mornings showing the greatest variability (Fig. 3.10). The undisturbed sites generally had higher minimum temperatures in the early mornings, and lower minimum temperatures during the rest of the day, compared to impact sites, corresponding to the lower variance of the undisturbed sites observed in overall temperatures. Minimum temperatures typically showed greater variability than maximum temperatures.

Thermal Landscape Structure - In the Pre-Nesting period (Fig. 3.14), thermal landscape structures did not differ from each other among sites in the Early Mornings; in all other seasonal and diel periods, sites differed from each other (Fig. 3.14 to Fig. 3.17; Table A.14). The thermal landscapes were typically smoothest (showed the least variability) within site during the early mornings and roughest (most variability) in the afternoons; the exceptions were F₁ and G₂ in the Summer and Pre-Hibernation periods (Fig 3.16 and Fig. 3.16), which were rougher in the early mornings. W₂ showed the smoothest thermal landscape structure of all the sites; G₂ generally had the roughest thermal landscape structure, except in Pre-Nesting and Nesting periods, where F₂ had the roughest thermal landscape structure (Fig 3.14 to Fig. 3.17).

Habitat Thermal Quality - All treatments showed significant thermal differences from T₀; all treatments were significantly colder than T₀, except for G₁, which was hotter (Table 3.1).

Median habitat thermal qualities values differed among sites ($X^2 = 700.20$, $df = 5$, $p < 0.01$); the

undisturbed sites showed the highest habitat thermal quality (fewest and least extreme deviations from thermal use range), and G₂ showed the lowest habitat thermal quality (most frequent and extreme deviations from thermal use range; Table 3.2). The undisturbed sites also showed the lowest variability in habitat thermal quality, while the impact sites had greater variability in thermal quality (Table 3.2).

Thermal Landscape as a Predictor of Habitat Thermal Quality - Akaike's Information Criterion selected one model out of nine possibilities. Landscape thermal structure and mean diel temperature, and the interaction of time of day with those variables, showed the strongest predictive utility for habitat thermal quality ($R^2 = 0.86$; Table 3.3). The strongest single variable was thermal landscape structure ($R^2 = 0.18$; Table 3.3). Interestingly, 'site' did not appear in the most supported model (Table 3.3).

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, where all treatments were near similar baseline 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 considerably cooler and less variable than the impact sites, particularly W₂. W₂ also had the smoothest thermal landscape structure in nearly all cases, or was at least in the cluster of treatments with the smoothest structure (Fig. 3.14 to 3.17); W₂ had a more homogeneous physical landscape than the other sites, being solely jack pine plantation, which may have contributed to this smooth thermal landscape. In contrast, W₁

was a mix of natural riparian forest and jack pine plantation, F₁ and F₂ were alternating strips of red pine plantation and logged open ground, G₁ was a mix of early successional forest and open sand/gravel pit, and G₂ was a rehabilitated gravel pit (which was effectively grassland). The physical landscape mosaics of these treatments likely contributed their rougher thermal landscapes; however, the impact sites were still typically rougher than W₁ (Fig. 3.13 to 3.17). These findings largely support my prediction of cooler and less variable temperatures at the undisturbed sites compared to the impact sites; however, my 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.

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, prefer forested areas with moderate canopy cover; they thought that this reflected a trade-off between thermoregulatory vs. feeding needs for the species. Kaufmann (1992), Foscarini (1994), and Arvisais *et al.* (2004) all 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 commonly known as an edge species (Kaufmann, 1992; Compton *et al.*, 2002). This may explain why I typically found more wood turtles in and around W₁ than W₂ during the radiotelemetry study in Chapter 1; the higher variability in temperature/thermal structure at W₁ may make the site more attractive to wood turtles. 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 any distance from their home streams (Kaufmann, 1992); W_1 was much closer to the River than any of the other treatments. Several of the wood turtles radio-tracked in Chapter 1 were closer to W_1 than to W_2 , so researcher search effort may have biased my perception of a higher population density near W_1 , and thus my assumption of W_1 as 'good' wood turtle habitat. Nevertheless, even without such assumptions of relative quality, the two relatively undisturbed habitat sites showed clear differences in temperature and in thermal landscape structure to those of the impacted sites.

Resource extraction impacted the thermal quality of wood turtle habitat. Although all treatments strongly differed from T_0 (Table 3.1), the undisturbed sites showed the least frequent and least extreme median deviations from the wood turtle's thermal use range (Fig. 3.18); this low variability in habitat thermal quality compared to the impact sites shows that the undisturbed sites were more consistently of higher habitat thermal quality than the impact sites. These findings support my prediction; resource extraction degrades the thermal quality of wood turtle habitat. From a thermal perspective, my findings suggest that retaining natural forest cover provides the highest quality habitat, and studies on other turtle species corroborate my 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 far more terrestrial than either of those species, it is reasonable to hypothesize that forest cover is even more important to them. 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 to their habitat selection (Reagan, 1974). The two

resource extraction forms that I studied removed vegetation from the landscape, both in the canopy and the understory; vegetation removal has clear and well-studied thermal consequences to habitat (Liddle and Moore, 1974; Zhou *et al.*, 2007), which for wood turtles apparently translates into degradation of habitat.

The rehabilitated gravel pit, G₂, generally provided the least suitable thermal habitat (Table 3.2), and was the only site that was generally hotter than T₀ (Table 3.1). 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' (which carries no legal protection in Canada) by COSEWIC (2008), and five years before wood turtles were first officially recorded in this watershed (C. Blomme, pers. comm.). 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 listed as 'Threatened' in 2007 (COSEWIC, 2007), or when wood turtle habitat was officially protected by the government of Ontario in 2010 (OMNRF, 2010). Based on my 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 W₁. I believe that the most beneficial plan would be to plant native forest species such as white spruce, ash (*Fraxinus* sp.), white cedar (*Thuja occidentalis*), and maple (*Acer* sp.), once the successional state allows these species to grow successfully, while maintaining open patches of meadow and shrub thickets close to the River. Depressions in the soil would foster vernal pool development, important thermal refuges to the wood turtles during spring emergence (Greaves, 2007), and help maintain the open patches. Future rehabilitation plans in wood turtle habitat will be obligated to consider the species' needs,

and should avoid the plan implemented for G₂. In general, the forestry sites differed less from the recently undisturbed sites than the gravel sites, thermally-speaking, and it is less clear what my results would mean for forestry operations and/or regeneration objectives. The difference may be a result of the dominant tree species; I never observed wood turtles in red pine plantations (like F₁ and F₂) during field work, but I located several individuals in jack pine plantations (similar to W₂ and parts of W₁) incidentally and during the radio-telemetry study in Chapter 1. Anecdotally, the red pine plantations were noticeably drier than the jack pine plantations, with less understory or moss cover, including areas that had not been harvested. The forests that succeed from jack pine plantations with an understory maintained may be more beneficial for wood turtles. Further studies on the thermal and physical characteristics of different forest conditions are still required to provide operational guidance on the maintenance and/or enhancement of wood turtle habitat. Investigations on suitable ranges of stocking density and canopy closure, thinning practices, species composition, and the maximal patch sizes of clearings, are just a few research ideas that could better inform forest management planning and practices.

The thermal landscape concept can be used to predict the thermal quality of wood turtle habitat. My prediction was not supported, as habitat thermal quality generally increased with thermal landscape structure ($R^2 = 0.18$; Table 3.3), meaning that habitat thermal quality decreased with increasing thermal roughness; structure alone was also not the most predictive variable. The model with the highest predictive utility included mean diel temperature and structure, and accounted for the interactions of time of day with structure and mean temperature (Table 3.3). 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 take action as habitat thermal quality increases and decreases over the course of the day in particular areas of their home ranges. The 'site' variable's low effect on habitat thermal quality, both on its own and as a co-variate (Table 3.3), suggest that my thermal mapping technique can be easily applied in other studies to measure the thermal landscape.

In conclusion, resource extraction has thermal consequences for wood turtle habitat, both in absolute terms (temperature, thermal landscape structure) and in terms of habitat thermal quality. My first and second hypotheses were supported: temperatures and structure differed among the undisturbed sites and the impact sites, and the undisturbed sites differed from impact sites in thermal quality. My predictions were largely supported, in that the undisturbed sites were typically cooler, less variable, and higher quality than the impact sites, but not always. 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). My study shows the potential hazards of human tampering with wood turtle habitat, which should be taken into consideration, along with all of the other issues faced by the species that are contributing to its decline, when deciding management policies and best practices. Future studies should seek to map the thermal landscapes of undisturbed and impact types that I was unable to sample, such as agricultural fields, clear-cut forestry sites, and more-recently active

aggregate pits with less early-successional vegetation. Larger arrays of thermal models would also allow for more extensive and representative thermal landscape mapping; my arrays (1.8 ha) were considerably smaller than the mean home range of adult wood turtles in this population (~60 ha; Greaves, 2007). My third hypothesis was also supported, in that I showed that the thermal landscape concept can be used as a predictor of habitat thermal quality, although the strongest predictive model did not follow my predictions exactly. This represents a potential 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.

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CHAPTER 3 TABLES

TABLE 3.1 - ANOVA comparisons of mean temperatures (\pm standard deviation) selected by wood turtles (T_0) and mean temperatures of six sites in the 2015 field season: W_1 and W_2 represent pristine wood turtle (*Glyptemys insculpta*) habitat, F_1 and F_2 represent harvested forest, and G_1 and G_2 represent gravel pits.

Site	T_0 - Temp ($^{\circ}$ C)	Site - Temp ($^{\circ}$ C)	F-value	df	p-value
$T_0 \sim W_1$	19.01 \pm 4.83	15.89 \pm 5.59	397481	1, 6881	<0.01
$T_0 \sim W_2$	19.01 \pm 4.83	15.51 \pm 5.64	169666	1, 6894	<0.01
$T_0 \sim F_1$	19.01 \pm 4.83	17.43 \pm 7.90	134603	1, 6894	<0.01
$T_0 \sim F_2$	19.01 \pm 4.83	17.51 \pm 8.03	93263	1, 6894	<0.01
$T_0 \sim G_1$	19.01 \pm 4.83	17.77 \pm 8.03	88982	1, 6894	<0.01
$T_0 \sim G_2$	19.01 \pm 4.83	19.22 \pm 9.86	144880	1, 6894	<0.01

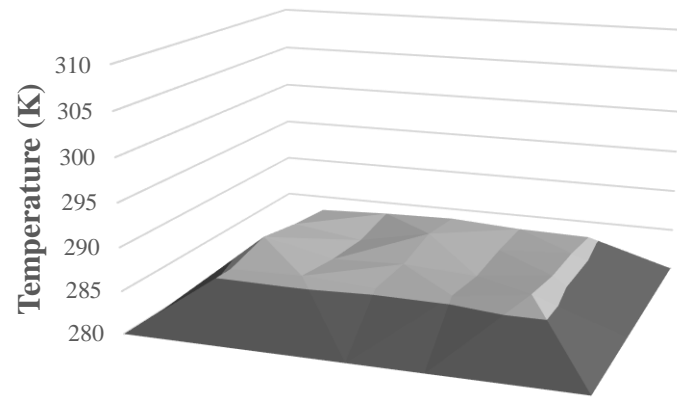
TABLE 3.2 - Median habitat thermal quality (interquartile range in parentheses) measured at six sites in Sudbury District, Ontario in the 2015 field season: W₁ and W₂ represent pristine wood turtle (*Glyptemys insculpta*) habitat, F₁ and F₂ represent harvested forest, and G₁ and G₂ represent gravel pits. Superscript letters represent post-hoc groupings in relation to W₁ and W₂ ($\alpha = 0.006$).

Site	D _e (Δ°C)
W ₁	^A 1.00 (4.00)
W ₂	^A 1.19 (4.17)
F ₁	2.00 (5.84)
F ₂	2.19 (6.52)
G ₁	1.84 (5.73)
G ₂	2.50 (7.85)

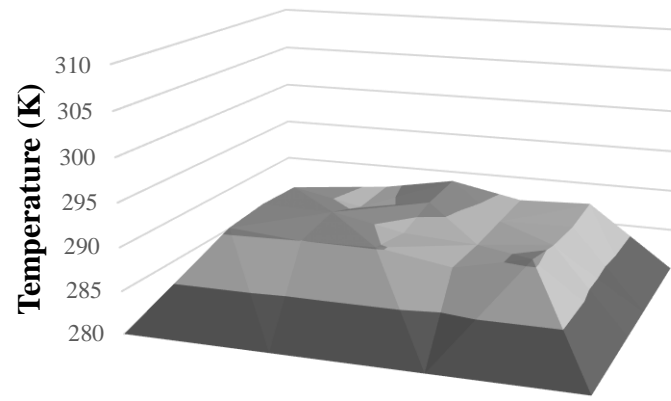
TABLE 3.3 - Model selection results using Akaike's Information Criterion (AIC) to select the strongest model predicting habitat thermal quality (D_e). Variable short forms are 'struc' (thermal landscape structure), 'mean.temp' (mean diel temperature), 'diel' (diel period), and 'site' (treatment). The model with the most support is highlighted in grey.

Model	AIC (df)	ΔAIC	R²	F-value	df	p-value
$D_e \sim \text{struc}$	17238.85 (03)	5542.81	0.175	665.20	1, 3122	<0.01
$D_e \sim \text{mean.temp}$	17841.73 (03)	6145.69	<0.001	0.50	1, 3122	0.5
$D_e \sim \text{diel}$	17307.85 (05)	5611.81	0.158	195.6	3, 3120	<0.01
$D_e \sim \text{site}$	17776.07 (07)	6080.03	0.022	14.98	5, 3118	<0.01
$D_e \sim \text{struc} + \text{mean.temp}$	16945.83 (04)	5249.79	0.250	520.00	2, 3121	<0.01
$D_e \sim \text{struc} + \text{mean.temp} + \text{diel}$	16534.97 (07)	4838.93	0.343	326.50	5, 3118	<0.01
$D_e \sim \text{struc} + \text{mean.temp} + \text{site}$	16919.34 (09)	5223.30	0.257	155.30	7, 3116	<0.01
$D_e \sim (\text{struc} + \text{mean.temp}) * \text{diel}$	11696.04 (13)	0	0.861	1753.00	11, 3112	<0.01
$D_e \sim (\text{struc} + \text{mean.temp}) * \text{site}$	16597.24 (19)	4901.20	0.332	92.26	17, 3106	<0.01

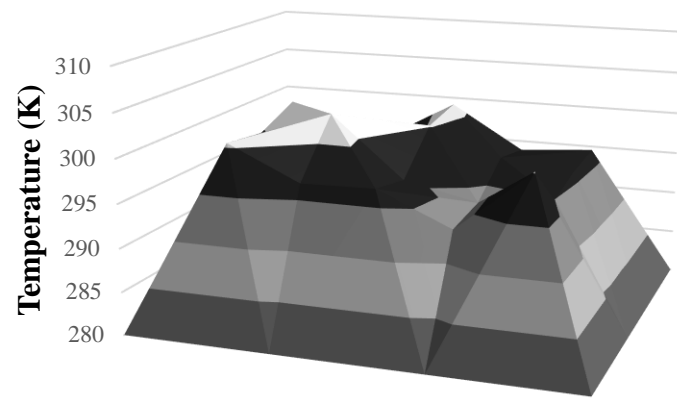
CHAPTER 3 FIGURES



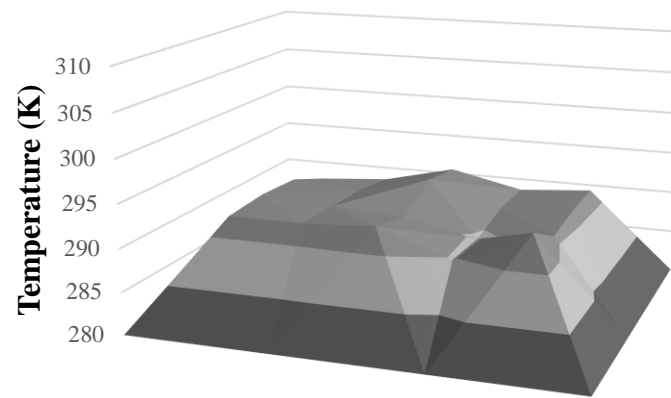
Early Morning ($V = 0.001$)



Late Morning ($V = 0.0024$)



Afternoon ($V = 0.0291$)



Evening ($V = 0.0044$)

FIGURE 3.1 - Thermal landscape maps from site G₁ (gravel impact site) on 21 June 2015 during four different 6-hour diel periods, showing correlation between 'roughness' of the thermal landscape and coefficient of variation (V). The dark gray band at the base is comprised of dummy data (280.00 K) to standardize the shape of the surface maps (graphical purposes only).

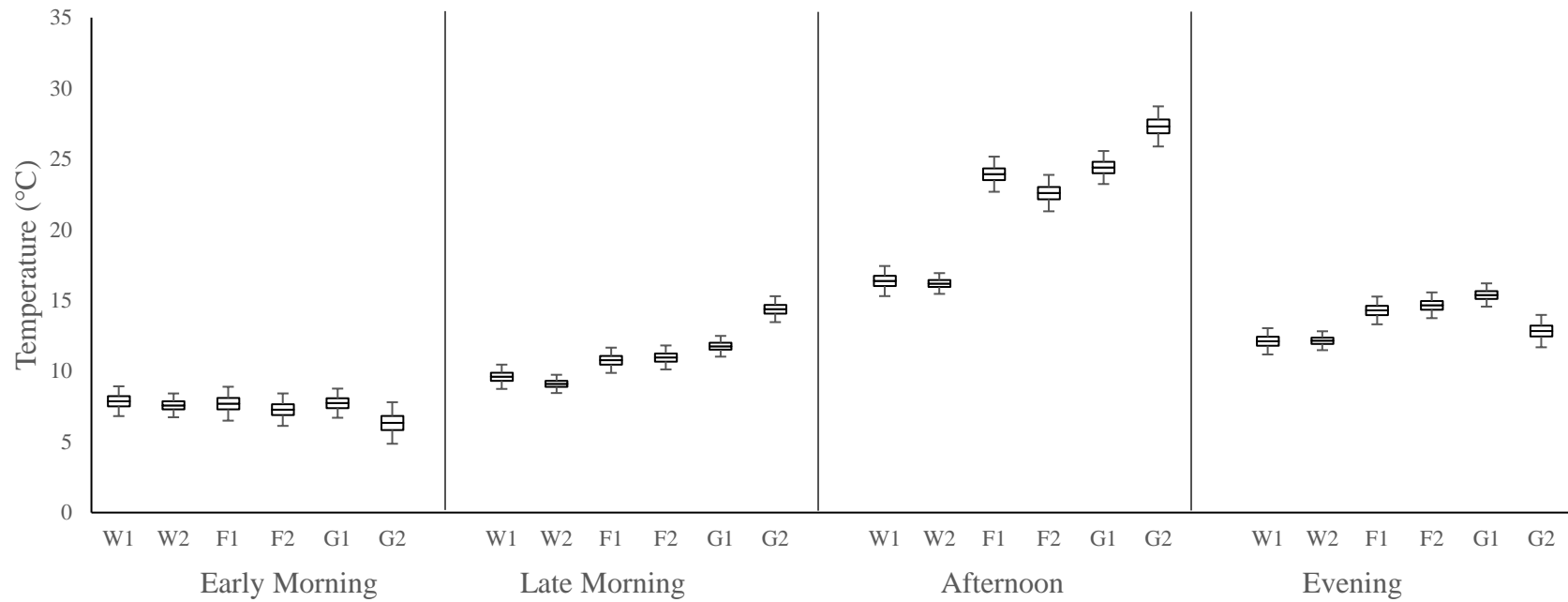


FIGURE 3.2 - Environmental temperatures measured at six sites in Sudbury District, Ontario in the Pre-Nesting period (1 May to 1 June) of the 2015 field season: W₁ and W₂ represent pristine wood turtle (*Glyptemys insculpta*) habitat, F₁ and F₂ represent harvested forest, and G₁ and G₂ represent gravel pits. Temperatures are divided into four six-hour diel periods. Middle line shows the mean temperature, boxes show standard error, and the whiskers show the 95% confidence interval.

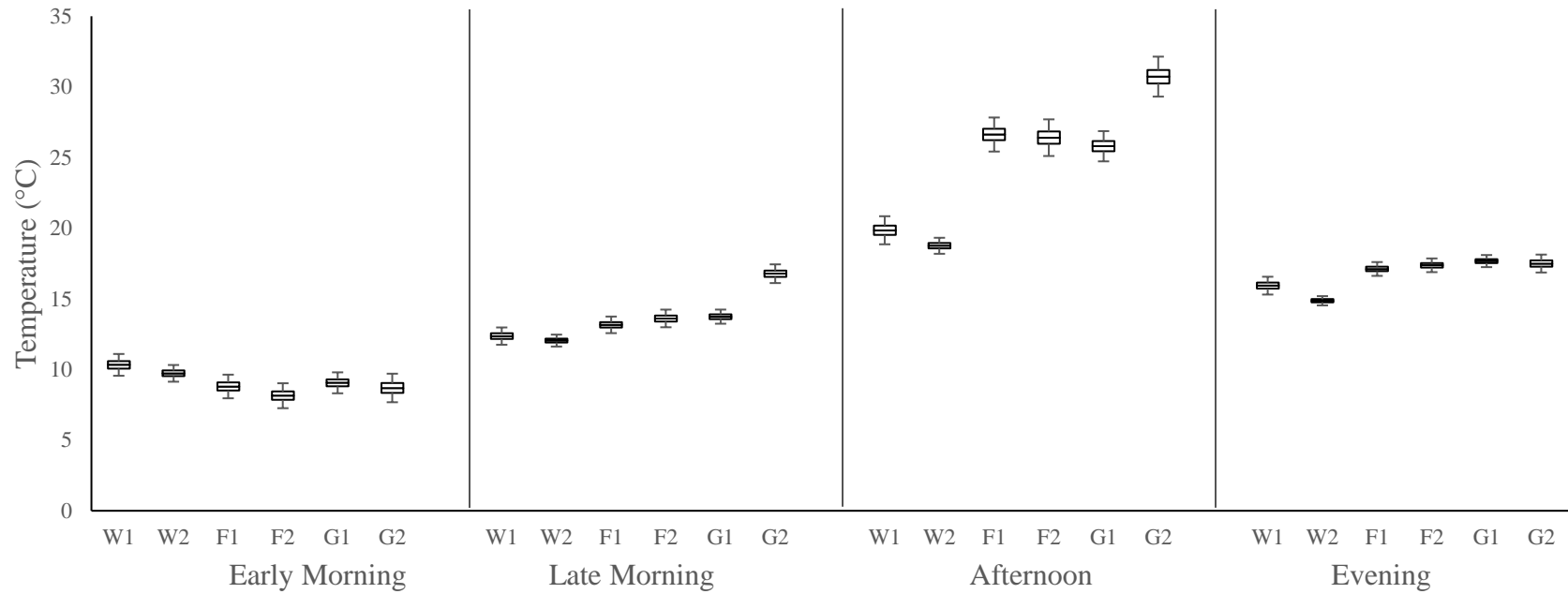


FIGURE 3.3 - Environmental temperatures measured at six sites in Sudbury District, Ontario in the Nesting period (2 June to 20 June) of the 2015 field season: W₁ and W₂ represent pristine wood turtle (*Glyptemys insculpta*) habitat, F₁ and F₂ represent harvested forest, and G₁ and G₂ represent gravel pits. Temperatures are divided into four six-hour diel periods. Middle line shows the mean temperature, boxes show standard error, and the whiskers show the 95% confidence interval.

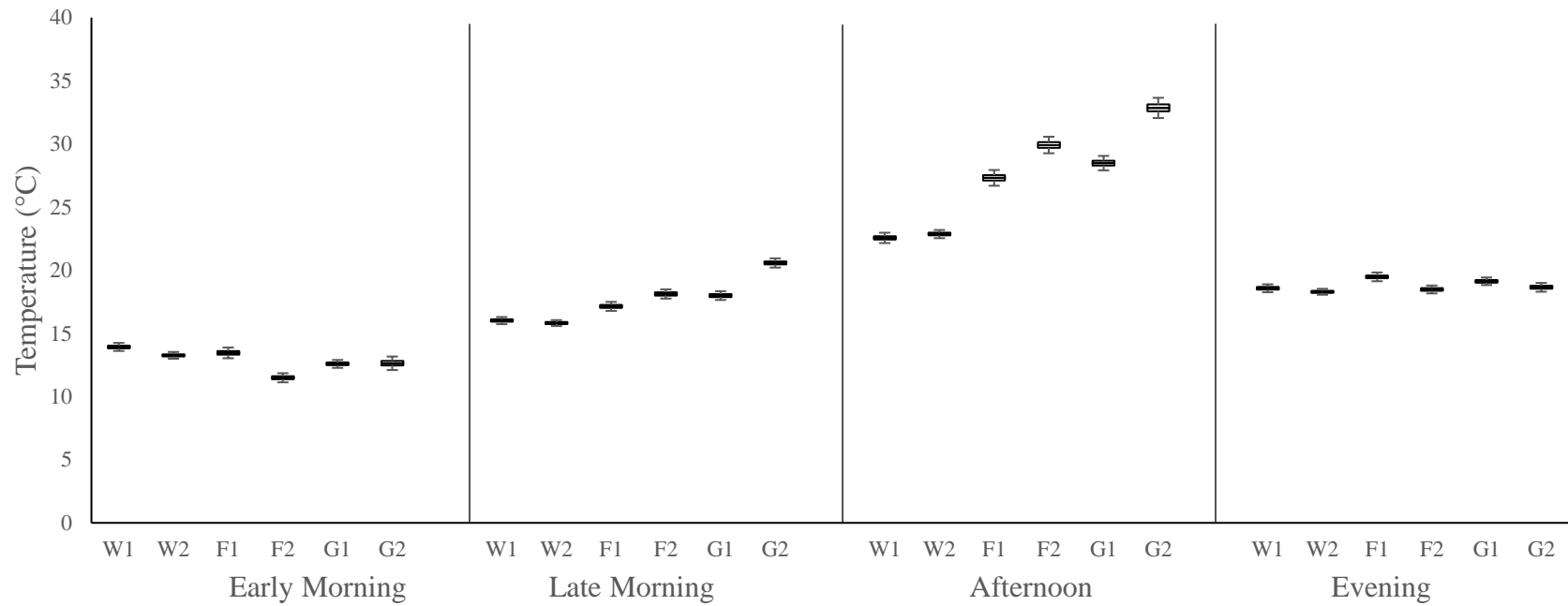


FIGURE 3.4 - Environmental temperatures measured at six sites in Sudbury District, Ontario in the Summer period (21 June to 10 September) of the 2015 field season: W₁ and W₂ represent pristine wood turtle (*Glyptemys insculpta*) habitat, F₁ and F₂ represent harvested forest, and G₁ and G₂ represent gravel pits. Temperatures are divided into four six-hour diel periods. Middle line shows the mean temperature, boxes show standard error, and the whiskers show the 95% confidence interval.

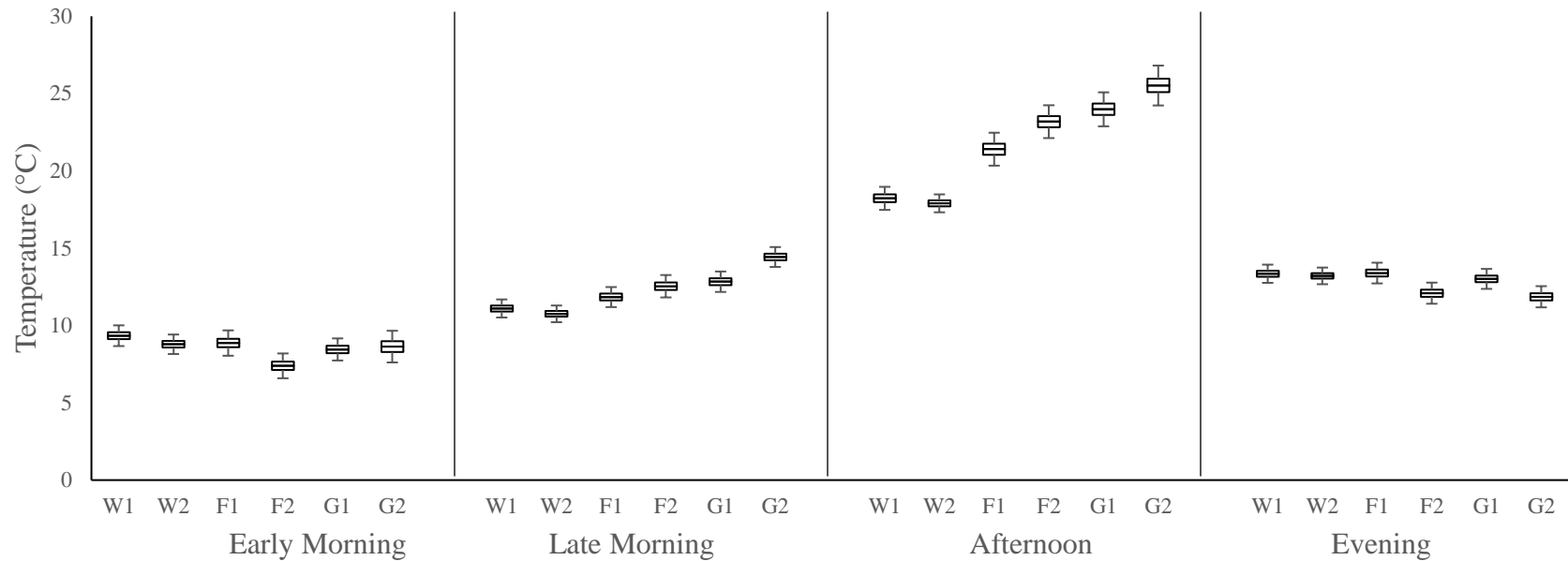


FIGURE 3.5 - Environmental temperatures measured at six sites in Sudbury District, Ontario in the Pre-Hibernation period (11 September to 30 September) of the 2015 field season: W₁ and W₂ represent pristine wood turtle (*Glyptemys insculpta*) habitat, F₁ and F₂ represent harvested forest, and G₁ and G₂ represent gravel pits. Temperatures are divided into four six-hour diel periods. Middle line shows the mean temperature, boxes show standard error, and the whiskers show the 95% confidence interval.

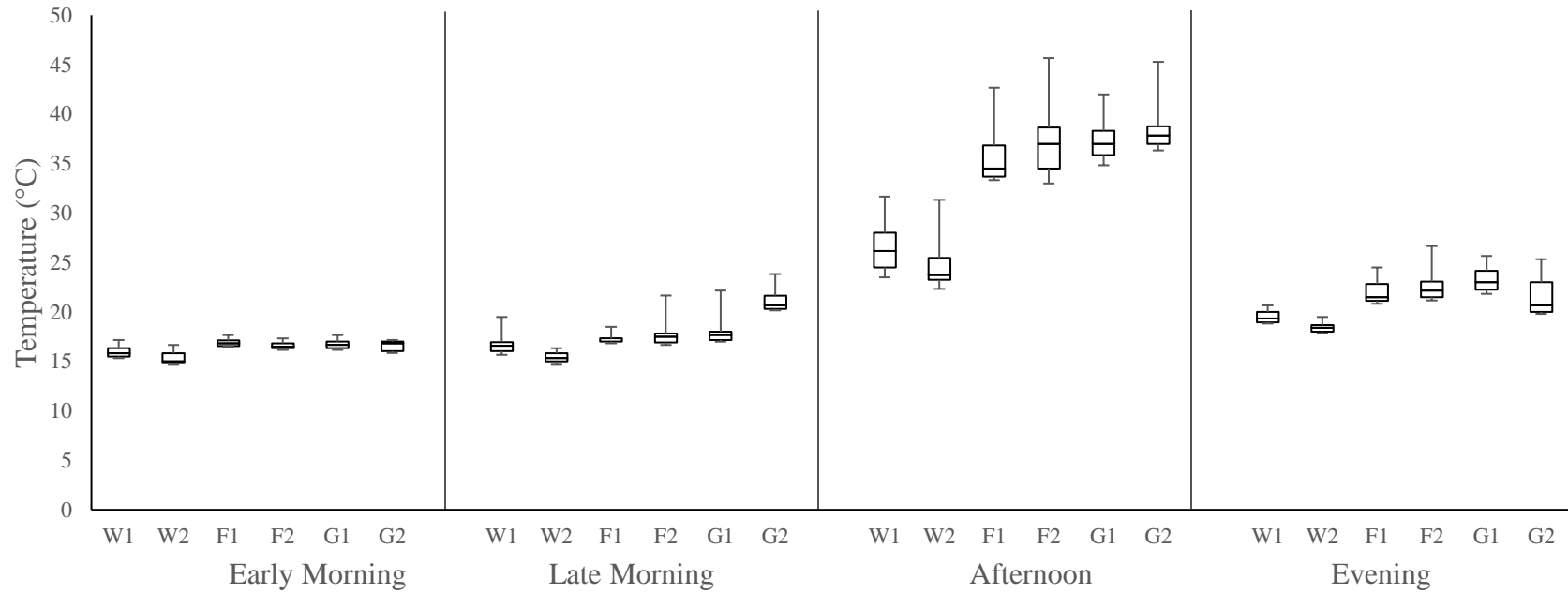


FIGURE 3.6 - Maximum environmental temperatures (90th percentile) measured at six sites in Sudbury District, Ontario in the Pre-Nesting period (1 May to 1 June) of the 2015 field season: W₁ and W₂ represent pristine wood turtle (*Glyptemys insculpta*) habitat, F₁ and F₂ represent harvested forest, and G₁ and G₂ represent gravel pits. Temperatures are divided into four six-hour diel periods. Middle line shows the median temperature, boxes show 1st to 3rd quartiles, and the whiskers show the total range.

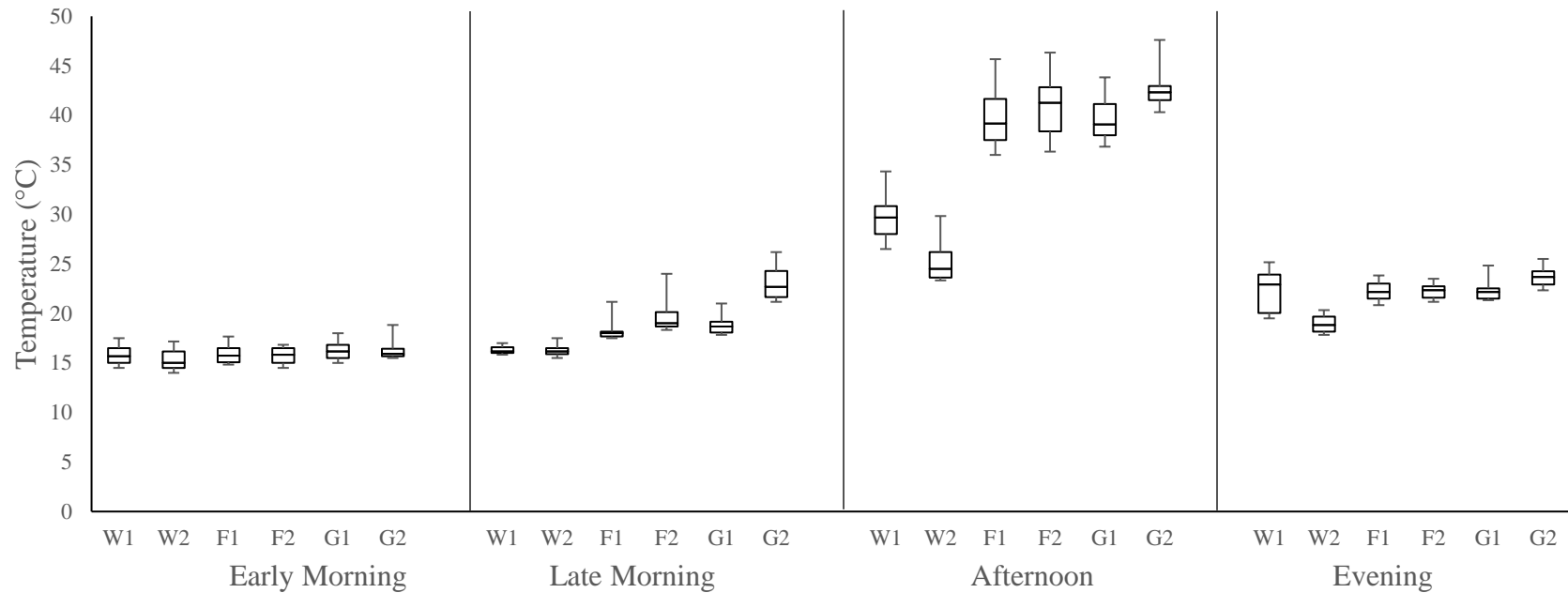


FIGURE 3.7 - Maximum environmental temperatures (90th percentile) measured at six sites in Sudbury District, Ontario in the Nesting period (2 June to 20 June) of the 2015 field season: W₁ and W₂ represent pristine wood turtle (*Glyptemys insculpta*) habitat, F₁ and F₂ represent harvested forest, and G₁ and G₂ represent gravel pits. Temperatures are divided into four six-hour diel periods. Middle line shows the median temperature, boxes show 1st to 3rd quartiles, and the whiskers show the total range.

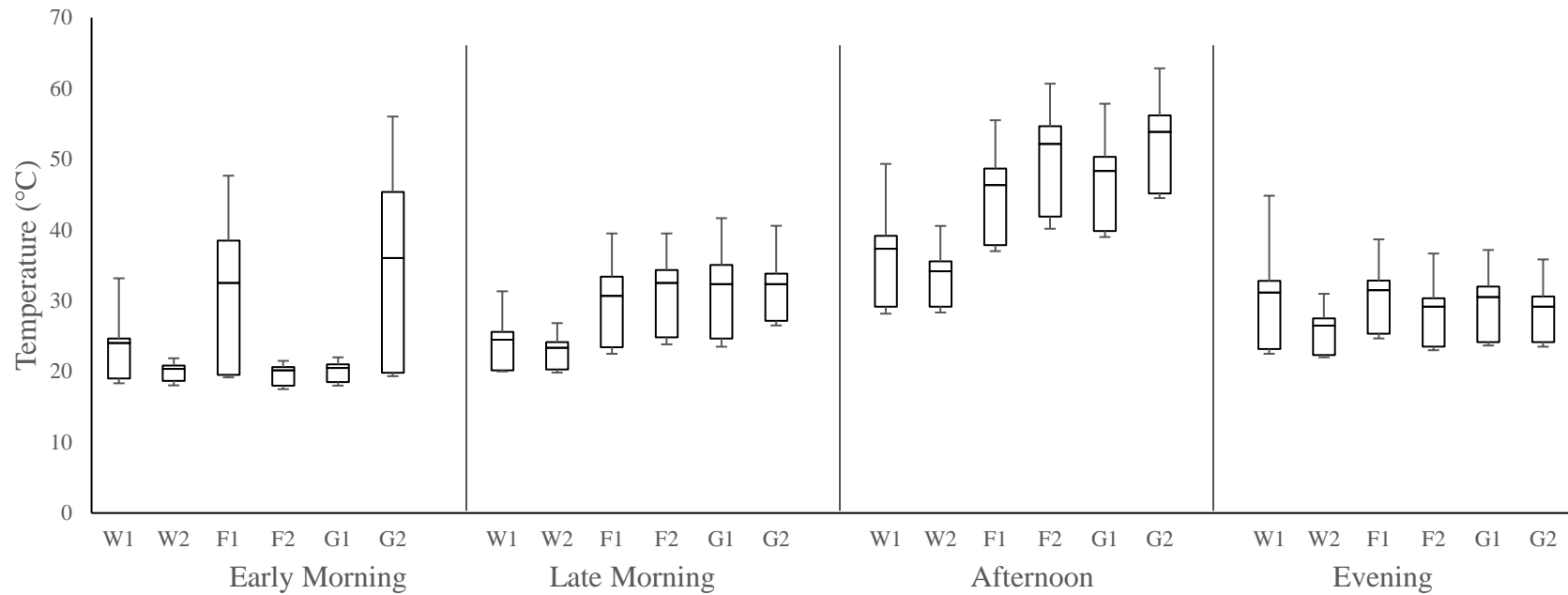


FIGURE 3.8 - Maximum environmental temperatures (90th percentile) measured at six sites in Sudbury District, Ontario in the Summer period (21 June to 10 September) of the 2015 field season: W₁ and W₂ represent pristine wood turtle (*Glyptemys insculpta*) habitat, F₁ and F₂ represent harvested forest, and G₁ and G₂ represent gravel pits. Temperatures are divided into four six-hour diel periods. Middle line shows the median temperature, boxes show 1st to 3rd quartiles, and the whiskers show the total range.

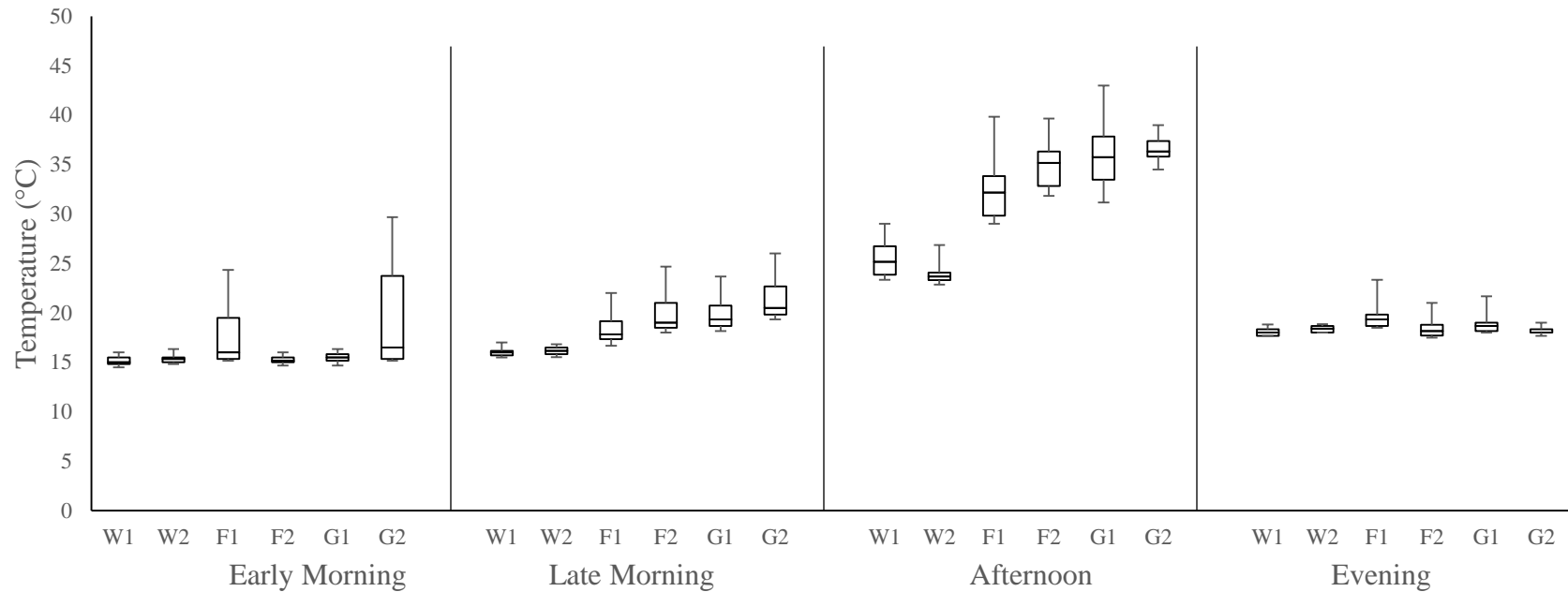


FIGURE 3.9 - Maximum environmental temperatures (90th percentile) measured at six sites in Sudbury District, Ontario in the Pre-Hibernation period (11 September to 30 September) of the 2015 field season: W₁ and W₂ represent pristine wood turtle (*Glyptemys insculpta*) habitat, F₁ and F₂ represent harvested forest, and G₁ and G₂ represent gravel pits. Temperatures are divided into four six-hour diel periods. Middle line shows the median temperature, boxes show 1st to 3rd quartiles, and the whiskers show the total range.

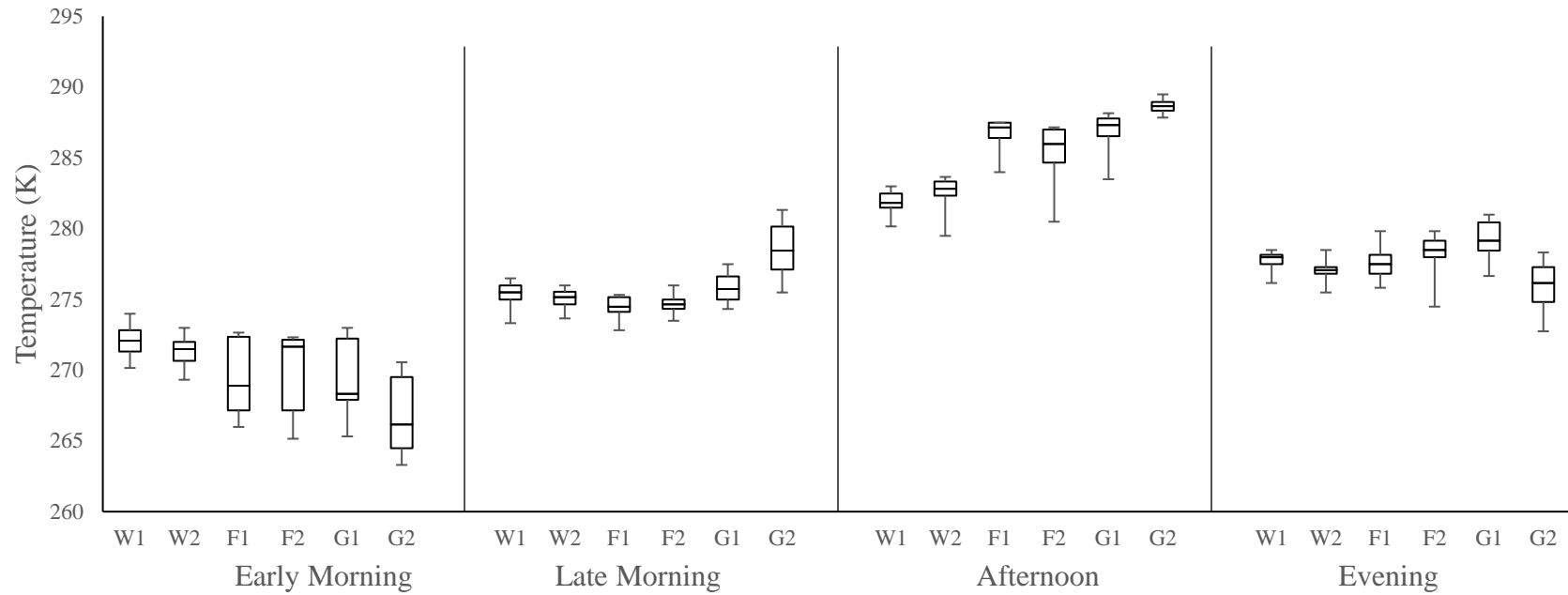


FIGURE 3.10 - Minimum environmental temperatures (10th percentile) measured at six sites in Sudbury District, Ontario in the Pre-Nesting period (1 May to 1 June) of the 2015 field season: W₁ and W₂ represent pristine wood turtle (*Glyptemys insculpta*) habitat, F₁ and F₂ represent harvested forest, and G₁ and G₂ represent gravel pits. Temperatures are divided into four six-hour diel periods. Middle line shows the median temperature, boxes show 1st to 3rd quartiles, and the whiskers show the total range.

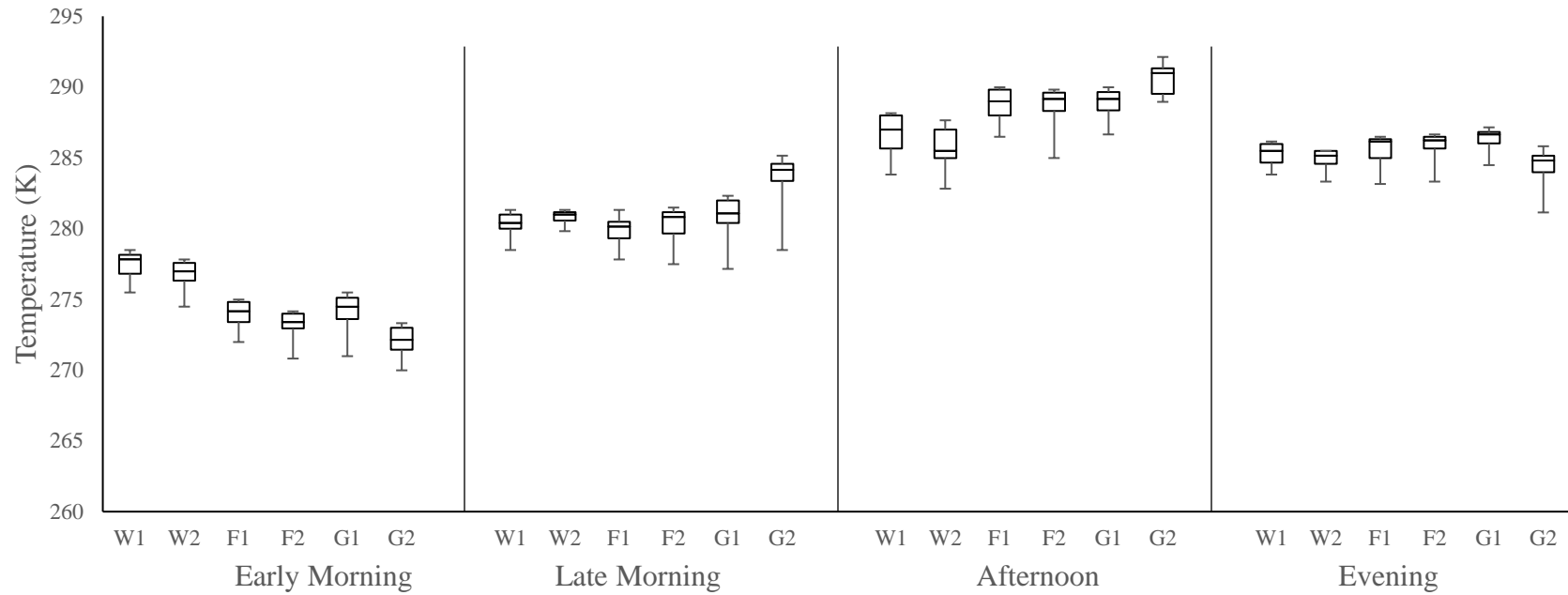


FIGURE 3.11 - Minimum environmental temperatures (10th percentile) measured at six sites in Sudbury District, Ontario in the Nesting period (2 June to 20 June) of the 2015 field season: W_1 and W_2 represent pristine wood turtle (*Glyptemys insculpta*) habitat, F_1 and F_2 represent harvested forest, and G_1 and G_2 represent gravel pits. Temperatures are divided into four six-hour diel periods. Middle line shows the median temperature, boxes show 1st to 3rd quartiles, and the whiskers show the total range.

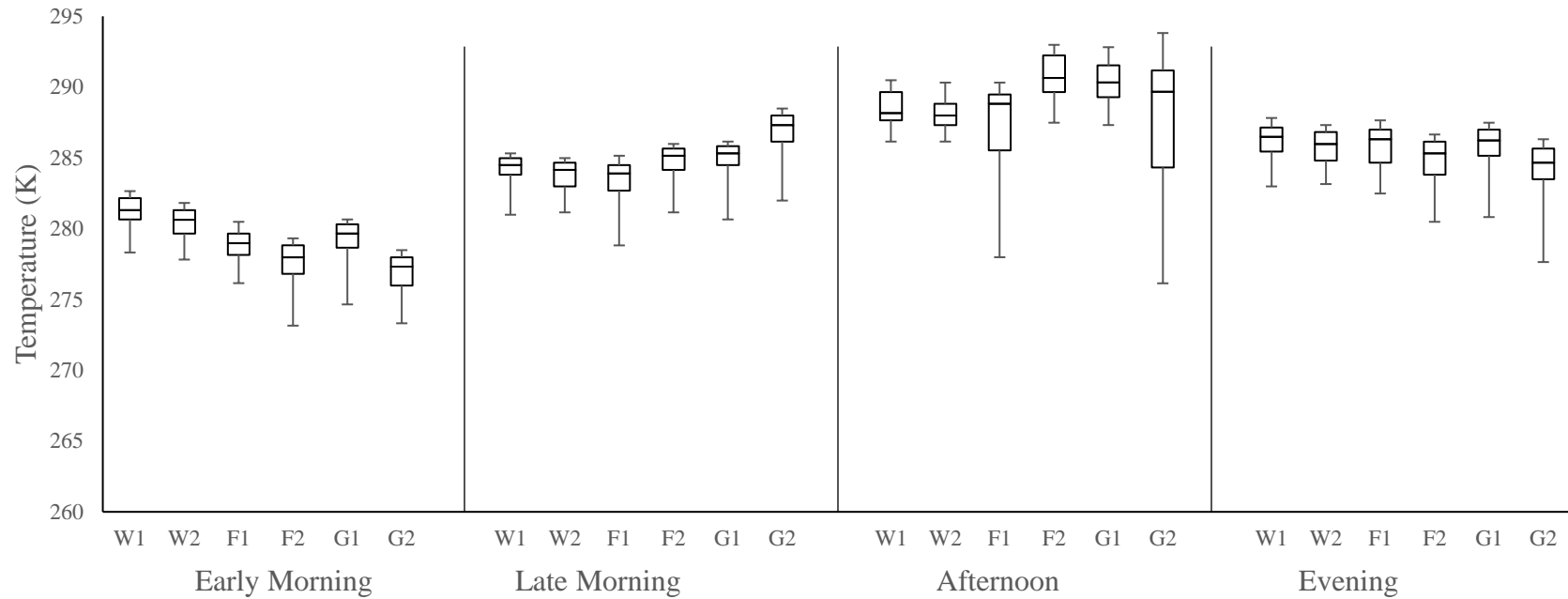


FIGURE 3.12 - Minimum environmental temperatures (10th percentile) measured at six sites in Sudbury District, Ontario in the Summer period (21 June to 10 September) of the 2015 field season: W₁ and W₂ represent pristine wood turtle (*Glyptemys insculpta*) habitat, F₁ and F₂ represent harvested forest, and G₁ and G₂ represent gravel pits. Temperatures are divided into four six-hour diel periods. Middle line shows the median temperature, boxes show 1st to 3rd quartiles, and the whiskers show the total range.

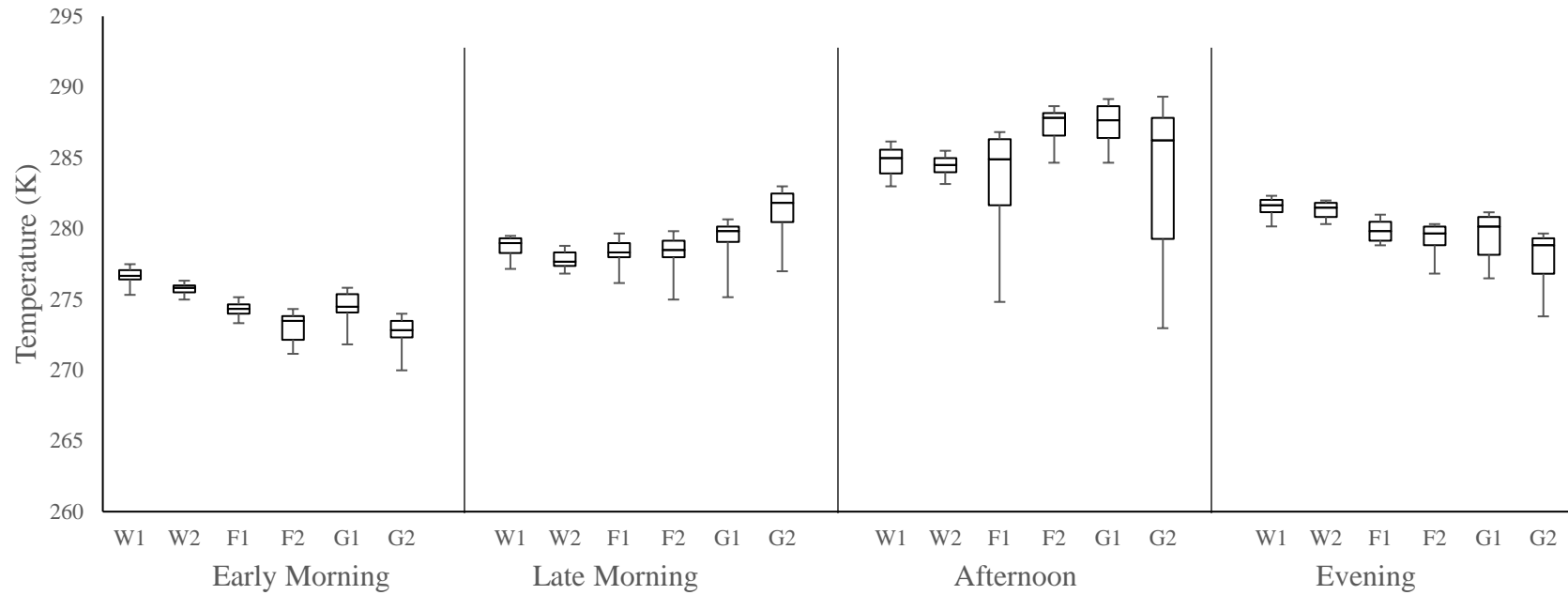


FIGURE 3.13 - Minimum environmental temperatures (10th percentile) measured at six sites in Sudbury District, Ontario in the Pre-Hibernation period (11 September to 30 September) of the 2015 field season: W_1 and W_2 represent pristine wood turtle (*Glyptemys insculpta*) habitat, F_1 and F_2 represent harvested forest, and G_1 and G_2 represent gravel pits. Temperatures are divided into four six-hour diel periods. Middle line shows the median temperature, boxes show 1st to 3rd quartiles, and the whiskers show the total range.

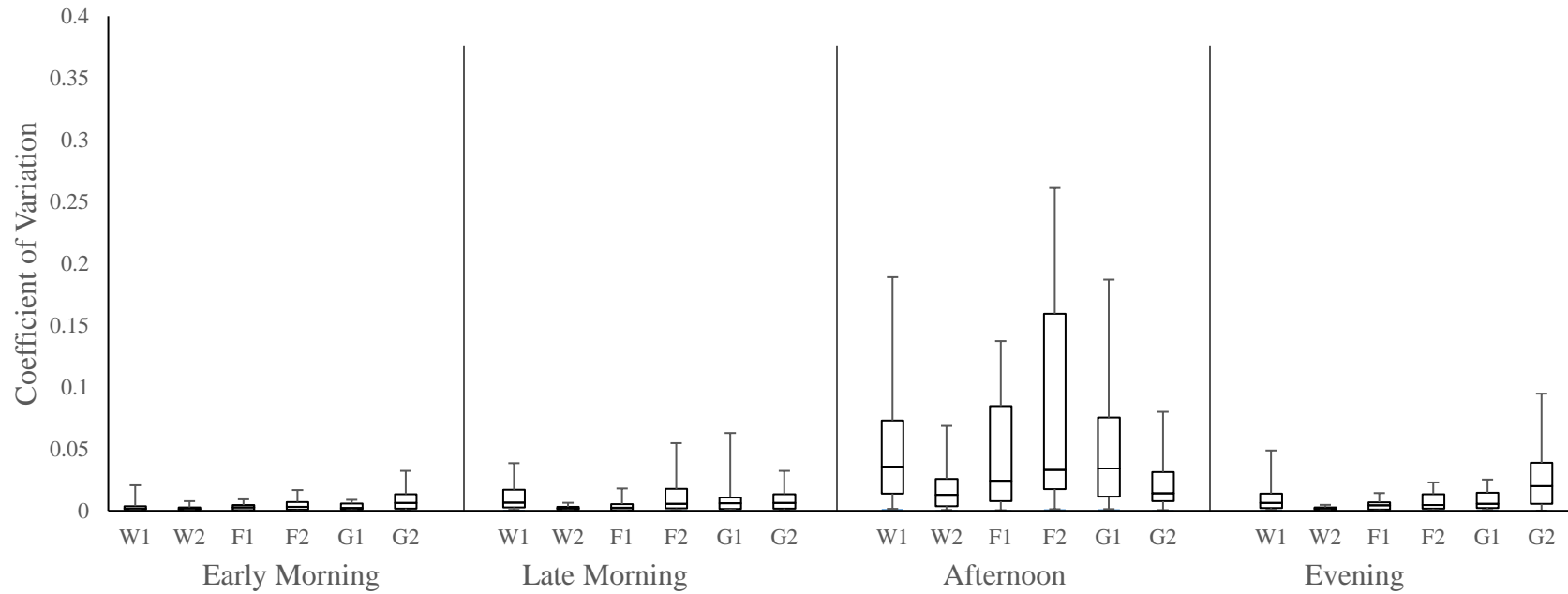


FIGURE 3.14 - Diel coefficients of variation (V) for all treatments, estimating thermal landscape structure measured at six sites in Sudbury District, Ontario in the Pre-Nesting period (1 May to 1 June) of the 2015 field season: W_1 and W_2 represent pristine wood turtle (*Glyptemys insculpta*) habitat, F_1 and F_2 represent harvested forest, and G_1 and G_2 represent gravel pits. Temperatures are divided into four six-hour diel periods. Middle line shows the median temperature, boxes show 1st to 3rd quartiles, and the whiskers show the total range.

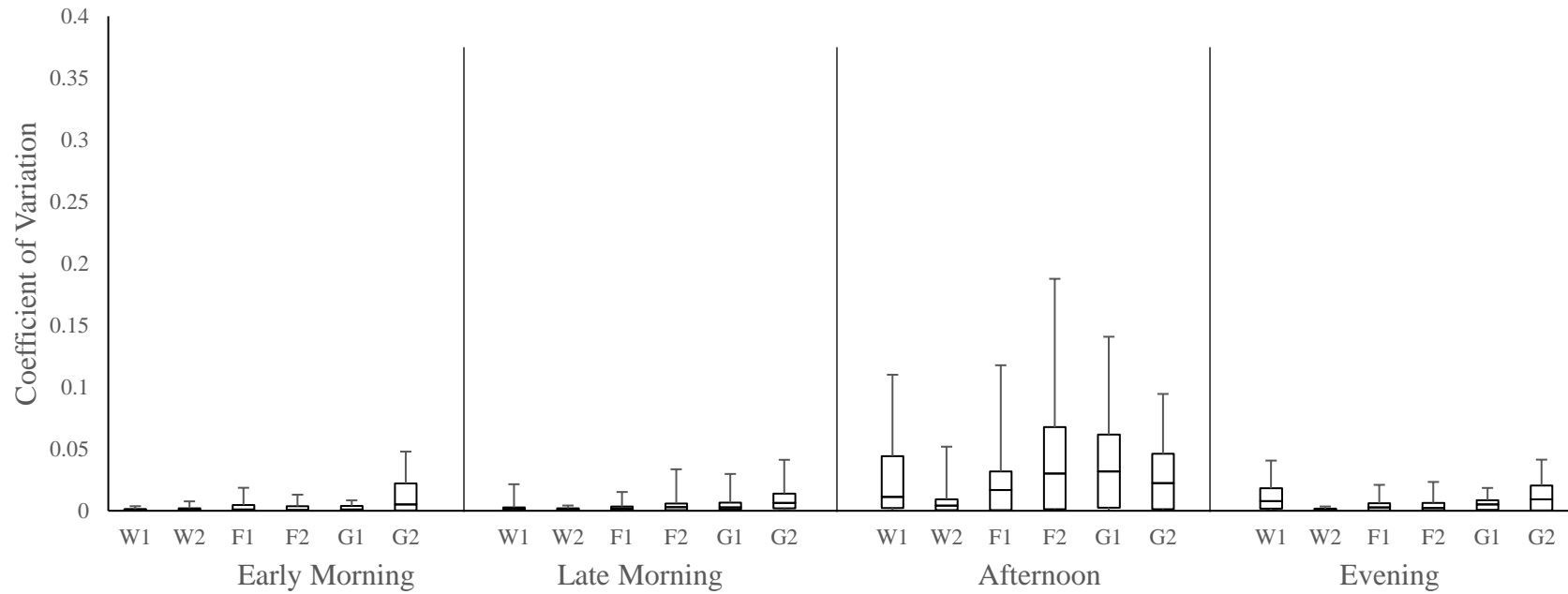


FIGURE 3.15 - Diel coefficients of variation (V) for all treatments, estimating thermal landscape structure measured at six sites in Sudbury District, Ontario in the Nesting period (2 June to 20 June) of the 2015 field season: W_1 and W_2 represent pristine wood turtle (*Glyptemys insculpta*) habitat, F_1 and F_2 represent harvested forest, and G_1 and G_2 represent gravel pits. Temperatures are divided into four six-hour diel periods. Middle line shows the median temperature, boxes show 1st to 3rd quartiles, and the whiskers show the total range.

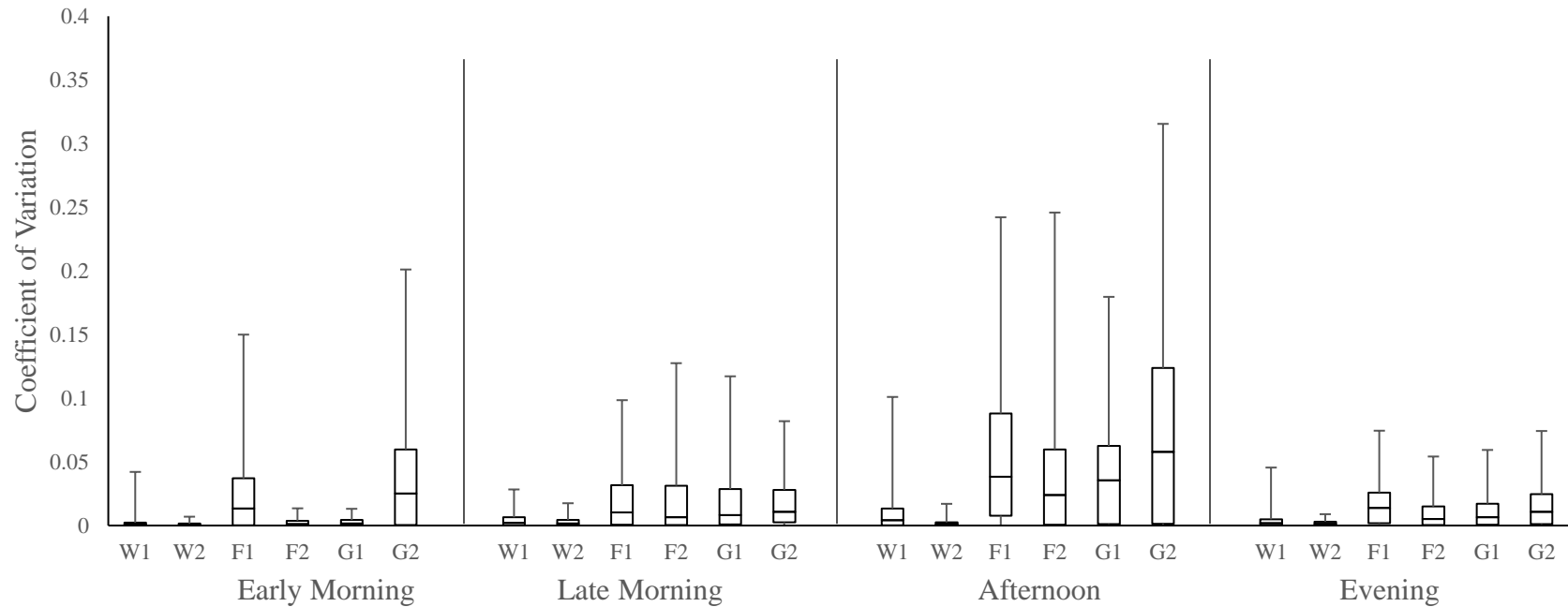


FIGURE 3.16 - Diel coefficients of variation (V) for all treatments, estimating thermal landscape structure measured at six sites in Sudbury District, Ontario in the Summer period (21 June to 10 September) of the 2015 field season: W_1 and W_2 represent pristine wood turtle (*Glyptemys insculpta*) habitat, F_1 and F_2 represent harvested forest, and G_1 and G_2 represent gravel pits. Temperatures are divided into four six-hour diel periods. Middle line shows the median temperature, boxes show 1st to 3rd quartiles, and the whiskers show the total range.

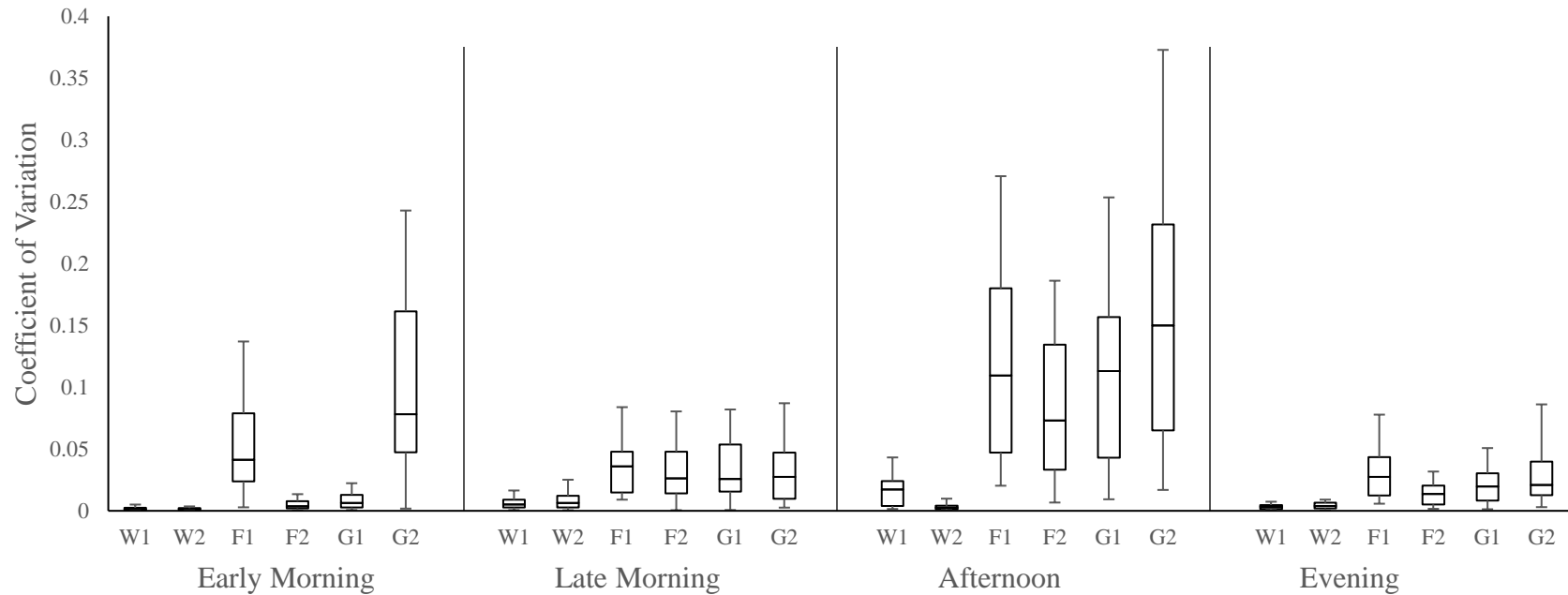


FIGURE 3.17 - Diel coefficients of variation (V) for all treatments, estimating thermal landscape structure measured at six sites in Sudbury District, Ontario in the Pre-Hibernation period (11 September to 30 September) of the 2015 field season: W_1 and W_2 represent pristine wood turtle (*Glyptemys insculpta*) habitat, F_1 and F_2 represent harvested forest, and G_1 and G_2 represent gravel pits. Temperatures are divided into four six-hour diel periods. Middle line shows the median temperature, boxes show 1st to 3rd quartiles, and the whiskers show the total range.

GENERAL CONCLUSIONS

Wood turtles (*Glyptemys insculpta*) are Species at Risk across their range, and chelonians in general are declining worldwide. The exploration of novel techniques to survey for general habitat and key habitat features, particularly while taking advantage of new technologies and new perspectives, would only be to the benefit of turtle conservation efforts in the future. I was prompted to perform this study partially to explore the idea of a "mammalian bias" on the part of human researchers; as endotherms, we may not be able to readily consider the perspectives of our reptilian study animals, who are thought to be far more affected by environmental temperatures than we are. Instead, my project showed that wood turtles, far from being at the mercy of the elements, are able to successfully exploit their environment to suit their needs. Home range level spatial selections were not strongly governed by temperature, and although wood turtles do need to thermoregulate behaviourally, they are apparently able to do so without great effort by exploiting their micro-habitats. Temperature is very important to incubating eggs, and surface temperature range generally seemed to be the principle cue by female wood turtles when selecting a nest site. However, as the surface temperature of the beaches co-varies with other, more tangible features, it is also possible that the females are selecting based on a suite of features rather than a single cue. These results suggest that wood turtles have a more complex relationship with the thermal landscape than I had predicted.

I explored the potential of thermal landscape mapping for future studies. Temperature is easier to measure than many other characteristics of the landscape, and does not require as much specialized training as other techniques, such as a forest inventory, would; if it proved useful in my studies, I believed it would allow for the development of more efficient surveying techniques. My studies, when taken in view of the existing literature on the subject, show that

future thermo-spatial studies are best focused on smaller-scale landscapes. I also had grand ambitions for the future of thermal imagery in reptile ecology studies. Thermal imagery technology will only become less expensive and more readily available in the future; I envisioned thermal images taken from aircraft or satellites giving ecologists tools to survey for undiscovered populations, or to look for suitable areas for potential re-introductions. I also envisioned using a thermal camera to determine if a particular beach was or could be a nesting beach, which would allow nest-site surveying outside of the nesting season. The thermal cameras that I used were expensive and cumbersome, however, and the techniques that I developed to use them did not provide the quality of results that I had hoped for. With stronger protocols for the use of the cameras, they could be useful tools for field work, but simpler mapping techniques, like the one that I used in Chapter 3 (an array of simple temperature monitoring stations) appeared to be more cost-effective and useful strategies for the immediate future.

I would recommend further development and refinement of the thermal mapping technique that I used in Chapters 1 and 3. Experimentation with different grid resolutions, timings of temperature readings, and methods of data collection redundancy could lead to a very useful strategy for assessing the quality of general habitat and key habitat features in future studies. My results from Chapter 3 can, I believe, provide useful insights for mitigation of sites impacted by natural resource extraction, by allowing for more thermally-targeted mitigation or rehabilitation projects. Long-term monitoring with this technique might also prove useful in the study of the effects of climate change at local levels. I also intend to continue exploration of the data set from Chapter 1 from a more seasonal approach, as this may reveal a greater dependence on the thermal landscape in the spring and fall, when ambient temperatures are less suitable for wood turtles. Future studies might also explore a potential 'social landscape', to determine how

much the presence/absence of conspecifics affects wood turtle spatial ecology. Over the last three field seasons, I and my field crew have often observed wood turtles basking in close proximity, typically male-female, female-female, or adult-juvenile pairs. Whether this is sought-after social interaction or mere tolerance of conspecifics would be a valuable insight into wood turtle ecology.

APPENDIX

TABLE A.1 - Daily mean temperature readings (\pm interquartile range) from usage zones on wood turtle (*Glyptemys insculpta*) nesting beaches in Sudbury District, ON, in 2016. Kruskal-Wallis test results display differences in daily temperature; asterisks show post-hoc groupings in relation to high use zones.

M-BEACH	M-NU	M-LU	M-HU	X²-value	df	p-value
Date	Mean Temp (°C)	Mean Temp (°C)	Mean Temp (°C)			
6 June	*14.0 (\pm 0.4)	*14.1 (\pm 0.5)	*13.8 (\pm 0.7)	2.09	2	0.35
9 June	8.1 (\pm 1.9)	11.9 (\pm 1.0)	9.7 (\pm 4.5)	13.42	2	<0.01
10 June	11.9 (\pm 0.7)	14.6 (\pm 1.5)	13.0 (\pm 4.1)	10.87	2	<0.01
W-BEACH	W-NU	W-LU	W-HU	X²-value	df	p-value
Date	Mean Temp (°C)	Mean Temp (°C)	Mean Temp (°C)			
5 June	*19.2 (\pm 0.4)	*19.1 (\pm 0.6)	*19.4 (\pm 0.4)	1.11	2	0.57
6 June	*19.1 (\pm 0.8)	*19.2 (\pm 0.2)	*19.4 (\pm 0.6)	1.01	2	0.60
8 June	*17.3 (\pm 7.3)	*17.1 (\pm 5.9)	*16.9 (\pm 7.8)	0.54	2	0.76
11 June	*28.9 (\pm 5.3)	*29.2 (\pm 4.8)	*29.1 (\pm 6.2)	0.10	2	0.95
B-NU	B-HU	X²-value	df	p-value		
Date	Mean Temp (°C)					
9 June	*13.7 (\pm 3.8)	*13.8 (\pm 3.3)	0.39	1	0.53	
10 June	*15.0 (\pm 3.4)	*13.8 (\pm 3.3)	1.76	1	0.19	
11 June	*17.7 (\pm 5.4)	*17.1 (\pm 5.0)	0.52	1	0.47	

TABLE A.2 - Daily temperature range readings (\pm interquartile range) from usage zones on wood turtle (*Glyptemys insculpta*) nesting beaches in Sudbury District, ON, in 2016. Kruskal-Wallis test results display differences in daily temperature; asterisks show post-hoc groupings in relation to high use zones.

M-BEACH	M-NU	M-LU	M-HU			
Date	Mean Temp (°C)	Mean Temp (°C)	Mean Temp (°C)	X²-value	df	p-value
6 June	*3.0 (\pm 0.8)	*3.0 (\pm 0.8)	*2.6 (\pm 0.3)	4.84	2	0.09
9 June	9.8 (\pm 1.0)	7.5 (\pm 0.7)	5.4 (\pm 1.2)	15.63	2	<0.01
10 June	*5.5 (\pm 2.1)	*5.1 (\pm 0.5)	*3.9 (\pm 0.7)	3.32	2	0.19
W-BEACH	W-NU	W-LU	W-HU			
Date	Mean Temp (°C)	Mean Temp (°C)	Mean Temp (°C)	X²-value	df	p-value
5 June	2.6 (\pm 0.6)	2.8 (\pm 0.4)	1.9 (\pm 0.1)	16.77	2	<0.01
6 June	3.4 (\pm 0.7)	4.0 (\pm 0.5)	1.8 (\pm 0.3)	18.79	2	<0.01
8 June	3.0 (\pm 0.4)	2.4 (\pm 0.9)	3.3 (\pm 1.8)	8.44	2	0.02
11 June	3.7 (\pm 0.6)	3.1 (\pm 0.6)	2.4 (\pm 0.5)	14.76	2	<0.01
	B-NU	B-HU				
Date	Mean Temp (°C)	Mean Temp (°C)	X²-value	df	p-value	
9 June	1.3 (\pm 0.6)	2.7 (\pm 1.1)	5.30	1	0.02	
10 June	*1.7 (\pm 0.5)	*1.9 (\pm 0.2)	1.13	1	0.29	
11 June	*1.3 (\pm 0.3)	*1.8 (\pm 0.5)	2.41	1	0.12	

TABLE A.3 - Comparisons of medians of daily mean temperature and daily temperature ranges (\pm interquartile range) among high use zones of wood turtle (*Glyptemys insculpta*) nesting beaches in the Sudbury District, ON, in 2016. Kruskal-Wallis test results display differences in daily temperature; asterisks show post-hoc groupings.

Date	Beaches	M Mean Temp (°C)	W Mean Temp (°C)	B Mean Temp (°C)	X ² -value	df	p-value
6 June	M, W	13.8 (\pm 0.7)	19.4 (\pm 0.6)		13.60	1	<0.01
9 June	B, M	*9.7 (\pm 4.5)		*13.5 (\pm 3.7)	0.51	1	0.48
10 June	B, M	*13.0 (\pm 4.1)		*13.8 (\pm 3.3)	0.43	1	0.51
11 June	B, W		29.1 (\pm 6.2)	19.9 (\pm 3.4)	14.30	1	<0.01

Date	Beaches	M Temp Range (Δ °C)	W Temp Range (Δ °C)	B Temp Range (Δ °C)	X ² -value	df	p-value
6 June	M, W	2.6 (\pm 0.3)	1.8 (\pm 0.3)		13.40	1	<0.01
9 June	B, M	5.3 (\pm 0.3)		1.7 (\pm 1.1)	13.57	1	<0.01
10 June	B, M	3.9 (\pm 1.7)		2.0 (\pm 0.7)	13.21	1	<0.01
11 June	B, W		*2.4 (\pm 0.5)	*2.0 (\pm 0.7)	0.76	1	0.38

TABLE A.4 - Median daily moisture readings for all usage zones on wood turtle (*Glyptemys insculpta*) nesting beaches in the Sudbury District (ON) in 2016. Moisture readings are in percent soil content (\pm interquartile range). Kruskal-Wallis test results display differences in daily soil moisture; asterisks show post-hoc groupings in relation to high use zones. Precipitation data are taken from Environment Canada.

M-BEACH		M-NU	M-LU	M-HU	X²-value	df	p-value
Date	Precipitation (mm)	Moisture (%)	Moisture (%)	Moisture (%)			
	0.0	*2.1 (\pm 1.2)	*1.1 (\pm 0.7)	*1.1 (\pm 0.4)	15.78	2	0.06
4 June	0.0	*3.2 (\pm 2.5)	*1.2 (\pm 1.0)	*1.3 (\pm 0.4)	1.54	2	0.46
5 June	16.4	8.7 (\pm 5.8)	*5.3 (\pm 1.5)	*5.8 (\pm 2.2)	6.31	2	0.04
6 June	5.8	12.6 (\pm 3.8)	6.3 (\pm 1.2)	2.5 (\pm 1.7)	11.77	2	<0.01
7 June	0.6	8.6 (\pm 3.3)	*3.4 (\pm 2.1)	*1.9 (\pm 1.5)	10.64	2	<0.01
8 June	0.4	*8.7 (\pm 9.6)	*2.4 (\pm 1.0)	*1.6 (\pm 2.2)	5.33	2	0.07
9 June	0.0	7.5 (\pm 3.8)	*2.3 (\pm 1.6)	*1.4 (\pm 0.1)	8.33	2	0.02
10 June	1.2	4.8 (\pm 2.8)	*1.6 (\pm 0.6)	*1.3 (\pm 0.5)	5.12	2	0.08
11 June	1.0	*5.1 (\pm 2.8)	*1.7 (\pm 0.1)	*1.5 (\pm 0.2)	10.60	2	<0.01

W-BEACH		W-NU	W-LU	W-HU	X²-value	df	p-value
Date	Precipitation (mm)	Moisture (%)	Moisture (%)	Moisture (%)			
3 June	0.0	*2.3 (\pm 1.3)	*1.7 (\pm 0.5)	*1.5 (\pm 0.9)	2.77	2	0.25
4 June	0.0	2.6 (\pm 0.9)	*2.5 (\pm 0.5)	*2.0 (\pm 0.7)	7.92	2	0.02
5 June	16.4	3.0 (\pm 0.9)	*4.4 (\pm 2.0)	*3.7 (\pm 1.8)	8.17	2	0.02
6 June	5.8	*2.8 (\pm 1.0)	*3.7 (\pm 2.0)	*3.0 (\pm 2.2)	2.14	2	0.34
7 June	0.6	*2.9 (\pm 0.7)	*2.5 (\pm 0.4)	*2.3 (\pm 1.3)	3.12	2	0.21
8 June	0.4	2.6 (\pm 0.5)	*2.1 (\pm 0.5)	*1.9 (\pm 0.8)	13.63	2	<0.01
9 June	0.0	2.7 (\pm 0.9)	2.5 (\pm 0.6)	1.8 (\pm 0.9)	8.60	2	0.01
10 June	1.2	2.3 (\pm 0.5)	*2.3 (\pm 1.4)	*1.8 (\pm 0.5)	8.91	2	0.01
11 June	1.0	*2.4 (\pm 0.7)	*2.6 (\pm 0.3)	*2.1 (\pm 0.4)	5.31	2	0.07

B-BEACH		B-NU	B-HU	X²-value	df	p-value
Date	Precipitation (mm)	Moisture (%)	Moisture (%)			
3 June	0.0	*0.9 (\pm 0.5)	*0.6 (\pm 1.1)	0.25	1	0.61
4 June	0.0	*0.9 (\pm 0.2)	*0.6 (\pm 0.4)	3.69	1	0.06
5 June	16.4	*8.8 (\pm 3.6)	*9.9 (\pm 1.4)	1.67	1	0.47
6 June	5.8	*8.1 (\pm 1.8)	*10.0 (\pm 4.9)	1.65	1	0.20
7 June	0.6	*5.2 (\pm 1.1)	*6.1 (\pm 3.9)	3.46	1	0.06
8 June	0.4	*3.8 (\pm 1.0)	*5.4 (\pm 1.7)	3.46	1	0.06
9 June	0.0	*2.9 (\pm 0.5)	*4.4 (\pm 1.4)	1.68	1	0.20
10 June	1.2	*2.9 (\pm 0.4)	*3.4 (\pm 1.0)	1.15	1	0.28
11 June	1.0	*3.0 (\pm 0.7)	*2.9 (\pm 1.0)	0.74	1	0.39

TABLE A.5 - Comparisons of median daily soil moisture content (\pm interquartile range) among high use zones of wood turtle (*Glyptemys insculpta*) nesting beaches in the Sudbury District, ON, in 2016. Asterisks show post-hoc groupings.

Date	M Moisture (%)	W Moisture (%)	B Moisture (%)	X²-value	df	p-value
3 June	*1.1 (\pm 0.4)	1.5 (\pm 0.9)	*0.6 (\pm 1.1)	6.02	2	0.05
4 June	1.3 (\pm 0.4)	2.0 (\pm 0.7)	0.6 (\pm 0.4)	20.38	2	<0.01
5 June	*5.8 (\pm 2.1)	*3.7 (\pm 1.8)	9.9 (\pm 1.4)	8.45	2	0.02
6 June	*2.5 (\pm 1.7)	*3.0 (\pm 2.2)	10.0 (\pm 4.9)	15.34	2	<0.01
7 June	*1.9 (\pm 1.5)	*2.3 (\pm 1.3)	6.1 (\pm 3.9)	15.60	2	<0.01
8 June	*1.6 (\pm 2.2)	*1.9 (\pm 0.8)	5.4 (\pm 1.7)	9.16	2	0.01
9 June	1.4 (\pm 0.1)	1.8 (\pm 0.9)	4.4 (\pm 1.4)	7.23	2	0.03
10 June	*1.3 (\pm 0.5)	*1.8 (\pm 0.5)	3.4 (\pm 1.0)	11.74	2	<0.01
11 June	1.5 (\pm 0.2)	2.1 (\pm 0.4)	2.9 (\pm 1.0)	18.78	2	<0.01

TABLE A.6 - Median grain size distributions for all usage zones on wood turtle (*Glyptemys insculpta*) nesting beaches in the Sudbury District (ON) in 2016. Size distributions are in percent soil by mass (\pm interquartile range). Kruskal-Wallis test results display differences in grain size class; asterisks show post-hoc groupings in relation to high use zones.

M-BEACH						
Grain Size Class	M-NU (%)	M-LU (%)	M-HU (%)	X²-value	df	p-value
Gravel	0.3 (\pm 0.1)	0.9 (\pm 0.8)	0.0 (\pm 0.0)	10.39	2	0.01
Very Coarse Sand	1.9 (\pm 1.2)	10.5 (\pm 4.9)	0.1 (\pm 0.1)	10.02	2	0.01
Coarse Sand	17.4 (\pm 11.7)	42.6 (\pm 2.4)	4.3 (\pm 1.1)	8.35	2	0.02
Medium Sand	39.9 (\pm 3.4)	*27.9 (\pm 9.1)	*28.5 (\pm 16.0)	7.39	2	0.03
Fine Sand	26.6 (\pm 10.0)	13.0 (\pm 1.4)	56.2 (\pm 13.5)	8.35	2	0.02
Very Fine Sand	*6.3 (\pm 3.2)	*2.5 (\pm 0.7)	*10.0 (\pm 3.7)	4.77	2	0.09
Fines	*0.9 (\pm 0.4)	*0.2 (\pm 0.1)	*0.8 (\pm 0.3)	5.02	2	0.08
W-BEACH						
Grain Size Class	W-NU (%)	W-LU (%)	W-HU (%)	X²-value	df	p-value
Gravel	57.2 (\pm 7.8)	*1.3 (\pm 3.1)	*2.4 (\pm 2.5)	7.42	2	0.03
Very Coarse Sand	*8.7 (\pm 1.4)	*15.2 (\pm 18.2)	*18.3 (\pm 18.4)	1.08	2	0.58
Coarse Sand	10.1 (\pm 1.8)	*43.0 (\pm 5.7)	*35.7 (\pm 9.8)	8.00	2	0.02
Medium Sand	*14.1 (\pm 2.7)	*17.2 (\pm 13.7)	*17.4 (\pm 17.4)	0.04	2	0.98
Fine Sand	*6.1 (\pm 0.6)	*12.8 (\pm 3.2)	*11.0 (\pm 13.1)	4.50	2	0.11
Very Fine Sand	1.4 (\pm 0.4)	*5.6 (\pm 1.2)	*4.3 (\pm 4.0)	6.29	2	0.04
Fines	*0.3 (\pm 0.0)	*1.3 (\pm 0.5)	*0.9 (\pm 1.0)	5.02	2	0.08
B-BEACH						
Grain Size Class	B-NU (%)		B-HU (%)	X²-value	df	p-value
Gravel	0.4 (\pm 0.2)		1.9 (\pm 0.9)	5.33	1	0.02
Very Coarse Sand	2.3 (\pm 0.4)		3.9 (\pm 0.1)	5.46	1	0.02
Coarse Sand	17.3 (\pm 2.0)		23.8 (\pm 0.9)	5.40	1	0.02
Medium Sand	45.8 (\pm 1.4)		51.8 (\pm 1.5)	4.08	1	0.04
Fine Sand	24.9 (\pm 1.6)		12.8 (\pm 1.6)	5.33	1	0.02
Very Fine Sand	4.0 (\pm 0.6)		2.3 (\pm 0.6)	5.33	1	0.02
Fines	*5.1 (\pm 0.9)		*3.5 (\pm 1.0)	3.56	1	0.06

TABLE A.7 - Comparisons of median soil grain size distributions (\pm interquartile range) among high use zones of wood turtle (*Glyptemys insculpta*) nesting beaches in the Sudbury District, ON, in 2016. Kruskal-Wallis test results display differences in grain size class; asterisks show post-hoc groupings.

Date	M Content (%)	W Content (%)	B Content (%)	X²-value	df	p-value
Gravel	0.0 (\pm 0.0)	*2.4 (\pm 2.5)	*1.9 (\pm 0.9)	7.65	2	0.02
Very Coarse Sand	0.1 (\pm 0.0)	*18.3 (\pm 18.5)	*3.9 (\pm 0.1)	8.14	2	0.02
Coarse Sand	4.3 (\pm 1.2)	*35.7 (\pm 9.8)	*23.8 (\pm 0.8)	8.03	2	0.02
Medium Sand	*28.5 (\pm 16.1)	*17.4 (\pm 17.4)	51.8 (\pm 1.5)	8.00	2	0.02
Fine Sand	56.2 (\pm 13.5)	*11.0 (\pm 13.1)	*12.9 (\pm 1.6)	7.42	2	0.02
Very Fine Sand	*10.0 (\pm 3.7)	*4.3 (\pm 4.0)	*2.3 (\pm 0.6)	5.54	2	0.06
Fines	*0.8 (\pm 0.3)	*0.9 (\pm 1.0)	3.5 (\pm 1.0)	7.42	2	0.02

TABLE A.8 - Utility of different logistic models in predicting female wood turtle (*Glyptemys insculpta*) nest-searching attention on M-beach, a nesting beach in Sudbury District, ON, in 2016. Relative Akaike's Information Criterion scores are displayed for multiple iterations of multinomial logistic regression models, using mean surface temperature ('Temperature'), range of surface temperatures ('Range'), soil moisture content ('Water'), and soil grain size distribution ('Soil') as predictor variables.

Date	Iteration	Temperature (df = 8)	Range (df = 8)	Water (df = 8)	Soil (df = 16)
6 June	1	33.59	33.28	23.18	32.00
	2	31.58	21.98	18.41	32.00
	3	29.65	32.77	18.54	32.00
	4	32.08	30.99	21.87	32.00
	5	32.79	29.99	20.86	32.00
9 June	1	27.09	30.22	24.82	32.00
	2	23.54	10.09	24.92	32.00
	3	29.37	16.40	25.12	32.00
	4	27.92	17.37	18.53	32.00
	5	20.44	29.33	18.91	32.00
10 June	1	24.50	22.55	17.98	32.00
	2	23.49	22.82	29.97	32.00
	3	29.10	34.09	28.67	32.00
	4	28.44	32.94	28.66	32.00
	5	30.09	33.79	29.89	32.00

TABLE A.9 - Utility of different logistic models in predicting female wood turtle (*Glyptemys insculpta*) nest-searching attention on W-beach, a nesting beach in Sudbury District, ON, in 2016. Relative Akaike's Information Criterion scores are displayed for multiple iterations of multinomial logistic regression models, using mean surface temperature ('Temperature'), range of surface temperatures ('Range'), soil moisture content ('Water'), and soil grain size distribution ('Soil') as predictor variables.

Date	Iteration	Temperature (df = 8)	Range (df = 8)	Water (df = 8)	Soil (df = 16)
5 June	1	26.08	18.11	32.97	33.63
	2	34.36	19.48	23.09	33.63
	3	33.87	17.96	33.55	33.63
	4	27.81	21.87	33.82	33.63
	5	30.73	19.21	25.87	33.63
6 June	1	31.67	17.66	32.54	33.63
	2	32.51	16.08	32.22	33.63
	3	31.96	14.03	30.63	33.63
	4	33.90	21.68	29.98	33.63
	5	34.12	16.34	30.13	33.63
8 June	1	32.91	29.79	17.74	33.63
	2	31.78	32.27	27.70	33.63
	3	31.98	30.42	32.73	33.63
	4	32.44	27.95	32.90	33.63
	5	30.77	10.96	29.6	33.63
11 June	1	34.31	19.60	31.58	33.63
	2	32.33	15.40	26.97	33.63
	3	32.16	29.37	34.09	33.63
	4	30.77	23.44	25.47	33.63
	5	33.47	30.84	33.63	33.63

TABLE A.10 - Utility of different logistic models in predicting female wood turtle (*Glyptemys insculpta*) nest-searching attention on B-beach, a nesting beach in Sudbury District, ON, in 2016. Relative Akaike's Information Criterion scores are displayed for multiple iterations of multinomial logistic regression models, using mean surface temperature ('Temperature'), range of surface temperatures ('Range'), soil moisture content ('Water'), and soil grain size distribution ('Soil') as predictor variables.

Date	Iteration	Temperature (df = 4)	Range (df = 4)	Water (df = 4)	Soil (df = 8)
9 June	1	15.07	4.20	4.01	16.00
	2	10.08	4.59	15.09	16.00
	3	11.67	5.07	12.31	16.00
	4	15.08	12.92	13.02	16.00
	5	14.61	12.7	13.42	16.00
10 June	1	14.95	14.83	12.86	16.00
	2	5.66	14.67	14.48	16.00
	3	13.71	15.08	11.62	16.00
	4	14.8	4.89	12.40	16.00
	5	13.16	15.08	13.16	16.00
11 June	1	8.43	14.34	13.11	16.00
	2	15.08	15.08	14.85	16.00
	3	14.99	14.98	15.09	16.00
	4	14.96	13.98	14.09	16.00
	5	12.91	4.05	10.66	16.00

Table A.11 - Mean environmental temperatures (\pm standard deviation) measured at six sites in Sudbury District, Ontario in the 2015 field season: W₁ and W₂ represent pristine wood turtle (*Glyptemys insculpta*) habitat, F₁ and F₂ represent harvested forest, and G₁ and G₂ represent gravel pits. Temperatures are divided into four six-hour diel periods, and four seasonal periods, based on observed activity of wood turtles. ANOVA results are on the bottom of each section: superscript letters represent post-hoc groupings in relation to W₁ and W₂ ($\alpha = 0.006$).

Pre-Nesting	Early Morning (°C)	Late Morning (°C)	Afternoon (°C)	Evening (°C)
W ₁	^A 7.87 \pm 5.28	^{AB} 9.60 \pm 4.31	^A 16.37 \pm 5.33	^A 12.11 \pm 4.66
W ₂	^A 7.58 \pm 5.40	^A 9.10 \pm 4.14	^A 16.20 \pm 4.72	^A 12.15 \pm 4.29
F ₁	^A 7.70 \pm 6.68	^B 10.77 \pm 4.98	23.93 \pm 6.93	14.29 \pm 5.47
F ₂	^A 7.28 \pm 6.69	^B 10.97 \pm 4.86	22.59 \pm 7.39	14.66 \pm 5.23
G ₁	^A 7.74 \pm 6.42	11.76 \pm 4.57	24.40 \pm 7.28	15.39 \pm 5.12
G ₂	^A 6.33 \pm 7.19	14.38 \pm 4.49	27.31 \pm 6.95	^A 12.83 \pm 5.61
F _(5,1686)	1.84	41.80	132.00	22.86
p-value	0.10	<0.01	<0.01	<0.01
Nesting	Early Morning (°C)	Late Morning (°C)	Afternoon (°C)	Evening (°C)
W ₁	^{AB} 10.32 \pm 3.59	^{AB} 12.35 \pm 2.81	^A 19.73 \pm 4.50	15.92 \pm 2.86
W ₂	^{ABC} 9.75 \pm 3.71	^A 12.10 \pm 2.64	^A 18.92 \pm 3.70	14.90 \pm 2.06
F ₁	^C 8.73 \pm 4.96	^B 13.10 \pm 3.49	26.57 \pm 6.99	17.05 \pm 2.88
F ₂	8.14 \pm 5.20	13.61 \pm 3.64	26.08 \pm 7.57	17.38 \pm 2.83
G ₁	^{AB} 9.01 \pm 4.79	13.79 \pm 3.19	26.07 \pm 7.01	17.75 \pm 2.75
G ₂	8.59 \pm 5.60	16.95 \pm 3.72	30.83 \pm 7.77	17.30 \pm 3.58
F _(5,1875)	7.83	82.72	143.90	50.08
p-value	<0.01	<0.01	<0.01	<0.01
Summer	Early Morning (°C)	Late Morning (°C)	Afternoon (°C)	Evening (°C)
W ₁	^A 13.39 \pm 3.49	^A 16.01 \pm 3.08	^A 22.56 \pm 4.47	^A 18.57 \pm 3.45
W ₂	^B 13.26 \pm 3.52	^A 15.82 \pm 3.08	^A 22.86 \pm 4.26	^A 18.29 \pm 3.08
F ₁	^{AB} 13.46 \pm 4.97	17.14 \pm 4.19	27.31 \pm 7.32	19.47 \pm 4.07
F ₂	11.49 \pm 4.33	18.12 \pm 4.36	29.91 \pm 7.86	^A 18.48 \pm 3.76
G ₁	12.58 \pm 3.87	17.99 \pm 4.33	28.48 \pm 7.12	19.12 \pm 3.74
G ₂	12.63 \pm 6.24	20.57 \pm 4.26	32.85 \pm 9.31	^A 18.65 \pm 4.07
F _(5,7559)	43.98	243.80	418.10	18.7
p-value	<0.01	<0.01	<0.01	<0.01
Pre-Hibernation	Early Morning (°C)	Late Morning (°C)	Afternoon (°C)	Evening (°C)
W ₁	^A 9.34 \pm 3.60	^{AB} 11.10 \pm 3.13	^A 18.22 \pm 4.00	^A 13.35 \pm 3.16
W ₂	^A 8.78 \pm 3.94	^A 10.75 \pm 3.37	^A 17.90 \pm 3.62	^A 13.21 \pm 3.37
F ₁	^A 8.86 \pm 4.85	^B 11.84 \pm 3.82	21.40 \pm 6.30	^A 13.39 \pm 3.96
F ₂	7.39 \pm 4.60	12.54 \pm 4.15	23.18 \pm 6.08	12.09 \pm 3.92
G ₁	^A 8.45 \pm 4.22	12.83 \pm 3.90	23.98 \pm 6.50	^A 13.01 \pm 3.92
G ₂	^A 8.63 \pm 6.05	14.43 \pm 3.81	25.52 \pm 7.62	11.86 \pm 4.04
F _(5,1794)	5.60	39.53	85.40	9.60
p-value	<0.01	<0.01	<0.01	<0.01

Table A.12 - Median environmental temperatures in the 90th percentile (interquartile range in parentheses) measured at six sites in Sudbury District, Ontario in the 2015 field season: W₁ and W₂ represent pristine wood turtle (*Glyptemys insculpta*) habitat, F₁ and F₂ represent harvested forest, and G₁ and G₂ represent gravel pits. Temperatures are divided into four six-hour diel periods, and four seasonal periods, based on observed activity of wood turtles. ANOVA results are on the bottom of each section: superscript letters represent post-hoc groupings in relation to W₁ and W₂ ($\alpha = 0.006$).

Pre-Nesting	Early Morning (°C)	Late Morning (°C)	Afternoon (°C)	Evening (°C)
W ₁	15.83 (0.83)	16.58 (0.92)	^A 26.17 (3.50)	19.33 (1.04)
W ₂	15.00 (1.00)	15.33 (0.83)	^A 23.75 (2.21)	18.42 (0.67)
F ₁	16.83 (0.58)	17.00 (0.33)	34.50 (3.17)	21.50 (1.71)
F ₂	16.50 (0.50)	17.50 (0.92)	37.00 (4.17)	22.17 (1.58)
G ₁	16.67 (0.67)	17.67 (0.83)	37.00 (2.46)	23.00 (1.92)
G ₂	16.83 (0.95)	20.69 (1.35)	37.83 (1.79)	20.67 (3.00)
X ² (5)	105.92	139.84	133.02	137.18
p-value	<0.01	<0.01	<0.01	<0.01
Nesting	Early Morning (°C)	Late Morning (°C)	Afternoon (°C)	Evening (°C)
W ₁	^A 15.67 (1.50)	^A 16.17 (0.58)	29.67 (2.83)	^A 22.92 (3.88)
W ₂	^{AB} 15.00 (1.67)	^A 16.17 (0.63)	24.50 (2.58)	18.83 (1.50)
F ₁	^A 15.75 (1.42)	18.00 (0.50)	39.17 (4.17)	^A 22.17 (1.50)
F ₂	^{AB} 15.83 (1.50)	19.00 (1.46)	41.25 (4.46)	^A 22.23 (1.17)
G ₁	^A 16.17 (1.33)	18.67 (1.08)	39.08 (3.13)	^A 22.17 (1.04)
G ₂	^A 15.92 (0.75)	22.68 (2.61)	42.33 (1.41)	23.67 (1.33)
X ² (5)	21.11	169.64	140.84	112.13
p-value	<0.01	<0.01	<0.01	<0.01
Summer	Early Morning (°C)	Late Morning (°C)	Afternoon (°C)	Evening (°C)
W ₁	^A 19.17 (0.83)	^A 20.67 (1.58)	^A 30.33 (3.00)	^A 24.33 (2.79)
W ₂	^{AB} 19.17 (0.98)	^A 20.83 (1.39)	^A 29.94 (2.17)	23.17 (1.84)
F ₁	20.17 (6.67)	24.33 (3.67)	39.33 (3.83)	26.17 (2.17)
F ₂	19.00 (1.46)	26.17 (3.17)	44.67 (5.29)	^A 24.50 (2.17)
G ₁	^B 19.17 (1.17)	25.83 (3.88)	42.00 (4.17)	25.33 (2.67)
G ₂	20.83 (10.36)	27.92 (2.23)	46.83 (4.00)	24.83 (2.08)
X ² (5)	302.48	543.86	622.68	264.87
p-value	<0.01	<0.01	<0.01	<0.01
Pre-Hibernation	Early Morning (°C)	Late Morning (°C)	Afternoon (°C)	Evening (°C)
W ₁	^A 15.00 (0.67)	^A 16.00 (0.46)	^A 25.17 (2.88)	^A 18.00 (0.67)
W ₂	^A 15.33 (0.50)	^A 16.17 (0.67)	^A 23.67 (0.76)	^{AB} 18.42 (0.67)
F ₁	16.00 (4.17)	17.83 (1.83)	32.17 (4.00)	19.33 (1.17)
F ₂	15.17 (0.50)	19.00 (2.50)	35.17 (3.50)	^{AB} 18.17 (1.08)
G ₁	^A 15.50 (0.67)	19.33 (2.08)	35.75 (4.38)	^B 18.67 (0.83)
G ₂	16.50 (8.40)	20.50 (2.83)	36.33 (1.58)	^A 18.00 (0.33)
X ² (5)	51.90	140.71	143.59	69.51
p-value	<0.01	<0.01	<0.01	<0.01

Table A.13 - Median environmental temperatures in the 10th percentile (interquartile range in parentheses) measured at six sites in Sudbury District, Ontario in the 2015 field season: W₁ and W₂ represent pristine wood turtle (*Glyptemys insculpta*) habitat, F₁ and F₂ represent harvested forest, and G₁ and G₂ represent gravel pits. Temperatures are divided into four six-hour diel periods, and four seasonal periods, based on observed activity of wood turtles. ANOVA results are on the bottom of each section: superscript letters represent post-hoc groupings in relation to W₁ and W₂ ($\alpha = 0.006$).

Pre-Nesting	Early Morning (°C)	Late Morning (°C)	Afternoon (°C)	Evening (°C)
W ₁	^A -1.08 (1.50)	^A 2.33 (1.00)	8.67 (1.00)	^A 4.83 (0.67)
W ₂	^{AB} -1.67 (1.33)	^A 2.17 (1.00)	9.67 (1.00)	^B 3.92 (0.46)
F ₁	^B -4.25 (5.21)	1.33 (1.04)	14.00 (1.08)	^{AB} 4.33 (1.33)
F ₂	^B -1.50 (5.00)	1.50 (0.67)	12.83 (2.33)	^{AB} 5.33 (1.17)
G ₁	^A -3.83 (4.83)	^A 2.58 (1.63)	14.17 (1.25)	6.00 (2.00)
G ₂	-7.00 (5.03)	5.30 (3.04)	15.50 (0.62)	^B 3.00 (2.45)
X ² (5)	42.74	80.35	145.37	81.89
p-value	<0.01	<0.01	<0.01	<0.01
Nesting	Early Morning (°C)	Late Morning (°C)	Afternoon (°C)	Evening (°C)
W ₁	^A 4.67 (1.33)	^{AB} 7.25 (1.00)	^A 13.83 (2.33)	^{AB} 12.33 (1.33)
W ₂	^A 3.83 (1.25)	^{ABC} 7.83 (0.58)	^A 12.33 (2.00)	^{AC} 12.00 (0.92)
F ₁	1.00 (1.42)	^A 7.00 (1.17)	15.83 (1.83)	^{AB} 13.00 (1.33)
F ₂	0.25 (1.04)	^{AB} 7.67 (1.50)	16.00 (1.29)	13.08 (0.83)
G ₁	1.33 (1.50)	^C 7.92 (1.58)	16.00 (1.29)	13.50 (0.79)
G ₂	-1.00 (1.55)	11.00 (1.19)	17.83 (1.81)	^C 11.67 (1.16)
X ² (5)	153.32	66.42	124.32	76.68
p-value	<0.01	<0.01	<0.01	<0.01
Summer	Early Morning (°C)	Late Morning (°C)	Afternoon (°C)	Evening (°C)
W ₁	8.17 (1.50)	11.33 (1.17)	^A 15.00 (2.00)	^A 13.33 (1.71)
W ₂	7.48 (1.67)	^A 11.00 (1.67)	^A 14.83 (1.50)	^B 12.83 (2.00)
F ₁	5.83 (1.50)	^A 10.75 (1.79)	^A 15.67 (2.58)	^{AB} 13.17 (2.33)
F ₂	4.83 (2.00)	12.00 (1.50)	17.50 (2.58)	12.17 (2.33)
G ₁	6.50 (1.67)	12.17 (1.33)	17.17 (2.25)	^{AB} 13.08 (1.83)
G ₂	4.17 (2.00)	14.17 (1.83)	16.52 (6.85)	11.50 (2.17)
X ² (5)	517.80	349.37	242.47	139.09
p-value	<0.01	<0.01	<0.01	<0.01
Pre-Hibernation	Early Morning (°C)	Late Morning (°C)	Afternoon (°C)	Evening (°C)
W ₁	^A 3.50 (0.67)	^A 5.83 (1.04)	11.83 (1.67)	^A 8.50 (0.88)
W ₂	^{AB} 2.67 (0.50)	^A 4.50 (0.95)	11.33 (1.00)	^A 8.33 (1.00)
F ₁	^B 1.17 (0.67)	5.17 (1.00)	11.75 (4.67)	6.67 (1.33)
F ₂	^B 0.33 (1.67)	5.33 (1.17)	14.67 (1.58)	6.50 (1.33)
G ₁	^A 1.33 (1.29)	^A 6.67 (1.08)	14.50 (2.25)	7.00 (2.67)
G ₂	-0.33 (1.17)	8.67 (2.04)	13.08 (8.54)	5.67 (2.51)
X ² (5)	139.14	96.78	72.34	134.33
p-value	<0.01	<0.01	<0.01	<0.01

Table A.14 - Median coefficients of variation (V) (interquartile range in parentheses) of mean temperatures measured at six sites in Sudbury District, Ontario in the 2015 field season: W_1 and W_2 represent pristine wood turtle (*Glyptemys insculpta*) habitat, F_1 and F_2 represent harvested forest, and G_1 and G_2 represent gravel pits. Measures of V are divided into four six-hour diel periods, and four seasonal periods, based on observed activity of wood turtles. ANOVA results are on the bottom of each section: superscript letters represent post-hoc groupings in relation to W_1 and W_2 ($\alpha = 0.006$).

Pre-Nesting	Early Morning (°C)	Late Morning (°C)	Afternoon (°C)	Evening (°C)
W_1	^A 0.0015 (0.0020)	^A 0.0058 (0.0114)	^A 0.0342 (0.0453)	^A 0.0056 (0.0096)
W_2	^A 0.0011 (0.0013)	^B 0.0016 (0.0012)	^B 0.0123 (0.0184)	^B 0.0014 (0.0011)
F_1	^A 0.0026 (0.0034)	^{AB} 0.0024 (0.0044)	^{AB} 0.0237 (0.0693)	^{AB} 0.0041 (0.0046)
F_2	^A 0.0029 (0.0050)	^A 0.0051 (0.0138)	^A 0.0318 (0.1243)	^A 0.0041 (0.0100)
G_1	^A 0.0019 (0.0038)	^A 0.0053 (0.0076)	^{AB} 0.0328 (0.0527)	^A 0.0048 (0.0098)
G_2	^A 0.0062 (0.0097)	0.0062 (0.0097)	^{AB} 0.0135 (0.0160)	^A 0.0199 (0.0275)
$X^2_{(5)}$	7.16	22.02	14.07	31.44
p-value	0.21	<0.01	0.02	<0.01
Nesting	Early Morning (°C)	Late Morning (°C)	Afternoon (°C)	Evening (°C)
W_1	^A 0.0011 (0.0016)	^{AB} 0.0022 (0.0103)	^{AB} 0.0421 (0.0503)	^A 0.0165 (0.0174)
W_2	^A 0.0017 (0.0024)	^B 0.0016 (0.0010)	^B 0.0087 (0.0162)	0.0011 (0.0002)
F_1	^A 0.0043 (0.0069)	^A 0.0032 (0.0161)	^A 0.0312 (0.0873)	0.0058 (0.0050)
F_2	^A 0.0034 (0.0085)	^A 0.0054 (0.0330)	^A 0.0664 (0.1399)	0.0061 (0.0081)
G_1	^A 0.0034 (0.0043)	^A 0.0057 (0.0200)	^A 0.0592 (0.0655)	^A 0.0078 (0.0108)
G_2	0.0217 (0.0326)	0.0120 (0.0450)	^{AB} 0.0448 (0.0409)	^A 0.0201 (0.0437)
$X^2_{(5)}$	24.92	34.66	19.37	47.25
p-value	<0.01	<0.01	<0.01	<0.01
Summer	Early Morning (°C)	Late Morning (°C)	Afternoon (°C)	Evening (°C)
W_1	^A 0.0021 (0.0083)	^A 0.0062 (0.0100)	0.0132 (0.0229)	^A 0.0047 (0.0193)
W_2	0.0013 (0.0014)	^A 0.0041 (0.0099)	0.0023 (0.0043)	0.0029 (0.0029)
F_1	0.0368 (0.0526)	0.0310 (0.0432)	0.0803 (0.0923)	0.0241 (0.0210)
F_2	^A 0.0036 (0.0052)	0.0309 (0.0440)	0.0592 (0.0920)	^A 0.0145 (0.0153)
G_1	^A 0.0041 (0.0049)	0.0277 (0.0543)	0.0614 (0.0722)	0.0166 (0.0227)
G_2	0.0593 (0.0945)	0.0256 (0.0350)	0.1224 (0.1559)	0.0234 (0.0305)
$X^2_{(5)}$	250.76	123.91	242.10	151.34
p-value	<0.01	<0.01	<0.01	<0.01
Pre-Hibernation	Early Morning (°C)	Late Morning (°C)	Afternoon (°C)	Evening (°C)
W_1	^A 0.0009 (0.0013)	^A 0.0045 (0.0037)	0.0158 (0.0164)	^A 0.0025 (0.0018)
W_2	^A 0.0011 (0.0009)	^A 0.0059 (0.0067)	0.0020 (0.0018)	^A 0.0036 (0.0026)
F_1	0.0386 (0.0313)	0.0269 (0.0183)	0.0890 (0.0857)	0.0216 (0.0186)
F_2	0.0033 (0.0039)	0.0259 (0.0194)	0.0663 (0.0681)	0.0119 (0.0100)
G_1	0.0058 (0.0076)	0.0251 (0.0226)	0.1038 (0.0710)	0.0184 (0.0139)
G_2	0.0764 (0.0669)	0.0249 (0.0279)	0.1329 (0.1015)	0.0178 (0.0145)
$X^2_{(5)}$	77.33	41.42	70.26	64.16
p-value	<0.01	<0.01	<0.01	<0.01