Behavioural ecology and population dynamics of freshwater turtles in a semi-urban landscape at their northern range limit

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Abstract

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Species are faced with a variety of challenges in the environment, including natural challenges, such as variability in ambient temperature, and anthropogenic threats, such as habitat transformation associated with urbanisation. Understanding how animals respond to these kinds of challenges can advance the field of behavioural ecology and guide management decisions for wild species. Yet, we still have limited understanding of the extent of natural and human-caused impacts on animal behaviour and population dynamics, and lack robust assessment of behaviour in free-ranging animals. Using novel miniaturised biologging technologies, I characterised and validated behaviour in two freshwater turtle species: Blanding’s turtles (*Emydoidea blandingii*) and Painted turtles (*Chrysemys picta*). Further, I investigated how these two ectothermic species navigate a thermally heterogeneous landscape near their northern range limit, by comparing selected and available ambient temperatures. I showed that turtles preferred locations that were, on average, warmer and less variable in temperature than the available environment, and that this thermal sensitivity was greatest early in the year, and at fine spatial scales that likely matched the species' perception of the environment. Lastly, I assessed whether urban development was compatible with long-term viability of a

Blanding's turtle population, by monitoring habitat change and turtle survival over one decade of ongoing residential and road development. I found that Blanding's turtle habitat quantity and connectivity declined in the area, which coincided with high road mortality and severe declines in turtle survival and population size, especially in adult females. I concluded that urban development and current road mortality rates are incompatible with the long-term viability of this at-risk turtle population. Overall, my findings demonstrate the importance of variation in the thermal environment and anthropogenic impacts on habitat in shaping the behaviour and population dynamics of this species-at-risk.

Keywords: animal behaviour, accelerometer, biologging, habitat selection, ectotherms, temperature, urbanisation

Preface

This thesis was written in manuscript format, as each chapter will be published in the peer-reviewed literature. Chapter 2 is in revision for *PLOS ONE.* Chapter 3 is in preparation for submission to *Oecologia*. Chapter 4 is in preparation for submission to *Biological Conservation*. Each chapter is therefore written as a stand-alone manuscript and is written in the style of the journal to which it was submitted to or prepared for. I am first author on all the manuscripts, but all of my research has been in collaboration with others, therefore the plural “we” is used throughout the text of the research chapters. Each chapter also presents the list of people whose contribution was sufficient to merit authorship.

Acknowledgments

This dissertation could not have been completed without the support of my supervisor Dr. Dennis Murray, who allowed me the freedom to pursue new research questions, encouraged me to follow alternate research paths, and provided ample critical feedback. This ultimately gave me not only a multifaceted thesis, but also a more rounded skillset. I would not be where I am today if it was not for all your help and support. A big thank you also goes to my co-supervisor Dr. Gabriel Blouin-Demers, for very valuable feedback, comments, alternate ideas, prompts to always think about my research critically, and yearly visits to the field. Thank you also to Dr. James Schaefer, my third committee member, for providing stimulating discussions and ideas, helpful commentary and support. Thank you to everyone who helped with fieldwork: Matteo Petti for helping me get the hang of turtle capturing and processing, Grace McKinney for being a helpful, kind, and fun field buddy, and Devin Empey for going above and beyond – even willing to go scuba-diving to find turtles in mucky ponds. Thank you to all the Murray lab members for providing helpful feedback and ideas during lab meetings.

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Last but not least, a special thank you to my biggest supporter, my partner Paul Prior, for always keeping me grounded and sane, having confidence in me, and always supporting me no matter what. I quite literally could not have done it without you.

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Chapter 1: General Introduction

Free-ranging animals are often faced with a variety of challenges in the environment, including abiotic, natural stressors such as extremes in temperature (e.g. Angilletta, 2009), precipitation (e.g. Farooq et al., 2012), or solar radiation (e.g. Sevi et al., 2001). Additional challenges can be of anthropogenic origin, including loss of habitat due to agriculture and urban expansion (Baillie et al., 2004; Purvis et al., 2000; Sala et al., 2000). All challenges may elicit responses at the level of the individual, population, or community, depending on the intensity of exposure and whether core functions are affected (Danchin 2008). Ultimately, the effects of natural and human-caused variation in the environment depend on the ability of animals to respond to these changes through behavioural plasticity, and potentially, adaptation (Deutsch et al., 2008; Kearney et al., 2009; Moiron et al., 2020). Understanding how animal behaviour can shape population dynamics in response to challenges is important, as it not only advances the field of behavioural ecology but it also guides management decisions for free-ranging animals (e.g. Attum and Cutshall, 2015; Tetzlaff et al., 2019). Yet, our understanding of how and when threats can be impactful to animals still remains in its infancy. To accurately predict responses to environmental and anthropogenic threats, robust assessments of behaviour and demographics in wild animals are necessary, and advancements in bio-logging technologies are extremely valuable in this pursuit, provided that they are appropriately tested and validated (Brown et al., 2013; Wilson et al., 2015).

Quantifying behaviour and activity with bio-loggers

Novel, miniaturised bio-loggers such as accelerometers are particularly useful in monitoring fine-scale behaviour and activity, especially among cryptic species and in inaccessible habitats (Brown et al., 2013; Wilson et al., 2015). These devices are now commonly deployed in animal behaviour studies (e.g. Hertel et al., 2021; Shuert et al., 2019; Wilson et al., 2019), and robust classification of data is necessary to reliably interpret behaviour and activity states (Patterson et al., 2019a; Shepard et al., 2010). However, many accelerometer-based behavioural studies do not objectively assess data or neglect validation of models or decision trees for classifying animal behaviour (Bidder et al., 2015; Collins et al., 2015). Moreover, while the need for species-specific classification is often highlighted in the literature (e.g. Halsey, 2013), over-arching models that describe behaviour based on accelerometer data in more than one species could streamline the classification process. Yet, how transferable behavioural classification models are between closely-related species is still largely unknown. Considering the increased use of accelerometers in animal studies, effectively scheduling these devices to ensure uninterrupted and efficient deployment in the field should be a priority. For example, recording acceleration at a low frequency would allow longer battery life, longer field deployment and lower computational processing power (Khan et al., 2016). In this thesis, I used accelerometers and water sensors to characterise and validate activity states in free-ranging freshwater turtles and I investigated inter-species transferability (or generality) and the effect of low sampling frequencies on classification accuracy.

Responses to environmental temperature heterogeneity

Environmental temperature has wide-ranging impacts on organisms by influencing their distribution (e.g. Lembrechts et al., 2019) or home ranges (e.g. van Beest et al., 2011), shaping movement (e.g. Gibert et al., 2016), activity patterns (e.g. Attias et al., 2018), or habitat preferences (e.g. Alston et al., 2020). In ectothermic species, ambient temperature is considered the most important environmental resource, because it directly affects body temperature and physiological processes, and over the long term, can determine their survival, productivity and fitness (Huey, 1991; Huey and Stevenson, 1979). Ectothermic animals can control their body temperature through thermoregulatory behaviour (i.e. by adjusting activity time, posture or selecting thermally suitable locations), thereby making environmental temperature a key driver in ectotherm resource use and behaviour (Christian and Tracy, 1981; Cunnington et al., 2008; Huey, 1982; Huey and Kingsolver, 1989). Hence, for many species we should expect a strong link between the thermal environment and habitat selection (Fitzgerald and Nelson, 2011; Huey, 1991). In heterogeneous landscapes animals are exposed to a variety of thermal conditions and should demonstrate plastic behaviour to maximise thermoregulatory performance (Sears and Angilletta, 2015; Sears et al., 2016a). Theoretical models show that absolute and relative ambient temperatures are equally important in influencing behaviour (Sears and Angilletta, 2015; Sears et al., 2011), but how free-ranging animals navigate heterogeneous thermal landscapes is still unclear (Sears and Angilletta, 2015).

When investigating animal responses to environmental resources or threats, it is necessary to assess landscape characteristics at a spatial scale that is appropriate to the biology of the organism (Morin et al., 2005; Sears et al., 2011). Because different selection pressures vary across space, and because animal perception of their surroundings can vary depending on their body size, mobility and other life-history traits, rigorous animal behaviour assessment may require a multi-scale analysis (Luck, 2002; Morin et al., 2005). However, ecological research often fails to address the multi-scalar nature of animal responses to their environment (McGarigal et al., 2016). Habitat selection behaviour not only depends on the availability and distribution of thermal resources, but also on thermal properties of the habitat or the animals themselves (Seebacher et al., 1999; Turner, 1987). For example, thermal sensitivity should vary depending on animal body size and mass, as well as the surrounding environment (water vs. air) due to differences in thermal inertia (Turner, 1987; Turner and Tracy, 1985). Moreover, resource availability and biological needs of animals often vary over time (Arnall et al., 2019; Grgurovic and Sievert, 2005; Helm et al., 2017). For example, activities related to foraging, growth and reproduction are highly seasonal in many species. This seasonality can affect energetic demands and influence thermal responses of animals (Congdon and Tinkle, 1982; Schofield et al., 2007). Thus, to gain a deeper understanding of thermal ecology, it is necessary to investigate the role of the thermal landscape in shaping animal behaviour in a framework that considers multiple factors. In this thesis, I tested the hypothesis that ectotherms at their northern range limit navigate the thermal landscape by selecting warmer and less thermally variable locations. I also expected that their thermal sensitivity will vary depending on the spatial scale of analysis, season and species.

Demographic impacts of urbanisation

Human influences on the environment can lead to changes in microclimates (e.g. Cai et al., 2019), introduction of new species (e.g. Bertelsmeier, 2021), or diseases (e.g. Connolly et al., 2021), but the main consequences of anthropogenic land-use change are arguably loss of habitat quality, quantity and connectivity (Olejniczak et al., 2018; Shochat et al., 2006). Habitat transformation due to agricultural and urban expansion is considered one of the most immediate threats to biodiversity (Sala et al., 2000), contributing to reduced resource availability (e.g. Shochat et al., 2006), changes in population structure (e.g. Bowne et al., 2018), and over the long term, potential reduction in recruitment and population extirpation (Gibbons et al., 2000). When landscapes are developed for human use, it is often assumed that impacts on the environment and wildlife can be avoided if habitat changes are offset by mitigation measures (Bull et al., 2016; Maron et al., 2012). However, the effectiveness of mitigation measures associated with urban development projects is a much-debated concern (Theis et al., 2020). Measures to reduce development impacts often lack testing and long-term monitoring and may thus provide only limited benefits for target species (van der Grift et al., 2013). If retaining biodiversity and healthy ecosystems in urbanised landscapes remains a priority (e.g. Green et al. 2016; Aronson et al. 2017), a robust understanding of the effects of urban growth on population viability of native species is crucial.

Some species may be able to respond to changes in the environment through adaption (Rees et al., 2009; Roe et al., 2011) or behavioural plasticity (e.g. Scheun et al., 2019; Thomas et al., 2018). But when urbanisation is occurring at a rapid rate and/or due to multiple threats, such as when habitat loss and road mortality interact, adaptation or plasticity do not necessarily ensure population persistence (Jenssen et al., 2015; Paterson et al., 2021; Piczak et al., 2019). Ultimately, the effects of anthropogenic disturbance on population viability depend on the severity and duration of disturbance (e.g. Piczak et al., 2019), the effectiveness of mitigation measures (e.g. Glista et al., 2009), animal behavioural flexibility (e.g. Tuomainen and Candolin, 2011), and species life-history traits, such as generation time or recruitment rate (Peñaranda and Simonetti, 2015; Richards et al., 2021). Long-lived species, for example, often lack the ability to respond favourably to rapid changes in the landscape (e.g. Edwards et al., 2019; Howell et al., 2019), and their persistence is often highly dependent on the survival of adult females (Enneson and Litzgus, 2008; Heppell, 1998). However, we still have limited understanding of the demographic changes or the rate at which populations of long-lived species decline following urbanisation. Therefore, to assess population viability in urbanised landscapes, long-term monitoring of populations is crucial to track their susceptibility to increased mortality within vulnerable age and reproductive classes. In this thesis, I tested the hypothesis that urban and road development and associated habitat loss impacted an endangered freshwater turtle population by altering demographics and causing direct mortality, thus decreasing long-term population viability.

Study system

Blanding's turtles (*Emydoidea blandingii*) and Painted turtles (*Chrysemys picta*) are long-lived, freshwater turtles with similar habitat requirements, inhabiting wetlands across eastern North America (Ernst and Lovich, 2009; Standing et al., 1999). The two species mostly use aquatic habitats for foraging and basking, and terrestrial habitats to varying degrees for inter-wetland travel or search for nesting or overwintering sites (Bowne et al., 2006; Hartwig and Kiviat, 2007). Both are relatively elusive species, making animal-borne bio-loggers particularly useful for behavioural studies.

Our study populations occur at their northern range limits where temperatures are generally colder and more temporally heterogeneous than in more temperate parts of their ranges, which can constitute an important constraint on physiological function and performance (Addo-Bediako et al., 2002; Huey and Slatkin, 1976). These northern environments offer semi-aquatic reptiles a diversity of microclimate choices, making it an ideal system to investigate thermal habitat selection. Turtles at their northern range margin have a short active period (April to October) during which they have to acquire sufficient energy for reproductive and foraging activities (Congdon, 1989; Huey, 1991). This active season can be divided into three distinct behavioural periods (Beaudry et al., 2009; Congdon, 1989; Rasmussen and Litzgus, 2010): pre-nesting season (April-May) and nesting season (June-July), when turtles are more active and bask often (Edwards and Blouin-Demers, 2007; Krawchuk and Brooks, 1998), and post-nesting season (July-October), when turtles reduce activity in advance of hibernation (Christensen, 2013). Like many freshwater turtles, Blanding's turtles are considered at-risk in most jurisdictions across their range, mainly due to habitat loss and road mortality (NatureServe 2009). As species with long generation times and a limited ability to withstand additional mortality or threats, e.g. due to environmental changes (Congdon et al., 1993, 1994; Enneson and Litzgus, 2008, 2009), assessing impacts of urbanisation on population persistence is necessary and could contribute to management plans for this and other species at risk.

Thesis goals

The overall objective of my thesis is to examine the relationships among environmental and anthropogenic challenges, freshwater turtle behaviour, and population viability. My research contributes to our understanding of the complex interaction between environmental temperature and animal behaviour, and of population responses to anthropogenic threats, challenging the assumption that urban development with mitigation and population persistence can be compatible. In Chapter 2, I developed and validated classification models to characterise activity states in Blanding’s and Painted turtles, using accelerometers and water sensors, and used these models to describe activity-budgets of the two species. In Chapter 3, I examined the effects of temperature variation on habitat selection across multiple spatial scales, and depending on season and species, I predicted that: (1) turtles select warmer and less variable microclimates; and expected this selection to be stronger (2) during spring; (3) at finer spatial scales; and (4) in the smaller Painted turtle. In Chapter 4, I investigated turtle habitat change, population structure and viability in response to ongoing residential and road development, using turtle capture-mark-recapture data spanning one decade. I hypothesized that urban development led to habitat loss and unsustainable rates of road mortality in the population, and specifically predicted: (1) loss of natural habitat; and (2) reduced habitat connectivity between turtle sub-populations in the area; leading to (3) decline of the turtle population; with a (4) more a pronounced decline in the female cohort. Finally, I synthesized my findings in Chapter 5.

Chapter 2: Using accelerometers and water sensors to classify activity in two species of freshwater turtles

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A version of this chapter is submitted to *PLoS ONE*

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Abstract

The success of research in animal ecology and evolution often depends on robust assessment and classification of activity in free-ranging animals. While traditional observations can be biased and time-consuming, new miniaturised bio-logging technologies are powerful tools to record activity. Using accelerometers to collect reliable activity data usually requires species-specific validation of classification models, but such validations often are neglected, and model transferability across closely-related species and habitat types is unknown. Here, we validated accelerometer signatures and water sensor data to classify activity states in two free-ranging freshwater turtle species (Blanding's turtle, *Emydoidea blandingii*, and Painted turtle, *Chrysemys picta*). First, using only accelerometer data, we developed a decision tree to distinguish motion from motionless states, and second, we included water sensor data to classify the animal as motionless or in motion on land or in water. We found that accelerometers separated in-motion from motionless behaviour with >83% accuracy, whereas models also including water sensor data predicted states in terrestrial and aquatic locations with >77% accuracy. Despite differences in thresholds between the two species, we found high model generality allowing cross-species application of these classification models. Reducing sampling frequency did not affect the predictive accuracy of our models up to a sampling frequency of 0.0625 Hz. For illustrative purposes, we provide novel activity-budgets for the two species, derived from our models. Finally, we highlight the need for similar studies validating the reliability of new

bio-logging tools for tracking free-living animals, and also stress the importance of cross-species assessments to obtain generalizable models.

Introduction

Advances in behavioural ecology often depend on effectively quantifying activity and behaviours in free-ranging animals (Danchin et al., 2008; Gosling and Sutherland, 2000). For example, closely-related species with overlapping ranges may co-exist through a variety of mechanisms including resource partitioning through differing activity patterns or space use (Giller, 2012; Schoener, 1974). Behavioural syndromes (e.g., bold/shy classification) can help explain factors such as individual behavioural responses to anthropogenic or environmental stressors, and often require quantification of behavioural response across a stress gradient (e.g. Buchholz et al., 2019). Likewise, knowledge of behavioural responses of individuals of species-at-risk can guide management decisions such as design of dispersal corridors (e.g. Balbi et al., 2019) or establishment of captive breeding programs (e.g. Allard et al., 2019). Accordingly, collecting robust, fine-scale activity and behavioural data should be a high priority in ecology and conservation biology.

Traditionally, activity and behavioural data are collected via direct observation of captive (e.g. Kiik et al., 2016) and wild (e.g. Wittig and Boesch, 2003) animals, or via a variety of remote-monitoring technologies such as radio or acoustic telemetry (Bégout and Lagardère, 2004; Crofoot et al., 2010). These traditional methods, however, can be imprecise and possibly biased due to coarse or inaccurate data (Cagnacci et al., 2010;

Samuni et al., 2014). For elusive species, traditional measurements may also yield fragmented data and thus be of limited use for quantifying sources of variation in behaviour. However, new miniaturized bio-logging technologies may be particularly useful for monitoring activity and behaviour of cryptic species or those living in inaccessible habitats if they can characterize activity and behaviours at a scale and level of precision that is commensurate with contemporary research questions. In particular, modern bio-loggers record information about animal location, body position, or physiology continuously and at a very fine scale (e.g. Kemp et al. 1998; Rattenborg et al. 2008; Williams et al. 2020). Global positioning system (GPS) devices and accelerometers are now commonly deployed on wild animals and are often coupled with different environmental sensors such as thermometers or magnetometers (Gutowsky et al., 2016; Nathan et al., 2012). In the last two decades, accelerometry has become increasingly popular for studying animal activity, behaviour, and energy expenditure (Wilson et al., 2006) by recording high-resolution body acceleration in three dimensions and thereby providing information about animal posture and activity levels (Gleiss et al., 2011; Yoda et al., 1999). Acceleration data, either alone or in combination with data from other devices such as temperature or acoustic sensors, can precisely distinguish between behaviours in a variety of animals and settings (Graf et al. 2015; Studd et al. 2019).

Accelerometers are highly miniaturized and are included as a standard add-on in many radio-telemetry packages. It follows that large amounts of accelerometry data can be collected (e.g. Dickinson et al., 2020; Ward et al., 2019), but *a priori* validation is essential for assessing the effectiveness of this technology in capturing activity and behaviours and testing classification success (Patterson et al., 2019b). Yet, many research studies using accelerometers only involve subjective assessment of the data and omit proper validation (Bidder et al., 2014; Collins et al., 2015). This shortcoming could be due to difficulties in obtaining sources to validate an accelerometer-based behavioural classification, such as direct observations or video recordings of (often elusive) animals in the wild (Dickinson et al., 2020). Regardless, it is generally not appropriate to use accelerometry data for behavioural assessment without validation, but the extent of validation needed and the generality of models or statistical decision trees used to classify and assign behaviours across species or populations are largely unknown. Indeed, because accelerometer signatures are influenced by species-specific body sizes, shapes and movement patterns, validation of behavioural classification across groups is often recommended (Brown et al., 2013). However, it is generally unknown how transferable these classifications are when derived from accelerometers deployed on similar species or in different environments (Collins et al., 2015; but see Ferdinandy et al., 2020). It follows that if species- and habitat-specific classifications are not necessary, then accelerometers can be deployed broadly across closely-related species with limited need for species-specific validation. These conditions could improve efficiencies while also encouraging broader adoption of accelerometers to support animal behaviour studies. Finally, as a framework for collecting reliable activity and behavioural data from accelerometers, it is important to use device programming schedules in accordance with the ecology of target species (Moreau et al. 2009; Dickinson et al. 2020), with slower-moving animals or those with simpler behavioural repertoires potentially receiving accelerometers programmed with a lower sampling frequency to extend battery life and monitoring period (Khan et al., 2016).

In this study, we used accelerometers and water sensors to characterize activity and assess time budgets of two free-ranging, sympatric freshwater turtles: Blanding's turtles (*Emydoidea blandingii*) and Painted turtles (*Chrysemys picta*). These turtles have similar life history and habitat requirements, and co-occur in shallow ponds and marshes across eastern North America (Ernst and Lovich, 2009; Standing et al., 1999). Both species spend considerable time basking or under water, and use terrestrial habitats to varying degrees when travelling between wetlands and for nesting (Hartwig and Kiviat, 2007). First, we manually developed and validated a decision tree (or 'classification model') to classify Blanding's and Painted turtles as in motion or motionless while in water or on land (Figure 1). Second, we compared performance of behavioural classification models for each species, based on acceleration signatures. Third, we tested the generality of our species-specific classification via cross-species comparison. Fourth, we investigated the effect of sampling frequency on classification accuracy by rarefying our data from 1 Hz (1 reading per second) to 0.0625 Hz (1 per 16 seconds). Finally, we used our classification models to describe daily activity-budgets of our two turtle species. Thus, our study, which is the first to develop a robust accelerometer-based activity calibration and validation method for freshwater turtles, serves as a template for similar approaches in other species.

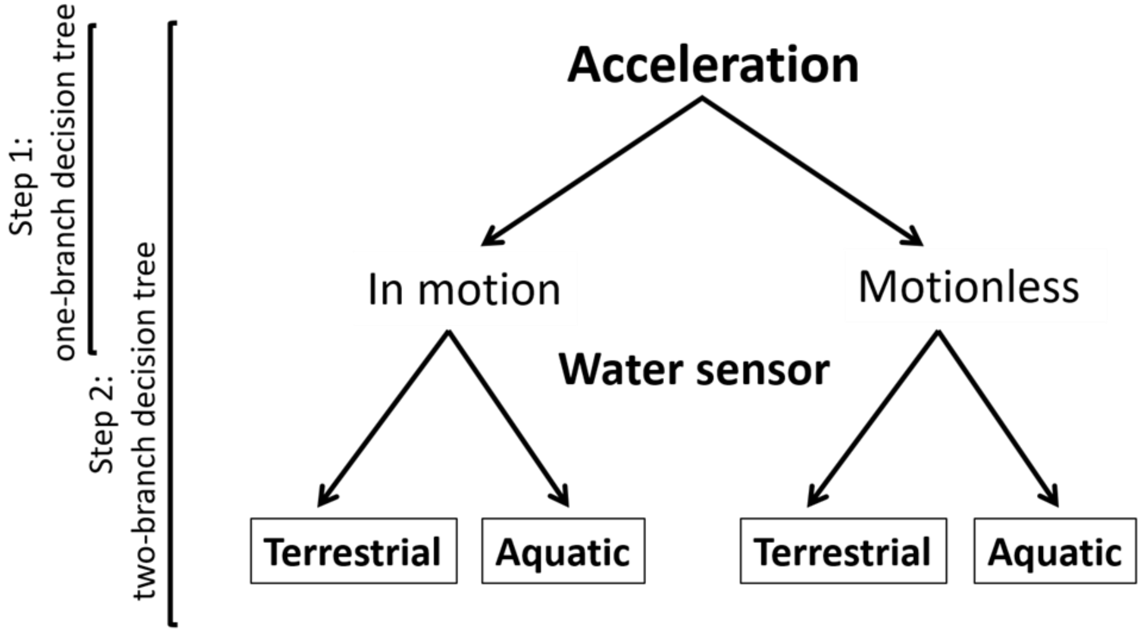

Figure 1: Two-step decision tree for classifying the main activities of freshwater turtles. Acceleration data are first binned according to activity level (Step 1) based on visual observation and acceleration thresholds, and then further classified according to habitat type (Step 2) based on a water conductivity sensor deployed in tandem with the accelerometer. The same process was used to classify activity in both turtle species, resulting in four categories.

Methods

Field methods and data collection

We studied Blanding's and Painted turtles in the South March Highlands Conservation Forest in Ottawa, Ontario, Canada (45°20ˈ N, 75°56′ W) in the summers 2018-2020. Turtles (Blanding's [n = 16]; Painted [n = 23]) were captured using baited hoop-nets or by hand and each was fitted with a GPS/tri-axial accelerometer data logger (model AxyTrek, Technosmart, Rome, Italy) and VHF transmitter (model SI-2, Holohil, Carp, Canada) bolted to the carapace margin (9th to 11th scute), respectively (Appendix A, Figure 1). Both units comprised <10% of turtle body mass and position of loggers was kept constant to ensure comparability. Data loggers recorded water conductivity and acceleration at a frequency of 1 Hz (10 bit resolution, ± 2 g_{force}). For activity classification and validation, videos of 8 Blanding's and 9 Painted turtles were recorded with a Smartphone camera (Motorola Moto G6) after being released at the capture site until they were out of sight (range: 1 min 57 s to 23 min 38 s). During recordings, we remained distant from the animals to avoid disturbing natural behaviour and censored observations that were notably influenced by our activities. All turtles were re-captured at the end of each summer to retrieve data loggers.

Activity annotation and time synchronisation

Using video footage recorded in the field, we categorized turtle activity per second. Locomotion (walking and swimming, hereafter referred to as "in-motion") was defined as forward movement lasting longer than 2 s. Terrestrial-motionless were turtles immobile out of water, whereas aquatic-motionless included sitting or floating in water. Annotating acceleration data with activity using video and external time devices introduces potential time synchronisation errors (Studd et al., 2019a). We synchronised start and end time of videos with accelerometer time (received from satellite systems) and time noted on an Android GPS app (GPS test, Chartcross Limited). Additionally, we compared time-specific repetitive motion signatures on accelerometers we recorded before deployment to the GPS time app. These signatures consisted of 30 s shaking and 30 s lying still on the ground and are visualised by plotting acceleration data. Finally, to confirm that activity annotation based on videos aligned with accelerometer time, we investigated abrupt transition in observed movement (e.g., motionless to in-motion) in each individual and corrected the time, if necessary (Studd et al., 2019a). To avoid time synchronisation uncertainty, we excluded the first and last second of each activity bout from analysis, and also censored bouts <2 s.

Calculation of acceleration metrics

From raw tri-axial acceleration data, we calculated six metrics of dynamic body acceleration (DBA) known to be relevant to activity and behavioural classification (e.g. Qasem et al. 2012; Studd et al. 2019a; Hounslow et al. 2019):

1) Total overall dynamic body acceleration (ODBA), as:

$$TODBA = \sum_{i=1}^{t} |X_{d,i} + Y_{d,i} + Z_{d,i}|$$

2) Total vectorial dynamic body acceleration (VeDBA), as:

$$TVeDBA = \sum_{i=1}^{t} \sqrt{(X_{d,i}^2 + Y_{d,i}^2 + Z_{d,i}^2)}$$

3) Delta ODBA, as:

$$\Delta ODBA = \sum_{i=1}^{t} \left|(X_{d,i+1} - X_{d,i}) + (Y_{d,i+1} - Y_{d,i}) + (Z_{d,i+1} - Z_{d,i})\right|$$

4) Delta VeDBA, as:

$$\Delta VeDBA = \sum_{i=1}^{t} \sqrt{(X_{d,i+1} - X_{d,i})^2 + (Y_{d,i+1} - Y_{d,i})^2 + (Z_{d,i+1} - Z_{d,i})^2}$$

5) Standard deviation of ODBA, as:

$$SDODBA = \sigma(\left|X_{d,i} + Y_{d,i} + Z_{d,i}\right|)_{i=1}^{t}$$

6) Standard deviation of VeDBA, as:

$$SVeDBA = \sigma(\sqrt{(X_{d,i}^2 + Y_{d,i}^2 + Z_{d,i}^2)})_{i=1}^{t},$$

where $X_{d,i}$, $Y_{d,i}$ and $Z_{d,i}$ are dynamic accelerations in each direction at time i, t is the sampling window and σ is standard deviation. The sampling window of 10 s was based on the shortest mean duration of each natural activity bout, ensuring sufficient resolution (see Studd et al., 2019).

Smoothing window sensitivity analysis

DBA represents average raw acceleration in each axis over time, resulting in static acceleration, which is subtracted from raw acceleration, yielding the dynamic portion caused by movement (Wilson et al., 2006). The averaging window is dependent on stroke duration, and DBA sensitivity should be assessed relative to the duration of the smoothing window (Shepard et al., 2008). We investigated ODBA variation derived from running median durations ranging from 3 to 131 s using data from video-recorded trials for each activity mode and species separately (Shepard et al., 2008). We visually inspected ODBA plots and selected the smoothing window with the lowest ODBA variability (Shepard et al., 2008). We then calculated the greatest mean ODBA value within 95% of the maximum and chose the corresponding smoothing window. A two-tailed paired t-test (Shepard et al., 2008) served to determine if ODBA values differed between selected windows and the next longest window.

Metric and threshold value selection

We randomly divided the dataset into training (70%) and testing (30%) (see Liu and Cocea 2017). In the training data set, all six DBA metrics were calculated per individual using the selected smoothing window. For each species, accelerometer data were used to distinguish in-motion and motionless states (Figure 1). We plotted histograms of each DBA metric for each pair of states (terrestrial in-motion vs. motionless; aquatic in-motion vs. motionless) and calculated percent overlap between states (Collins et al. 2015). The appropriate metric was chosen based on how clearly it separated target states. Based on histograms of the chosen metric, we calculated classification accuracy, sensitivity and specificity using a range of possible thresholds across overlapping ranges, in 0.1 increments (Collins et al., 2015). The point where all three evaluation metrics were highest was chosen as the threshold to separate state pairs. As a second step, we included water sensor data to determine if activity occurred in terrestrial (water sensor >500 V) or aquatic habitat (≤500 V). The 500 V threshold was determined by separate trials involving leaving transmitters in and out of water (A. Auge, unpubl.). Finally, from a decision tree that combined the two steps (Figure 1), we calculated confusion matrices as well as accuracy, sensitivity and specificity of state classification to the test data set based on threshold DBA values and water sensor data, and to evaluate classification performance (Figure 1) (Chakravarty et al., 2019). Confusion matrices and accuracy, sensitivity and specificity measures were calculated using the R package *carat* (Kuhn, 2020).

Species comparison

We assessed the transferability of our classification system by testing performance measures from the Blanding's turtle classification tree on Painted turtle data, and *vice versa*. We used the smoothing window from one species to calculate acceleration metrics and find optimal threshold values for the other species, and then used threshold values from one species to determine accuracy, sensitivity and specificity in classifying activity for the other species.

Effect of sampling frequency

We assessed how recording frequency affects the classification tree by rarefying the original acceleration data set and selecting every 2nd, 4th, 8th and 16th datum point to simulate a sampling frequency of 0.5, 0.25, 0.125 and 0.0625 Hz, respectively. We then repeated the steps described previously for 1 Hz: selecting the appropriate smoothing window, determining the best DBA metric and thresholds via histogram separation, and calculating accuracy measurements.

Activity-budgets

To illustrate the type of inference possible from accelerometry modeling in freshwater turtles, we calculated average daily activity-budgets for each turtle during its entire monitoring period (summers 2018-2020). We compared activity-budgets between species using a Dirichlet regression, which accounts for the compositional characteristics of the activity-budgets (Maier, 2014) using the *DirichletReg* package (Maier, 2014b) in R, where proportion of time spent in each state and species were the response and predictor variables, respectively. Note that we also performed this analysis using a non-parametric PERMANOVA, which yielded qualitatively similar results; herein we report exclusively the parametric results. All analyses were performed using R version 4.0.2 (R Development Core Team, Vienna, Austria, 2020).

Results

Turtle video observations

After censoring accelerometer data, we had totals of 47 min 8 s (range: 57 s – 19 min 18 s per individual) and 73 min 3 s (range: 54 s – 16 min 52 s per individual) of activity data from Blanding's and Painted turtles, respectively. All four pre-defined activity categories were recorded during the video trials, with Blanding's turtle terrestrial in-motion and terrestrial-motionless being observed most frequently (55.3% and 28.5% of video minutes, respectively), followed by aquatic-motionless (9.8%) and aquatic in-motion (6.4%). In Painted turtles, terrestrial-motionless was observed most frequently (85.1%), followed by aquatic-motionless (7.1%), terrestrial in-motion (4.4%), and aquatic in-motion (3.4%) (Appendix A, Figure 2).

Smoothing window

For Blanding's turtles, 91 s was the threshold at which ODBA stabilised for terrestrial and aquatic in-motion, whereas for Painted turtles, ODBA stabilised at 91 s and 51 s for terrestrial and aquatic in-motion, respectively (Figure 2). After selecting the appropriate ODBA value (within 95% of the maximum value which was comparable to the next longest running mean duration), we found that for Blanding's turtles 91 s was the best smoothing duration for both terrestrial and aquatic in-motion. For Painted turtles, we found that 71 s and 31 s were the best smoothing windows for terrestrial and aquatic in-motion, respectively (Figure 2), of which we selected 71 s to smooth acceleration data in Painted turtles.

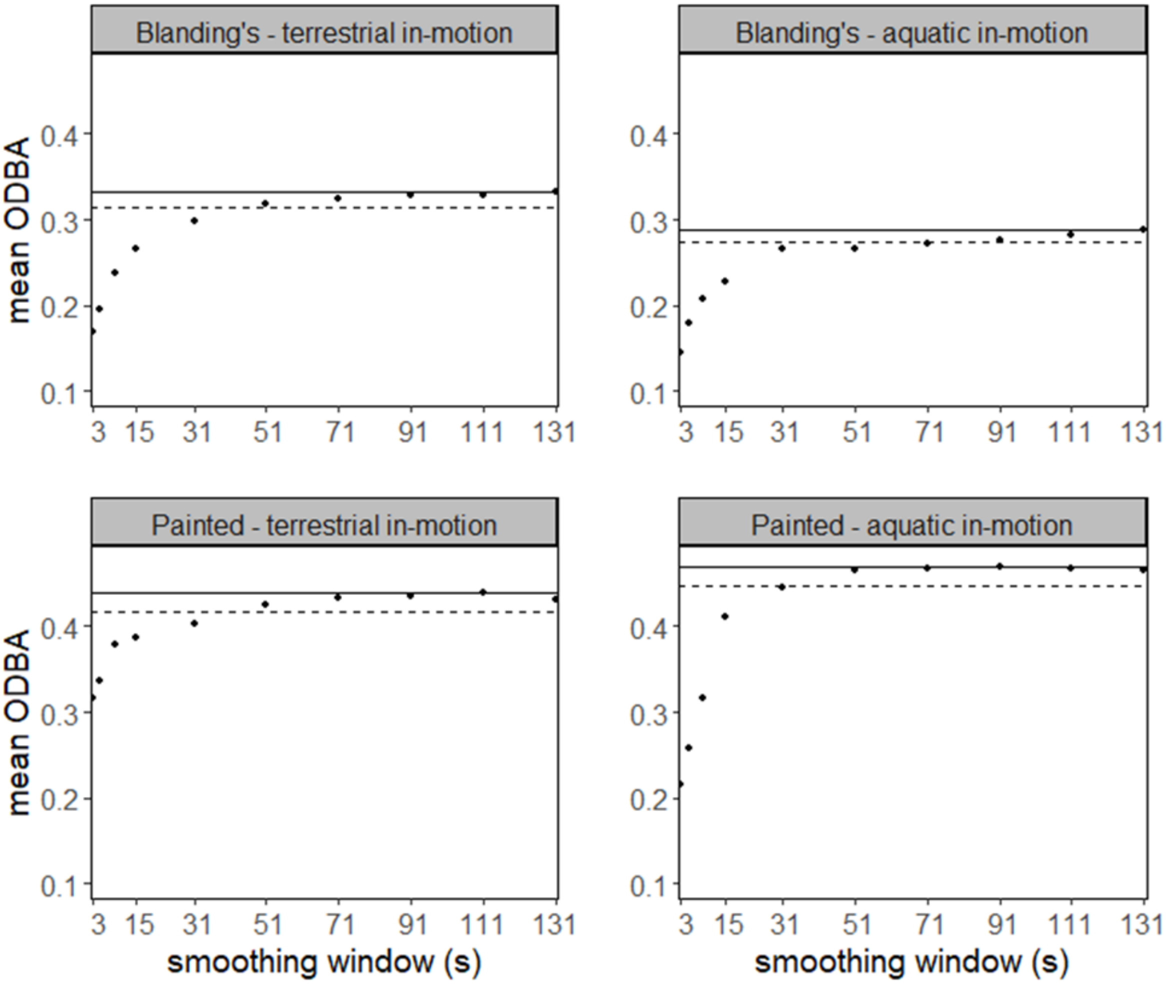

Figure 2: Mean overall dynamic body acceleration (ODBA) as a function of the duration of the smoothing window for Blanding's and Painted turtle terrestrial and aquatic motion, using accelerometer data sampled at 1 Hz. Maximum ODBA value (solid line) and 95% of the maximum ODBA value (dashed) are indicated.

Acceleration metrics and threshold values

Original dataset

The six acceleration metrics were all highly correlated (mean Pearson's correlation coefficient r = 0.83, range = 0.63-1.00, Appendix A, Table 2). Histogram separation of terrestrial and aquatic states indicated that generally ΔODBA and ΔVeDBA most clearly separated states in both species. Notably, ΔODBA was the summary statistic that separated aquatic states with the least overlap in both species (Appendix A, Table 1; Appendix A, Figure 3), which justified selection of this metric over all others. Within overlapping regions of the histograms, we tested performance of ΔODBA in assigning known activity and found that 0.6 was the best threshold separating terrestrial in-motion from motionless in Blanding's turtles (accuracy, sensitivity, specificity: all >98%, see Figure 3). In Blanding's turtles, a 1.3 threshold separated aquatic in-motion from motionless (accuracy, sensitivity, specificity: all >98%). For Painted turtles, a 0.3 threshold separated terrestrial activity (accuracy, sensitivity, specificity: >93%, see Figure 3). We found that threshold values of 1.4 and 1.5 were comparable in separating aquatic activity for Painted turtles (accuracy, sensitivity, specificity: all 100%). We chose the more conservative threshold (1.4) because of its higher overall accuracy, sensitivity, and specificity (Figure 3).

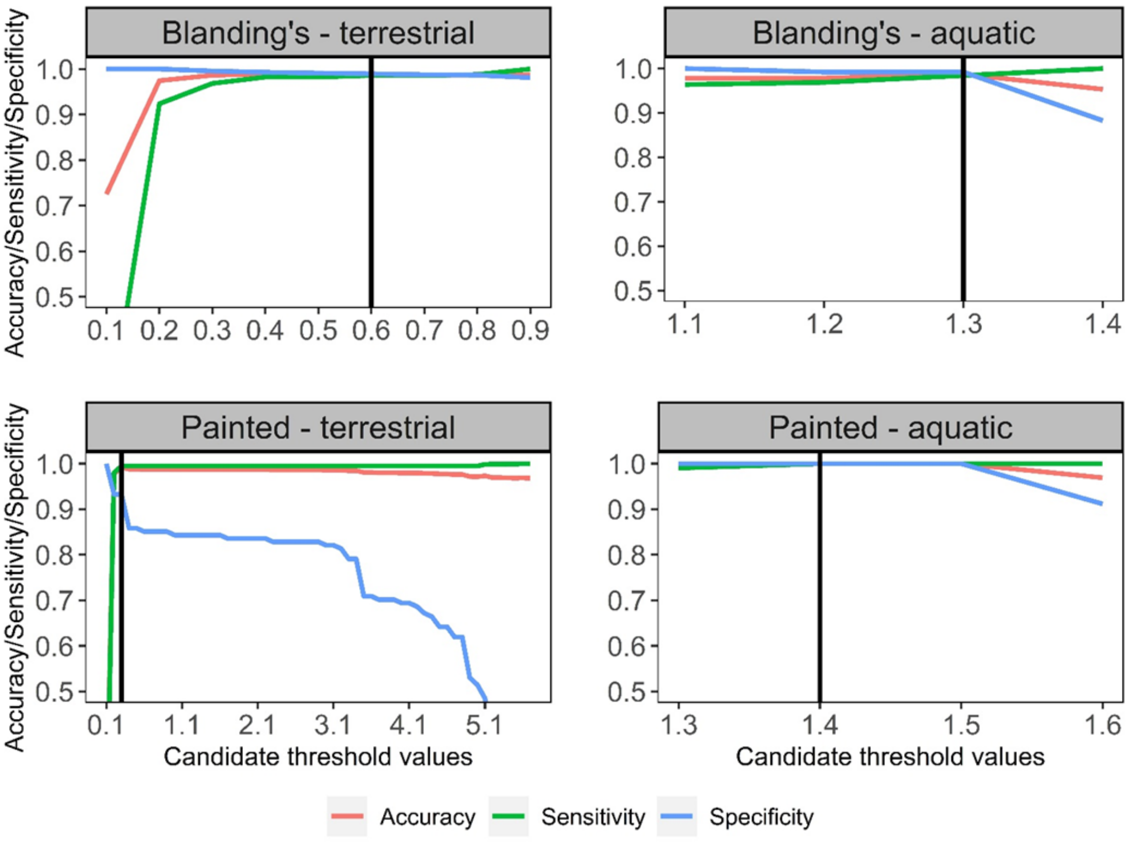

Figure 3: Qualitative selection of the most suitable threshold value (vertical line) relative to accuracy, sensitivity and specificity for Blanding's turtles and Painted turtles, using accelerometer data sampled at 1 Hz.

Cross-species comparison

Using a smoothing window of 71 s and 91 s for Blanding's and Painted turtles, respectively, and assessing histogram separation, ΔODBA was chosen to distinguish terrestrial in-motion from motionless and aquatic in-motion from motionless. In Blanding's turtles, ΔODBA and ΔVeDBA best distinguished terrestrial activity, while aquatic activity was distinguished using ΔODBA. In Painted turtles, ΔODBA, ΔVeDBA and SDVeDBA all distinguished terrestrial activity comparably, with ΔODBA separating aquatic activity with the least overlap (Appendix A, Table 1). Threshold values with highest accuracy were identical to those calculated with the original smoothing windows: in Blanding's turtles, threshold of 0.6 distinguished terrestrial activity (all metrics >98%) and 1.3 separated aquatic activity (all metrics >98%, Appendix A, Figure 4). In Painted turtles, threshold of 0.3 was selected to distinguish terrestrial activity (all metrics >93%) and threshold of 1.4 best distinguished aquatic activity, albeit comparably to the 1.5 threshold (all metrics >99%, Appendix A, Figure 4).

Performance of threshold values

Original dataset

Using our selected threshold values, terrestrial and aquatic activity were distinguished in Blanding's turtles with 99% and 84% accuracy, respectively, and in Painted turtles with 97% and 92% accuracy (Table 1). The main sources of error were misclassifying aquatic-motionless as aquatic in-motion in Blanding's turtles and Painted turtles (22/83 and 11/100 events, respectively), and terrestrial-motionless as terrestrial in-motion in Painted turtles (42/1136 events). Accuracy was slightly reduced with the inclusion of water sensor data (Blanding’s turtles: 92%; Painted turtles: 77%). Errors in assigning Blanding’s turtle state mainly arose from misclassifying aquatic-motionless as either terrestrial-motionless (18/83 events), aquatic in-motion (22/83 events) or terrestrial in-motion (10/83 events). Aquatic in-motion was falsely classified as terrestrial in-motion in a few instances (13/54 events) (Table 2). Errors in assigning Painted turtle state mainly arose from misclassifying terrestrial-motionless as aquatic-motionless (233/1136 events) or terrestrial in-motion (42/1136 events), as well as classifying terrestrial in-motion as aquatic in-motion (19/61 events) and aquatic-motionless as aquatic in-motion (11/100 events) (Table 2).

Table 1**:** Assignment accuracy for the testing data used to classify Blanding's turtle and Painted turtle activity based on accelerometry data, sampled at 1 Hz.

Species	**Separation of in-motion vs. motionless**	**Thresh-old**	**Accuracy (%) (95% CI)**	**Sensitivity (%)**	**Specificity (%)**
Blanding's	Terrestrial	0.6	99.3 (98.4, 99.7)	99.6	99.2
	Aquatic	1.3	83.9 (76.7, 89.7)	73.5	100
Painted	Terrestrial	0.3	96.5 (95.3, 97.5)	96.3	100
	Aquatic	1.4	91.8 (85.8, 95.8)	89.0	100

Table 2: Confusion matrix and assignment accuracy for the testing data used to classify Blanding’s turtle and Painted turtle activity based on accelerometry and water sensor data sampled at 1 Hz.

Observed

			Motionless (aquatic)	**Motionless (terrestrial)**	**In-motion (aquatic)**	**In-motion (terrestrial)**
Blanding`s	**Predicted**	Motionless (aquatic)	33	0	0	0
		Motionless (terrestrial)	18	242	0	4
		In-motion (aquatic)	22	0	41	0
		In-motion (terrestrial)	10	1	13	464
		Sensitivity (%)	39.8	99.6	75.9	99.2
		Specificity (%)	100	96.4	97.2	93.7

Overall accuracy (%): 92.0 (95% CI: 89.9, 93.7%)

			Motionless (aquatic)	**Motionless (terrestrial)**	**In-motion (aquatic)**	**In-motion (terrestrial)**
Painted	**Predicted**	Motionless (aquatic)	89	233	0	0
		Motionless (terrestrial)	0	861	0	0
		In-motion (aquatic)	11	0	34	19
		In-motion (terrestrial)	0	42	0	42
		Sensitivity (%)	89.0	75.8	100	68.9
		Specificity (%)	81.1	100	97.7	96.7

Overall accuracy (%): 77.1 (95% CI: 74.7, 79.3%)

Cross-species comparison

Cross-species comparison of activity state classification revealed high generality in our classification system. Painted turtle thresholds classified Blanding's turtle terrestrial and aquatic activity with 99% and 85% accuracy, respectively. Blanding's turtle thresholds distinguished Painted turtle terrestrial and aquatic activity with 98% and 91% accuracy, respectively (Table 3). When including water sensor data in the model, overall accuracy of Blanding's turtle classification using Painted turtle thresholds was 93%, with errors due to misclassification of aquatic-motionless as either terrestrial-motionless (6/83 events) or aquatic in-motion (20/83). Painted turtle decision tree accuracy when using Blanding's turtle thresholds was 78%, with main misclassifications due to assigning aquatic-motionless to terrestrial-motionless (233/1136), terrestrial in-motion to terrestrial-motionless (25/1136) and aquatic in-motion to aquatic-motionless (12/100) (Appendix A, Table 3).

Table 3: Assignment accuracy for the testing data used to classify Blanding's turtle and Painted turtle activity into states of in-motion vs. motionless in both habitat types based on accelerometry data, using the other species' threshold values.

Species	**Habitat**	**Thresh-old**	**Accuracy (%) (95% CI)**	**Sensitivity (%)**	**Specificity (%)**
Blanding's	Terrestrial	0.3	99.4 (98.6, 99.9)	99.6	99.4
	Aquatic	1.4	85.2 (78.4, 91.0)	75.9	100
Painted	Terrestrial	0.6	97.9 (96.9, 98.6)	97.8	100
	Aquatic	1.3	91.0 (84.8, 95.3)	89.0	100

Effect of sampling frequency

Smoothing windows using rarefied datasets were generally longer compared to the 1 Hz dataset in both species, except for 0.5 Hz Painted turtle data, which was slightly shorter (Appendix A, Table 4). Threshold values separating states using 0.5 and 0.25 Hz datasets were only marginally different from the original dataset, but were 17-75% higher using 0.125 and 0.0625 Hz datasets (Appendix A, Table 4). Similarly to the original dataset, we found that ΔODBA effectively distinguished terrestrial and aquatic activity in both species using all rarefied datasets. Lastly, we found that accuracy measurements of activity classification did not decrease with lower sampling frequencies. Accuracy of the two-branch decision tree (including both accelerometer and water sensor data) ranged from 79.4 to 91.9% (mean = 87.5%), when using sampling frequencies of 0.5, 0.25, 0.125 and 0.0625 Hz (Appendix A, Table 4).

Activity-budgets

To illustrate the application of our accelerometer-based activity classification for free-ranging turtles, we present activity-budgets for our study animals (Figure 4). Species exhibited similar activity in both aquatic and terrestrial environments, with only modest differences in time allocation: Both species spent most of their time motionless, with Blanding's turtles spending 84.0% (± SD 5.9%) and Painted turtles 78.1% (± 7.3%) of their day motionless under water (Dirichlet z-value = 0.647, p = 0.517); whereas Blanding's turtle spent 9.1% (± 6.0%) and Painted turtles 9.7% (± 4.4%) motionless on land (z = 1.528, p = 0.127). In contrast, Blanding's turtles spent 6.0% (± 3.5%) and Painted turtles 11.2% (± 5.8%) of the day in-motion under water (z = 2.511, p = 0.012).

In-motion on land occurred rarely, with Blanding's turtles spending 0.8% (± 1.0) and Painted turtles 1.0% (± 0.7) of the time engaging in terrestrial activity (z = 1.294, p = 0.196) (Figure 4).

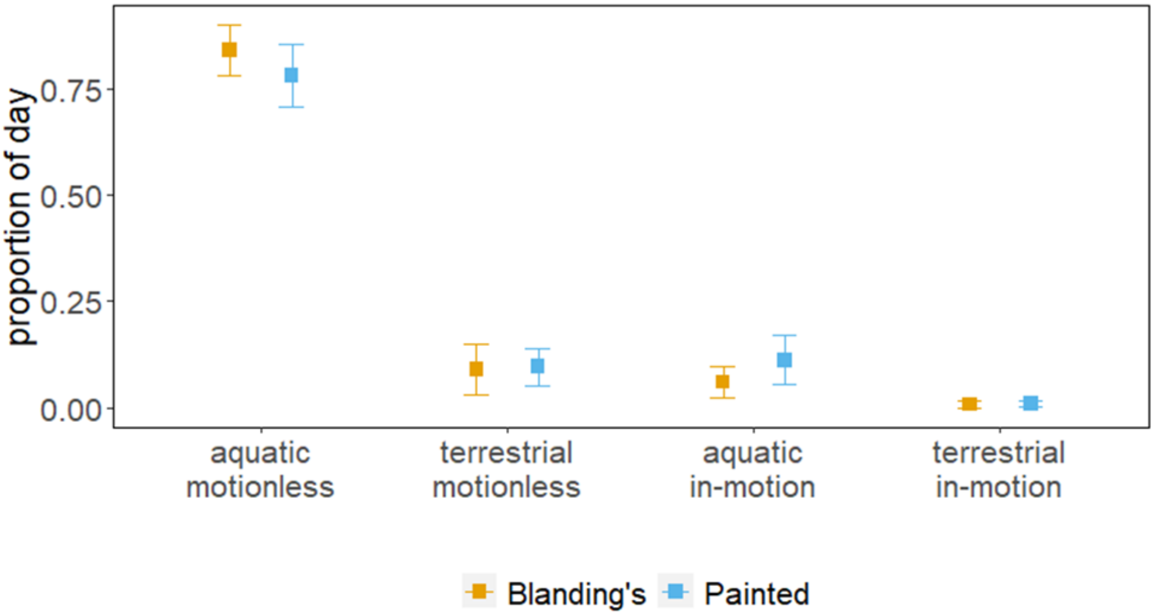

Figure 4**:** Daily activity-budget for Blanding's (n=16) and Painted turtles (n=23) in the South March Highlands, Ottawa. Shown are mean proportion (± SD) of time spent in each of the four states during a 24-hour period.

Discussion

Using a combination of accelerometers and water sensors, we classified activity of two free-ranging freshwater turtle species with high accuracy and achieved higher predictive accuracy when differentiating activity on land or in water separately using only accelerometer data (>83%) than when also considering water sensor data (accuracy >75%). Our model accuracy was comparable to studies classifying behaviours in other species exhibiting relatively simple behavioural repertoires (e.g. Hammond et al., 2016; Shamoun-Baranes et al., 2012), and in general threshold values distinguishing terrestrial and aquatic states were higher in the former environment. Unsurprisingly for our study species' simple and monotonous behaviours, sampling frequency down to a rate of 1 reading per 16 seconds did not affect classification performance. Interestingly, minor differences in classification threshold values between the two species did not impact the transferability of models between species, allowing us to conclude that accelerometry holds promise for broadly classifying activity of free-ranging freshwater turtles.

Smoothing window and acceleration metrics

A primary objective in calibrating accelerometry data is to determine the appropriate smoothing window to separate between activity and behaviours. For Blanding's turtles, the longer smoothing window can be explained by their larger body size and thus greater stroke length compared to Painted turtles (Sato et al., 2007). This is consistent with the results of Shepard et al. (2009) which show a positive relationship between stroke length and the running mean at which ODBA stabilised. For Painted turtles, we selected the longer plausible smoothing window to avoid underestimating the dynamic portion of acceleration (see Shepard et al., 2009). Generally, our smoothing windows were longer than those in many mammal or bird behavioural calibrations, which often ranged from 2-4 s (e.g. Graf et al., 2015; Patterson et al., 2019; Shepard et al., 2009); we ascribe this difference as being the result of slow movement and therefore long stroke length of our study animals relative to their body size. Regardless, despite small differences in optimal smoothing windows between our study species, cross-species validation suggests that these differences do not necessarily affect threshold values separating states or accuracy of activity predictions. ODBA is the most prevalent metric in the accelerometer literature, and its correlation with VeDBA has been demonstrated previously (e.g. Qasem et al. 2012; Wright et al. 2014). Accordingly, our choice of ODBA was appropriate and it seems likely that this metric will be well-suited for a wide range of species that are tracked via accelerometers (Brown et al., 2013; Wilson et al., 2006).

Effect of species and environment

While direct comparisons of accelerometer-derived behavioural signatures between species are rare in the literature, our findings are consistent with other studies showing some influence of body size and device attachment on accelerometer readings (Pagano et al., 2017; Patterson et al., 2019b). For example, the observation that terrestrial activity in Blanding’s turtles was separated by greater thresholds than in Painted turtles is likely due to the larger carapace of the former species. When accelerometers are attached to the carapace margin of the larger species, even small body movements might translate to higher acceleration due to a greater distance to the center of mass. Further, misclassification of in-water vs. out-of-water between species may be explained by relatively flat carapaces of Painted turtles requiring the water sensor to be mounted lower on the shell than for Blanding's turtles; as a consequence, Painted turtles were recorded as using aquatic habitat at shallower depths. Even though in our study system differences in threshold values between species due to turtle body shapes and sizes did not impact transferability of classification models between species, our findings highlight the need for careful placement of sensors, especially where accurate differentiation between aquatic and terrestrial activity is a high priority. Generally, larger ΔODBA thresholds separating motion from motionless states in aquatic compared to terrestrial environments is comparable to other studies showing that waves and water currents can lead to variation in measured acceleration due to passive motion (Whitford and Klimley, 2019). This effect is stronger in lighter animals, resulting in higher thresholds in aquatic (but not terrestrial) habitat for Painted turtles. Other studies emphasize the need to consider contribution of water currents or wind to accelerometer readings (Kelly and Klimley, 2012; Mitchell et al., 2015). Our results confirmed that comparable activity can vary in accelerometer signatures between environments, and thus require separate examination and validation across habitats. Nonetheless, despite decreased accuracy of the more complex classification model, more than one bio-sensor is usually preferred as it allows the description of much broader ecological contexts of behaviours (Brown et al., 2013).

Generality of activity classification model

Our study appears to be one of the first to assess the cross-species fit of accelerometer-based activity classification models, and our findings hold promise for future studies assessing the generality of such models in other taxa. We are aware of only one other case study assessing behavioural classification performance across species using accelerometers and gyroscopes; in a comparison of wolves (*Canis lupus*) to domestic dogs (*Canis familiaris*), cross-species model accuracy was considerably lower (≤51%) than what we observed for freshwater turtles (Ferdinandy et al., 2020). This difference could be related to the more restricted suite of behaviours under consideration and larger distinction in accelerometer readings between states in our study. Regardless, our findings are important because they show that deriving a single classification tree across similar species holds promise for improving model development and application. However, it should be noted that classification models are likely interchangeable only when accelerometer devices are identical and device position is consistent. Indeed, our preliminary trials using different accelerometers from two manufacturers, and even using different models from the same manufacturer, yielded >10% variation in activity classification (A. Auge, pers. obs.; see also Moreau et al. 2009). Therefore, researchers should consider cross-species application of classification models only for comparable devices and species with similar behavioural traits, and only after some testing and validation.

Sampling frequency

It is not especially surprising that lower sampling frequency up to 0.0625 Hz yields equally reliable activity information for slow-moving animals like freshwater turtles, thereby supporting findings from other studies showing classification success at similarly low sampling frequencies (e.g. Studd et al., 2019a). Assessing the impact of a range of sampling frequency on the performance of activity classification is an important step in studying behaviour of wild animals using accelerometers, as it serves as a validation exercise and allows refinement of accelerometer settings before deployment. High classification performance at low frequencies allows longer battery life, prolonged monitoring capacity, and, thus, longer field deployment duration. In addition, low-frequency accelerometer data require lower computational power for processing and analysis (Pagano et al., 2017). It is important to note, however, that species with more complex behaviour patterns and shorter bouts of behaviour may require high frequency accelerometry for reliable inference about behaviours (Brown et al., 2013; Sato et al., 2007).

Overall, our study demonstrates the successful application of accelerometry to distinguish between states in free-ranging turtles. Our findings highlight robust approaches for classifying activity and validating models that can serve as templates in other species. Ultimately, we conclude that accelerometers, combined with other bio-logging technologies, are powerful tools not only to characterise activity levels in free-ranging animals, but also to develop behavioural profiles of cryptic and elusive species with a high level of detail and accuracy (Brown et al., 2013; Wilson et al., 2019).

Accordingly, we predict that properly-validated application of accelerometry across a range of species and systems will provide a valuable tool for tracking animal behaviour across a variety of research and conservation or management contexts (Wilson et al., 2015).

Chapter 3: Effects of temperature and thermal heterogeneity on freshwater turtle habitat selection at their northern range limit

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A version of this chapter is submitted to *Oecologia*

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Abstract

Environmental temperature is a crucial resource for ectotherms, affecting their physiology, behaviour, and, ultimately, fitness. To maintain body temperatures within suitable ranges, ectotherms must select thermally-favourable locations, but selection of these sites may be challenging in environments with high spatio-temporal heterogeneity. We assessed thermal habitat selection in two freshwater turtles (Blanding's turtles: *Emydoidea blandingii*; Painted turtles: *Chrysemys picta*) within a thermally heterogeneous environment, where low temperatures may constitute a periodic physiological constraint. We investigated thermal habitat selection at two spatial scales (selection of home ranges and selection of habitats within home ranges) and across seasons by comparing temperatures at locations used by turtles to temperatures available in the environment. Turtles selected warmer locations compared to those available in both aquatic and terrestrial habitats, but selection occurred only at the scale of habitats within the home ranges rather than at the scale of habitats available outside home ranges. Moreover, turtles selected locations that were less variable in temperature than the surrounding environment, both at the home range scale and within home ranges. Thermal habitat selection was strongest during the colder and more thermally-variable pre-nesting season compared to later periods. Despite differences in body mass between species, both responded similarly to temperature variation. We conclude that microclimate selection by these reptiles at their northern range margin demonstrates the importance of ectotherm ability to select sites with

favourable temperatures and avoid temperature fluctuations within highly heterogeneous environments.

Introduction

For ectotherms, ambient temperature is often the primary environmental resource (Huey, 1991). Environmental temperature influences ectotherm body temperature, which translates to changes in physiology and behaviour that ultimately shape survival, reproduction, and, thus, fitness (Huey, 1991; Huey and Stevenson, 1979). To maintain body temperatures within a suitable range that maximizes physiological performance, ectotherms behaviourally thermoregulate by adjusting their body position, timing of activity, and selection of thermally-suitable locations (Christian and Tracy, 1981; Huey, 1982; Stevenson, 1985). Thermoregulation is thus a major driver of habitat selection in ectotherms, and ambient temperature is often more important in determining ectotherm habitat selection than are other resources such as food abundance and quality (Classen et al., 2015; Halliday and Blouin-Demers, 2016; Huey, 1991). Maintaining favourable body temperatures is particularly important in regions with climatic extremes such as near species' distribution margins (e.g. Blouin-Demers and Weatherhead, 2001; Picard et al., 2011) and in areas with high heterogeneity in ambient temperatures owing to variation in habitat or sun exposure (e.g. Pincebourde and Suppo, 2016; Scheffers et al., 2017; Sears et al., 2016).

Most landscapes are thermally heterogeneous and ectotherms can adjust their behaviour to exploit environmental disparities and avoid less favourable temperatures (Carroll et al., 2016; Huey, 1991; Sears et al., 2011). In fact, in a heterogeneous landscape, absolute and relative temperature may be equally important in influencing behaviour and physiological performance (Sears and Angilletta, 2015). While the link between habitat selection and thermoregulation has been demonstrated in a variety of ectotherms (e.g. Blouin-Demers and Weatherhead, 2001b; Harvey and Weatherhead, 2010), it is less clear how environments with high spatial and temporal heterogeneity in ambient temperatures can shape ectotherm behaviour.

Environmental heterogeneity and animal sensitivity to spatial variation in ambient temperatures are often a matter of scale (Luck, 2002; Morin et al., 2005). At which scale habitat selection occurs is related to the biology or physical traits of the species; for example, smaller animals often perceive their surroundings at finer spatial scales (Bowne and White, 2004; Mech and Zollner, 2002). While there is some evidence that ectotherms select macrohabitats at the scale of their home range (e.g. Carrière and Blouin-Demers, 2010; Edge et al., 2010), environmental temperature may be more important in determining behaviour at finer scales, as they can vary over short spaces. Therefore, responses to temperature heterogeneity within the home range seem plausible (Compton et al., 2002; Hughes, 2016). Hence, to ensure biologically-relevant interpretations of behavioural observations, habitat selection should be considered across multiple spatial scales (Compton et al., 2002; Markle and Chow-Fraser, 2014; Mayor et al., 2009).

Such scale-sensitive perceptions of the environment may be influenced by body size, but body size can also influence thermal inertia and the time required for body and ambient temperature to equilibrate: larger species or individuals require more time to heat up or cool down with changes in ambient temperature (Seebacher et al., 1999; Turner and Tracy, 1985). The relationship between body size and temperature balance can depend on the level of heterogeneity in the environment, through habitat-specific differences in heat transfer and capacity. Environments composed of both aquatic and terrestrial habitats are especially variable in their thermal properties, because water is more efficient in terms of heat transfer and retention than air (Turner, 1987). This means that body size and environmental thermal variation are likely to work in tandem to shape ectotherm habitat selection. Further, habitat selection may vary through time due to seasonal differences in temperature and varying biological needs of animals (Arnall et al., 2019; Arvisais et al., 2004; Grgurovic and Sievert, 2005). For example, in temperate environments animals may be more sensitive to thermal heterogeneity in spring, when mean ambient temperature is relatively low (Angilletta, 2009; Hadamová and Gvoždík, 2011). In spring, ectotherms may also be especially sensitive to thermal variation in the environment after their emergence from hibernation, which could prompt basking or other behavioural adjustments to raise their temperature and metabolic rate (Jackson, 1971; Krawchuk and Brooks, 1998). These spatial and temporal dynamics remain largely untested, however, especially for species occupying both aquatic and terrestrial habitats.

We assessed patterns of thermal site selection in two freshwater turtles (Blanding's turtles (*Emydoidea blandingii*) and Painted turtles (*Chrysemys picta*)), in a temperate region of southern Canada. In this region, both species are near their northern range limit, and near the northern range limit of reptiles generally. Thus, these species represent good candidates for evaluating ectotherm responses to large spatial and temporal variation in temperature. We hypothesized that thermal conditions dictate how turtles use the landscape, and expect that thermal site selection depends on the spatial scale of analysis and season. Specifically, we predicted that turtles should select locations that are (1) warmer, and (2) less variable in temperature compared to the surrounding environment. Furthermore, because of their relatively small size and restricted movements, we expected that turtles should exhibit thermal site selection at (3) a relatively fine spatial scale (i.e., locations within home ranges and within habitats, rather than across the landscape). Further, turtle selection for thermal sites should be (4) strongest during pre-nesting season, when mean ambient temperature is lower and animals are more sensitive to thermal heterogeneity. Finally, because both species differ to varying degrees in several traits, including diet, habitat preferences, colouration and, more noticeably, in body size (Bury and Germano, 2003; Ernst and Lovich, 2009), we expected that (5) species will differ in thermal habitat selection, with smaller Painted turtles, having lower thermal inertia, exhibiting stronger preference for warmer and less-variable thermal habitats compared to larger Blanding's turtles. We acknowledge limitations associated with two-species comparisons (Garland and Adolph, 1994), but recognize the substantial size variation between the two species and therefore approach the comparison with no adaptive inference (Garland and Adolph, 1994; Price, 1997).

Methods

Study species and site

We studied Blanding's and Painted turtles in the South March Highlands Conservation Forest in Ottawa, Ontario, Canada (45°20ˈ N, 75°56' W) during April-September 2019-2020. Both species inhabit wetlands, with Painted turtles being more generalist in habitat use compared to Blanding's turtles (Ernst and Lovich, 2009; Standing et al., 1999). The species differ in body size, with adult Blanding's turtles 10-80% larger and 160-420% heavier than adult Painted turtles (Congdon and Loben Sels, 1991a; Rowe et al., 2003). Both species use aquatic and terrestrial habitats to varying degrees, with the former being used primarily for foraging and basking and the latter serving mainly for inter-wetland travel or searching for nesting or overwintering sites (Bowne et al., 2006; Hartwig and Kiviat, 2007). Temperatures at our study location are generally colder than in more temperate parts of the species' range, which could constrain physiological performance (Addo-Bediako et al., 2002; Huey and Slatkin, 1976). Consequently, turtles in our area have a short active period (April to October) during which they must acquire sufficient energy and thermal resources for digestion, growth and reproductive activities (Congdon, 1989; Huey, 1991). The active season for turtles in our study region can be divided into distinct periods including pre-nesting

(April-May) and nesting (June-July), when turtles are more active and bask often (Edwards and Blouin-Demers, 2007; Krawchuk and Brooks, 1998), and post-nesting (July-October), when animals prepare for hibernation by reducing feeding and activity (Christensen, 2013; Rasmussen and Litzgus, 2010).

Our study area (~1000 ha) is composed of five main landcover or habitat types: deciduous and mixed forest (~51%), open field (~25%), marsh (~11%), swamp (~10%), and open water (~3%) (Appendix B, Figure 1). We captured Blanding's and Painted turtles using baited hoop-nets or by hand, weighed turtles and measured their carapace lengths, and fitted each of them with a combined GPS/temperature/water sensor data logger (model AxyTrek, Technosmart, Rome, Italy) and a VHF transmitter (model SI-2T, RI-2B, Holohil, Carp, Canada) bolted to the left and right carapace margins, respectively. Combined, both units comprised <10% (mean = 4.9%) of turtle body mass in air. Data loggers recorded water conductivity and temperature at a frequency of 1 Hz (temperature logger accuracy ± 0.1 °C, Technosmart). GPS transmitters recorded locations every hour, but because animals spent considerable time underwater and GPS data could not be collected when devices were submerged, the realised fix rate averaged across the entire study was 12.3% (12601 total fixes). Tests involving leaving GPS transmitters (n = 3) stationary in the field for six days revealed an average locational accuracy of 17.4 m (A. Auge, unpubl.). After transmitter attachment, turtles were released at their capture sites and re-captured at the end of the field season to retrieve data loggers. All animals were handled in accordance with guidelines from the Canadian Council on Animal Care (CCAC 2005) and procedures were approved by the Trent

University Animal Care Committee (Protocol No. 24729) and by the Ontario Ministry of Natural Resources and Forestry (MNRF, Permit No. KV-C-002-14).

Available and selected environmental temperatures

We recorded environmental temperatures in our study area by deploying data loggers (iButtons; Maxim model DS1921G-F5, accuracy ± 0.5 °C, Dallas Semiconductor, Sunnyvale, CA) in haphazard locations within the different habitats: forest (n = 3-8), open field (n = 2-4), marsh (n = 5-8), swamp (n = 4-6), and open water (n = 4-6) throughout the study period. Most loggers were placed >200 m from each other to reduce autocorrelation (A. Auge, unpubl.), although some locations received multiple loggers (i.e., water surface and ~1 m under water). Loggers recorded hourly temperature and were moved weekly several meters within the same site and habitat type to obtain a representative sample.

We calculated habitat-specific mean daily temperatures by averaging temperature recorded for each day and within each habitat. To test if daily temperatures within a habitat predict temperatures of the same habitat type in a different location, we randomly divided the dataset into training (70%) and testing (30%) data, each including similar ratios of habitat types (see Liu and Cocea, 2017). We found strong positive correlation between daily mean habitat temperature calculated from the training and test datasets (forest: R^2 = 0.94; field: R^2 = 0.94; marsh: R^2 = 0.72; swamp: R^2 = 0.89; open water: R^2 = 0.89). Differences between recorded mean habitat temperatures were generally consistent through both years of study, except for fields, where undersampling in 2019 led to unreliable estimates (A. Auge, unpubl.).

Accordingly, we adjusted estimates for fields by calculating their relative temperature in 2020 compared to forest habitat. We considered both quadratic ($R^2 = 0.83$; AICc = 17679) and linear ($R^2 = 0.81$, AICc = 18048) models when fitting field vs. forest temperatures, and note that the difference between AIC values (ΔAIC = 369) is large despite relatively small differences in R^2 which is not uncommon given Akaike Information Criterion calculation and interpretation (see Burnham and Anderson, 2002). Accordingly, we chose the more parsimonious model (quadratic) based on AIC. Further, we considered the quadratic relationship between forest and field temperature as most biologically plausible because at warmer ambient temperatures open field habitat should warm up faster than forest. Thus, we corrected 2019 field temperatures with the following model:

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

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

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

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

Data analyses

We assessed selection of the thermal environment at each of three spatial scales: home range (selected home ranges vs. study area), location within home range (selected locations across habitats vs. home range), location within aquatic and terrestrial habitats (selected locations in and out of water vs. aquatic and terrestrial habitats within home range, respectively). We used linear mixed effect models and compared selected mean temperature or temperature variability to those available at each spatial scale. For these analyses, daily mean temperature, or daily temperature C.V. was the response variable, and level (selected vs. available), species, and season were fixed effects. Note that despite aforementioned limitations regarding species comparisons (Garland and Adolph, 1994) we used a species variable (binary) rather than a continuous variable representing turtle body mass because of the large size differences between species (3X) and that body mass data were clearly bimodal (A.

Auge, unpubl.). We ran models both with a 3-way interaction (level x species x season) and with two 2-way interactions (level x species, level x season), and selected the top model using AIC. Each mixed effect model included turtle ID and level (selected vs. available) as random intercept and slope, and turtle ID and season as random intercept and slope, assuming random variation in temperature selection between individuals (Zuur et al., 2009). Mixed effect models were analysed using the R package *lme4* (Bates et al., 2015). Marginal and conditional R^2 values were computed using the R package *piecewiseSEM* (Lefcheck 2016). We identified discrete seasons as pre-nesting (April 28-May 31), nesting (June 1-July 21), and post-nesting (July 22-August 23) based on our field observations of both species (A. Auge, unpubl.). All data were analysed using R version 4.0.2 (R Development Core Team, Vienna, Austria, 2020).

Results

In 2019 and 2020, we captured 23 Blanding's and 25 Painted turtles. We collected temperature data from 17 Blanding's and 24 Painted turtles, and each was monitored on average 61.7 days (range: 8-121 days) and 74.6 days (range: 20-117 days), respectively. Because of our low GPS fix rate, we ended up with a smaller subsample of days for which environmental temperature around turtle locations could be calculated (Blanding's, mean days per individual: 32.6 days (range: 3-81); Painted, mean days per individual: 45.9 days (range: 6-97 days)). On average, monitored Blanding's turtles had 292 ± 14 mm carapace length, 149 ± 11 mm carapace width, and 1629 ± 244 g body mass. In contrast, Painted turtles had 153 ± 12 mm carapace length, 112 ± 8 cm carapace width, and 457 ± 118 g body mass. Thus, on average, Painted turtles in our sample had 67% of the shell length and 28% of the body mass of Blanding's turtles.

Selection of thermal home ranges

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

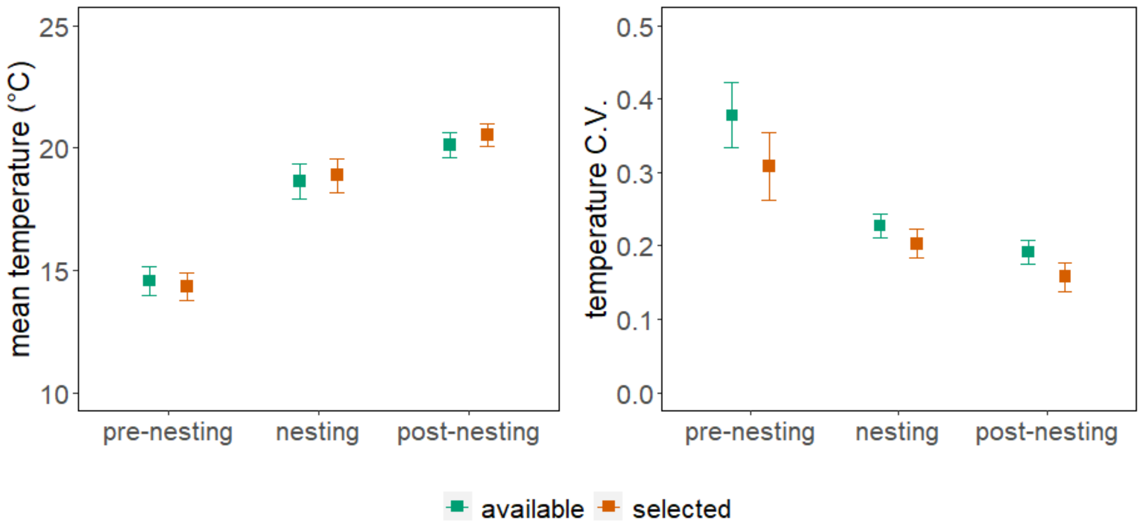

Figure 1: Thermal home range selection for Blanding's and Painted turtles in eastern Ontario, Canada. Mean temperatures (left) and temperature variability (C.V.) (right) in the available environment in the study area compared to selected turtle home ranges during each season. Displayed are marginal means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

Table 1: Thermal home range selection for Blanding's and Painted turtles in eastern Ontario, Canada. ANOVA results and R^2 values from mixed effect model comparing mean environmental temperature and mean temperature coefficient of variation (C.V.) of selected vs. available ('level') locations.

Response variable	**Fixed effect**	**Num. DF**	**Den. DF**	**F-value**	**p-value**	**Marg. R^2**	**Cond. R^2**
Mean temperature	Level	1	39.002	1.021	0.318	0.645	0.983
	Species	1	30.643	0.813	0.374		
	Season	2	28.962	182.069	<0.001		
	Level x species	1	38.386	1.657	0.206		
	Level x season	2	57.004	8.790	<0.001		
Mean temperature C.V.	Level	1	29.234	24.333	<0.001	0.402	0.911
	Species	1	26.245	0.018	0.893		
	Season	2	42.292	39.534	<0.001		
	Level x species	1	28.654	1.130	0.297		
	Level x season	2	76.419	6.888	0.002		

Num. DF: Numerator degrees of freedom; Den. DF: Denominator degrees of freedom;
Marg. R^2: Marginal R^2; Cond. R^2: Conditional R^2

Selection of thermal locations within home ranges

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

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

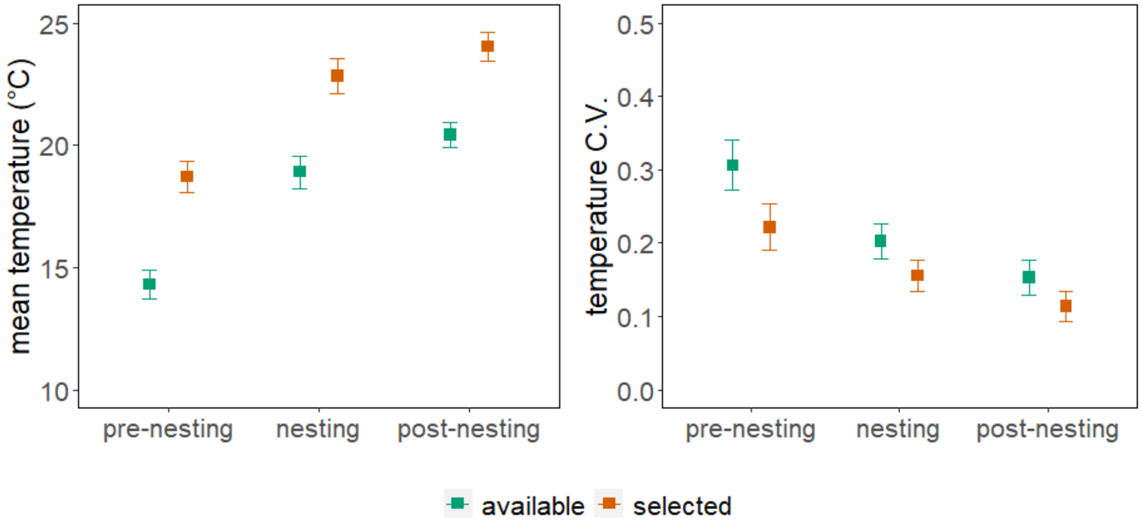

Figure 2: Temperature selection within home ranges for Blanding’s and Painted turtles in eastern Ontario, Canada. Mean temperatures (left) and temperature variability (C.V.) (right) selected by turtles compared to those available in their home ranges during each season. Displayed are marginal means as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

Table 2: Temperature selection within home ranges for Blanding's and Painted turtles in eastern Ontario, Canada. ANOVA results and R^2 values from mixed effect model comparing mean environmental temperature and mean temperature coefficient of variation (C.V.) of selected vs. available ('level') locations.

Response variable	**Fixed effect**	**Num. DF**	**Den. DF**	**F-value**	**p-value**	**Marg. R^2**	**Cond. R^2**
Mean temperature	Level	1	34.487	741.778	<0.001	0.734	0.967
	Species	1	27.533	1.662	0.208		
	Season	2	27.218	141.109	<0.001		
	Level x species	1	33.756	0.002	0.962		
	Level x season	2	55.434	4.415	0.017		
Mean temperature C.V.	Level	1	36.261	10.431	0.003	0.368	0.877
	Species	1	15.365	0.318	0.581		
	Season	2	30.209	42.242	<0.001		
	Level x species	1	35.953	1.639	0.209		
	Level x season	2	72.374	5.939	0.004		

Num. DF: Numerator degrees of freedom; Den. DF: Denominator degrees of freedom;
Marg. R^2: Marginal R^2; Cond. R^2: Conditional R^2

Selection of thermal locations in and out of water

At the scale of patches within habitats, turtles selected warmer than available temperatures, but this selection was less pronounced when they were in water compared to on land (Figure 3, Table 3). In water, turtles selected locations that were on average 3.1 °C (2.8-3.4) warmer than the surrounding aquatic habitat, whereas when out of water, turtles selected locations that were 8.2 °C (7.6-8.8) warmer compared to available terrestrial temperatures (Figure 3). Again, the magnitude of temperature selection both in and out of water differed by season, but not by species (Table 3). In water, the difference between selected and available temperature was greatest during pre-nesting and nesting season (≥3.2 °C) compared to post-nesting season, when selected locations were 2.6 °C (2.2-3.1) warmer than available water temperatures (Figure 3; Appendix B, Table 1). Out of water, selection for warmer locations was strongest during pre-nesting season (8.9 °C warmer, 8.1-9.7) compared to nesting and post-nesting season (≤8.1 °C; Appendix B, Table 1).

Overall, there was no evidence that turtles buffered daily temperature variability under water (Figure 3, Table 3), except during post-nesting, when they selected locations that were 1.7% (0.2-3.2) less variable in temperature than the surrounding aquatic habitat (Figure 3; Appendix B, Table 1). On land, temperature was generally more variable through the day, and turtles appeared to buffer this temperature variation by selecting locations that were overall 21.2% (17.0-25.4) less variable compared to the surrounding terrestrial environment (Figure 3; Appendix B, Table 1). The ability to buffer temperature on land varied by season, and was greatest during pre-nesting season, when turtles selected locations that were 26.3% (21.7-31.0) less variable than the available environment on land, compared to nesting and post-nesting season (≤17.7% less variable; Figure 3; Appendix B, Table 1).

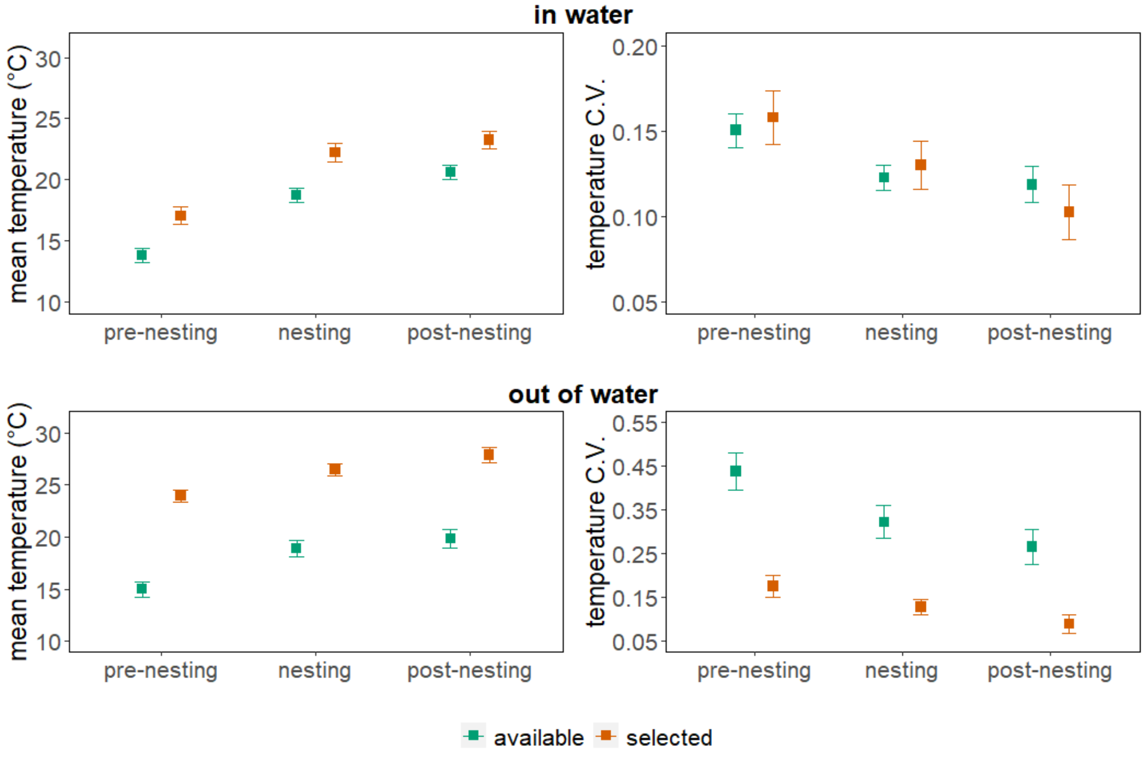

Figure 3: Temperature selection within habitats for Blanding's and Painted turtles in eastern Ontario, Canada. Mean temperatures and temperature variability (C.V.) selected by turtles when in and out of water compared to those available in aquatic and terrestrial habitat, respectively, during each season.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

Table 3: Temperature selection in and out of water for Blanding's and Painted turtles in eastern Ontario, Canada. ANOVA results and R^2 values from mixed effect models comparing mean environmental temperature and mean temperature coefficient of variation (C.V.) of selected vs. available ('level') locations within aquatic and terrestrial habitat types.

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

Num. DF: Numerator degrees of freedom; Den. DF: Denominator degrees of freedom;
Marg. R^2: Marginal R^2; Cond. R^2: Conditional R^2

Discussion

Our study revealed that, near the limits of these turtle species' ranges, the thermal landscape had an important influence on turtle habitat selection. Animals selected warmer than average available temperatures at the scale of habitats within home ranges, and in aquatic and terrestrial habitats, but not at the larger home range scale. Further, through their habitat preferences turtles experienced less variability in temperature than the surrounding environment at the scale of the home range, across habitat types within home ranges, and in terrestrial, but not aquatic habitat. As predicted, temperature selection was slightly stronger during pre-nesting season compared to nesting and post-nesting season, and was surprisingly consistent between species. This study illustrates selection for microclimate by ectotherms, contingent on spatial scale and season. It therefore highlights how temperature-sensitive animals navigate the thermal landscape by being sensitive to both mean temperature and the variation in temperature within their home range.

Our finding that turtles did not select home ranges according to mean environmental temperature likely reflects that at the home range scale, the spatial extent was too large for animals to perceive and respond rapidly to variation in ambient temperature (see also Hughes, 2016). This low sensitivity probably relates to the small body size and relatively low mobility of both species, and their inability to respond to large-scale temperature variation at the relatively short temporal scale at which this behaviour was assessed (Compton et al., 2002; Mayor et al., 2009; Mech and Zollner, 2002). However, there is evidence that animals use a variety of spatial scales when responding to environmental heterogeneity, depending on the resource requirements. For example, while ectotherms may traverse larger spatial scales in search of food, ambient temperature is usually perceived at a finer spatial scale (e.g. Compton et al., 2002). Indeed, microhabitats can be important thermal refugia, effectively buffering animals from temperature extremes and sometimes reducing temperature-related mortality (Scheffers et al., 2014). This level of thermal sensitivity is not exclusive to ectotherms and some endothermic species also show scale-dependent behavioural responses in thermally challenging landscapes (e.g. Alston et al., 2020; Attias et al., 2018; van Beest et al., 2012). Despite acknowledging the importance of analysing ecological and behavioural data at multiple scales, many studies still fail to do so (McGarigal et al., 2016) and our results demonstrate that without a multi-scale approach temperature-dependent habitat selection processes may be overlooked (see also Mayor et al., 2009).

The observation that turtles experienced markedly warmer and less variable temperatures relative to the environment when they were out of water is most likely related to the high temperatures that they experienced when basking (e.g. Millar et al., 2012). Indeed, many ectotherms bask on sun-exposed sites with little to no shade (Moll and Legler, 1969), which exhibit high temperatures with limited thermal variation throughout the day. In contrast, most other terrestrial habitats, including forests, experience considerable daily temperature variation. Open and sun-exposed environments can provide high thermal quality for a variety of ectotherms (e.g. Elzer et al., 2013; Row and Blouin-Demers, 2006), and can improve thermoregulatory effectiveness and maximise net energy gain (Lelièvre et al., 2010; Stellatelli et al., 2013). We interpret the observed weaker thermal site selection under water as a reflection of higher heat retention and efficient temperature transfer properties in water (Turner, 1987). Thus, we surmise that the more thermally homogeneous aquatic habitat provided animals with fewer opportunities to seek warmer and less thermally variable sites (Sears et al., 2016a). Overall, turtles likely were sensitive to divergent thermal change properties across the landscape, and thus were most selective in habitats with the highest thermal disparities, i.e. terrestrial habitat types. Generally, our results are consistent with the notion that temperature is an important driver in habitat selection in ectotherms at their northern range limit; such fine-scale selection should ultimately should maximise their physiological performance and fitness under extreme conditions (Huey, 1982, 1991).

Our results suggest that, despite their body mass differences, thermal site selection was consistent across the two species. However, we highlight the limitations of comparing two species at a single site, including our inability to infer adaptive evolution or to generalise results. Thus, in the absence of a more extensive effort to document species differences, we acknowledge that any observed behavioural differences may be due to random genetic drift or other morphological and physiological differences between species (Garland and Adolph, 1994). Nevertheless, the 3-fold mass advantage of Blanding's turtles could conceivably lead to lower thermal sensitivity (e.g. McNab, 2002; Peralta-Maraver and Rezende, 2020) because larger-bodied reptiles can retain heat longer and therefore should be less sensitive to temperature variation (e.g. Blake et al., 2021; Fitzgerald and Nelson, 2011). The two species were entirely syntopic in our study area (A. Auge, pers. obs.) and therefore exposed to the same thermal landscape. Accordingly, their comparable thermal responses could indicate that this resource was not sufficiently limiting during our study to elicit mass-related differences in response. Alternatively, comparing species across a wider breadth of body size/mass could have been more likely to reveal differences in thermal selection behaviour, although we note that our test had adequate statistical power to detect biologically-relevant variability given the roughly 3-fold body mass difference between species. Further, we acknowledge that other differential traits may contribute to temperature selection behaviour in the two species and could have compensated for any body-size-related behavioural differences.

The observed difference in turtle responses to the thermal environment across seasons is a phenomenon reported in many ectothermic species (Bouazza et al., 2016; Rasmussen and Litzgus, 2010; Row and Blouin-Demers, 2006a; Rowe et al., 2020), and is likely related to seasonal variation in ambient temperature. Average daily temperature is usually coldest early in the year, meaning that reptiles generally may be more sensitive to variation in temperature at that time because they require relatively high body temperature to accelerate metabolic activity to support growth and reproduction (Bouazza et al., 2016; Doughty and Shine, 1998; Shine, 2003). For example, turtles use up to ~50% of their total yearly energy to engage in activities like mating, nest searching, and egg development (Congdon and Tinkle, 1982; Krawchuk and Brooks, 1998), and species in temperate environments need to keep their body temperature between 24-

28 °C to assimilate this energy (Picard, 2008). Further, higher spatio-temporal heterogeneity in ambient temperature in the spring may force ectothermic animals to exploit relatively warmer thermal locations more efficiently (Sears and Angilletta, 2015; Sears et al., 2016a). In northern climates, animals experience shorter active seasons with ambient temperatures that are particularly cold and variable through space and time, compared to species or populations at lower latitudes (Tuttle and Gregory, 2012). It follows that northern ectotherms have limited time to assimilate sufficient energy for growth, and reproductive activities, and thus they must invest more effort into selecting higher temperatures early during the active season (Congdon, 1989; Tuttle and Gregory, 2012, 2014). Conversely, species at lower latitudes may exhibit less pronounced seasonal responses to ambient temperature variation (Sunday et al., 2011; Tuttle and Gregory, 2012).

Overall, our results imply that reptiles near their northern range limit exploit thermally heterogeneous landscapes, which advances our understanding of ectotherm ability to select thermal habitats. We surmise that turtles used a combination of actively moving between microclimates to stay within favourable temperature ranges, and selecting locations that are inherently warmer and/or that buffer temperature variation (see Woods et al., 2015). To better understand the intricate relationship between environmental temperature, thermoregulation, and habitat selection, we recommend that future studies incorporate animal activity or energetic data as well as animal body temperature in the analysis. Through the advent of new technologies like miniaturized bio-logging devices, it is now possible to obtain precise acceleration or body temperature measurements which then can be related to ambient temperature conditions (Wilson et al., 2015). Moreover, because we expect animals in more temperate regions to be less sensitive to thermal variation in the landscape, future work should examine habitat selection behaviour in response to thermal heterogeneity and mean ambient temperature in multiple populations across latitudinal gradients spanning species distributions and large variation in thermal properties. Collectively, these research efforts will support a better understanding of how ectotherms select habitats in a heterogenous landscape, and thus help predict how they will respond to future temperature variation in rapidly-changing environments.

Chapter 4: Urbanisation with mitigation is not compatible with sustainability in a Blanding's turtle population

Anne-Christine Auge, Gabriel Blouin-Demers, Dennis Murray

A version of this chapter is in preparation for submission to *Biological Conservation.*

Auge, A.-C., Blouin-Demers, G., Hasler, C., and Murray, D. Urbanisation with mitigation is not compatible with sustainability in a Blanding's turtle population. *In preparation for submission to Biological Conservation.*

Abstract

Habitat loss due to land-use change is one of the main drivers of biodiversity loss worldwide. Balancing urban development with environmental sustainability is a major societal challenge, and developers are often required to counter effects of habitat loss with mitigation measures intended to promote sustainability of indicator or at-risk species. Despite these efforts, we still have limited understanding of the efficacy of attempts to balance development and sustainability, specifically in terms of the demographic responses of populations that are targeted for protection. We studied an urban Blanding's turtle (*Emydoidea blandingii*) population in Ottawa, Ontario, Canada, to assess whether urban development and mitigation were sufficient to ensure long-term population viability. We assessed habitat change and turtle survival throughout one decade of ongoing residential and road development, using telemetry and capture-mark-recapture, to assess the magnitude of the effect of development on population viability through habitat loss, decreased survival, and lower population size. Between 2010 and 2020, Blanding's turtle habitat declined by 10%, and corridors connecting wetlands in the area were lost. This coincided with a severe reduction in survival and juvenile recruitment rates, resulting in a 70% decline in population size. Females experienced the most dramatic decline in numbers and were more likely to be found closer to roads than males; roadway deaths were a major source of mortality in the population. Population viability analysis revealed that an estimated 4 adult female road mortalities per year yielded population decline that was consistent with that observed. We infer that in our study area, despite mitigation measures implemented as part of the

development approval process, urbanization is not compatible with this at-risk turtle population viability. The broader implications of our findings are that development approval conditions, even in jurisdictions with robust species-at-risk legislation, can be inadequate for sustaining target species and therefore require considerably more stringent review during planning, approval, and implementation.

Introduction

Land-use change is one of the main drivers of biodiversity loss worldwide (Sala et al., 2000). Habitat change due to urban and agriculture land-use can reduce resource availability (e.g. Shochat et al., 2006), affect thermal or hydrological regimes (e.g. Lee et al., 2006), and, through fragmentation, reduce inter-population connectivity and gene flow (e.g. Fusco et al., 2021). These changes may lead to abnormal population structure (Reese and Welsh, 1998), reduced fitness of individuals, and, ultimately, population decline and potential extirpation. A primary, proximate outcome of urbanisation is higher mortality, for example, through higher rates of wildlife-vehicle collisions. Road mortality can be a major source of demographic change in urban wildlife populations, and sometimes these impacts can be disproportionate across demographic groups in the population (e.g. Gibbs and Steen 2005; Dorcas et al. 2007). Therefore, a major challenge in society is to balance increasing urban development with environmental sustainability (Hawkins et al., 2016), but the extent to which contemporary development and related activities can actually meet reasonable environmental standards over the long term is much-debated (Bull et al., 2016; Maron et al., 2012; Theis et al., 2020).

To reduce environmental impacts of urban development, projects may receive approval on the condition that mitigation measures are enacted. Mitigation can take a variety of forms, including efforts to reduce impacts on species and habitats while the development is first established and thereafter monitoring responses of species-at-risk. For example, developments may be required to avoid or buffer around sensitive habitats, or alter the placement of roads or other structures to minimize impacts on wildlife (Clevenger et al., 2001; Marshall et al., 2020). However, although effective conservation planning requires consideration and implementation of a variety of mitigation measures to reduce development impacts, often these measures lack rigorous testing and may provide limited protection of target species (van der Grift et al., 2013). Notably, rigorous evaluation of the responses of wildlife to development and mitigation may require intensive and long-term monitoring – before, during and after development – which is usually beyond the scope of activities or timelines mandated by the approval process (Pickett et al., 2013; Vasconcelos and Calhoun, 2006).

Freshwater turtles epitomize this challenge. These species have long generation times, delayed age to maturity, and naturally low nest survival, making them both vulnerable to new sources of disturbance and challenging to study in a demographic and response-to-disturbance context (Congdon et al., 1993). For example, many freshwater turtle species live in semi-urban areas where they occupy inter-connected wetlands and, to some degree, use terrestrial habitat, making them particularly vulnerable to disturbances due to development. Most turtle populations require high adult female survival to compensate for naturally low recruitment rates, but this can be problematic in an urbanisation context because of higher road mortality associated with inter-wetland movements near or across roads, or use of roadsides for nesting by females (Enneson and Litzgus, 2008; Steen and Gibbs, 2004; Steen et al., 2006). Despite the need to track freshwater turtle responses to urbanisation and assess the efficacy of mitigation measures on population viability, to date such studies have not spanned sufficiently long periods of time or modeled different disturbance scenarios for robust assessment (Beaudry et al., 2010; Howell and Seigel, 2019; Ross et al., 2020).

Here, we investigate the effects of recent urbanisation on the structure and viability of a population of Blanding’s turtles (*Emydoidea blandingii*) in Ottawa, Ontario, Canada. Blanding’s turtles can be strongly affected by land-use changes (Mui et al., 2017; Rhodin et al., 2018), especially by the compounding effects of habitat loss and road mortality (Beaudry et al., 2010; Howell and Seigel, 2019). We use 10 years of field data, combined with population and habitat analyses, to reconstruct changes in population size and structure and assess possible mechanisms for the observed changes. Specifically, we focus on the change in habitat connectivity between turtle sub-populations and on the potential effects of increased road mortality on population size. We hypothesized that urban development, including loss of natural habitat and establishment of a road network through the site, has impacted the local Blanding’s turtle population by causing direct loss of habitat and increased road mortality. Accordingly, we predicted: 1) loss of habitat suitable for turtles, 2) reduced habitat connectivity between turtle sub-populations leading to a 3) decline of the turtle population size with 4) a more pronounced decline in females due to their tendency to be closer to roads, including when searching for nest sites. Ultimately, we expected that our analyses would indicate unsustainable rates of road mortality on the study population, despite various mitigation measures. More broadly, our study is a case study of the robust assessment of impacts of urbanisation on a sensitive, long-lived species.

Methods

Study area and population

We studied Blanding's turtles in the South March Highlands in Ottawa, Ontario, Canada (45°20ˈ N, 75°56' W). The study site (~1000 ha) includes the protected South March Highlands conservation forest (SMH) in the north and a provincially-significant wetland (Kizell Cell Wetland) in the south, and is bounded by roads and residential areas (Appendix C, Figure 1). The study site has been impacted by substantial urban development during the past 40 years, including the extension of Terry Fox Drive, a major arterial route that now bisects the area, and development of two residential zones in the centre of the area (Appendix C, Figure 1). Following the road and residential development (starting in 2008), several mitigation measures were established including: ~2 km of wildlife fencing along Terry Fox Drive (2008), construction of 10 road culverts to allow turtle passage from SMH to Kizell Cell Wetland (2008), and construction of one artificial turtle nesting area (0.3 ha) and 2 ponds (2017; total area = 0.5 ha) (Dillon

Consulting Limited 2013; DST Consulting Engineers 2015). The Blanding's turtle population was previously monitored by the City of Ottawa (2010-2013, Hasler et al. 2015, Dillon Consulting Limited 2013) and we compare contemporary (2017-2020) site features and turtle population size to those observed by Hasler et al. (2015).

Turtle captures

During both study periods, Blanding's turtles were captured between May-September using baited hoop-nets or by hand, assigned age classes (hatchling, juvenile, adult) based on body size/mass (Congdon and Loben Sels, 1991b; Hasler et al., 2015), sexed based on secondary sexual characters (Congdon and Loben Sels, 1991b; Hamernick, 2000), and individually marked with carapace notches (Cagle, 1939). Because the 2010-2013 study included an extensive site to the north of the study area that was not sampled in 2017-2020 (approx. 110 ha), we excluded data (n = 9 turtles) from that site. Our 2017-2020 capture effort (i.e., number of traps, person-hours trapping) was ~50% of the earlier study; this disparity was integrated into population models (see below). All animals were handled in accordance with Canadian Council on Animal Care (CCAC) (2005) guidelines, and procedures were approved by Trent University Animal Care Committee (Protocol No. 24729) and the Ontario Ministry of Natural Resources and Forestry (MNRF, Permit No. KV-C-002-14).

Tracking and survival

In 2011-2013, 92 Blanding's turtles were captured, of which 21 were equipped with radio-transmitters and tracked for survival and location on average every 4 days (see Hasler et al. (2015), Dillon Consulting Limited 2013 for additional details). During

2017-2020, we captured 36 Blanding's turtles and equipped 31 adults with GPS (AxyTrek, Technosmart, Rome, Italy; GPS accuracy ± 17.4m) and VHF transmitters (SI-2, Holohil, Carp, Canada) (both <10% of turtle body mass). We retrieved data from 28 turtles. An additional 2 turtles were fitted with VHF transmitters only. GPS devices recorded locations hourly, which we then rarefied to one location per 4 days for comparison with less-extensively sampled VHF locations from 2010-2013 (see Mills et al. 2006). We assessed survival using VHF telemetry on a weekly basis and noted cause of death when mortalities were detected. Additionally, by driving and walking along roads, we surveyed Terry Fox Drive daily, and other roads surrounding the study area 3-4x per week for vehicle-caused mortalities, recognizing that observations of carcasses on the road might underestimate the true number of road mortalities because injured animals may move off the road before they die or road-killed turtles may be removed by scavengers or local residents (Row et al. 2007, DeGregorio et al. 2011). We considered the recovery rate of road-killed turtles that had been tagged as a crude rate of carcass detection.

Change in habitat and connectivity

We developed habitat maps of the study area and quantified the change in aquatic (open water, swamp, marsh) and terrestrial (forest, grassland/field) habitat, as well as settlement area between 2010 and 2020 (Appendix B, Table 1). We assessed habitat loss at two spatial scales: 1) within the entire study area and 2) within the combined home ranges of turtles in the central part of the study area in 2010-2013 (incl. developed areas). We applied a least-cost path model to estimate change in connectivity between patches of high-quality Category 1 habitat, using the habitat map as a resistance layer (lower resistance values in aquatic habitats; Appendix C, Table 2) (Mui et al., 2017). Category 1 habitat is considered highly sensitive habitat (including turtle nest and hibernation sites and 30 m buffer area), where species-at-risk have the lowest tolerance to alternation (MNR, 2021). Corridor modelling and mapping were performed in ArcGIS Pro 2.4.0 (Esri Inc., Redlands, CA, USA, 2019) (see Supplementary Information for additional details).

Statistical analyses

We compared male to female sex ratios and juvenile to adult ratios of turtles captured during 2010-2013 and 2017-2020 using a χ^2 goodness-of-fit test. We calculated turtle home ranges as 95% minimum convex polygons (MCP) (Row and Blouin-Demers, 2006b). We compared (log-transformed) home range sizes between study periods using a linear mixed model, including the turtle individual as a random effect to account for the ones that were monitored during both periods (Zuur et al., 2009). Based on 2017-2020 data, we estimated the proportion of time that turtles were on land from the realised GPS fix rate (obtained GPS locations / scheduled GPS locations), assuming that most missed fixes occurred when animals were submerged in water. We used ArcGIS to calculate distance of each turtle GPS location to the nearest road. We compared proportion of time on land and mean distance to roads during 2017-2020 nesting seasons (June to mid-July; A. Auge, unpubl.) between males and females using t-tests. We collected survival data for tracked animals during both study periods, and for the 2017-2020 period we calculated 30-day (May-September) survival probability using

Kaplan-Meier estimates (Murray and Bastille-Rousseau, 2020). Low sample sizes precluded calculating Kaplan-Meier survival rates during 2010-2013. Female and male survival rates were compared using a Cox proportional hazard (CPH) model; we confirmed that the model fit the proportional hazards assumption using Schoenfeld residuals (Murray and Bastille-Rousseau, 2020). Survival analysis was performed using the *survival* package (Therneau 2021) in R version 4.0.2 (R Development Core Team, Vienna, Austria, 2020).

Population size estimation

We estimated adult and juvenile turtle population size for each monitoring year (2010-2020) with Jolly-Seber (JS) models (POPAN formulation) (Schwarz and Arnason, 1996), using turtle capture histories from all 8 sampling years. JS models assume an open population, where deaths, emigration and immigration can occur (Pledger et al., 2010; Schwarz and Arnason, 1996). We assumed that weak connectivity with both the closest Blanding's turtle population outside our study area (Carp River system, approx. 3 km from our study area, see Dillon Consulting Limited 2013) and the northern portion of the study area that was not sampled during the 2017-2020 period meant that migration was possible, but unlikely in practice. This assumption was supported by the low estimated probability of entry into the population (p_{ent}, see results, but also Schwarz and Arnason 1996). Note that JS models are designed for open population estimation, but can serve to estimate apparent survival (Φ) in populations with negligible probability of immigration (e.g. Schneider et al. 2018; Cross et al. 2021; Kiss et al. 2021). Thus, JS models provided an alternate calculation of turtle survival probability, with JS estimates being the product of true (year-round) survival and site fidelity and explicitly consider imperfect detection (Lebreton et al., 1992). We constructed multiple JS models ranging from those with all parameters constant to others varying by sex, time and sampling period, and chose the best-fit model, given the need for model parsimony, using Akaike Information Criterion (AIC) (Burnham and Anderson, 2002). Differences in sampling effort across study periods were factored into the JS models as a covariate. We estimated population sizes first for the entire population and then separately for the northern conservation forest and southern Kizell wetland. Population size modeling was conducted using the R packages *marked* (Laake, 2013a) and *RMark* (Laake, 2013b).

Population Viability Analysis (PVA)

Turtle population viability was evaluated using demographic projection models (Morris and Doak 2002, Legendre 2020). Based on the 2010 adult female and juvenile turtle population size estimate from our JS models, we populated a 3-stage Leftkovich model representing turtle life stages (hatchlings (age 0-1 year), juveniles (age 1 to 14), and adults (age 14+)). Our base model was parameterized mostly using estimates from studies on Blanding's turtle populations subjected to few anthropogenic effects, to establish potential demographic conditions in our population prior to the 2010 pulse in urban development. In particular, annual baseline survival rates were derived from a long-term Blanding's turtle study in Michigan with low human access (Congdon et al., 1993, 2011), productivity rates from a study in Maine (Beaudry et al., 2010), and initial population sizes and proportion of breeding females were from our study (Table 1). Because sex of juvenile Blanding's turtles was not determined, we assumed the juvenile sex ratio to be similar to the adult sex ratio at the start of the study (see below). Based on the number of eggs per clutch, the proportion of reproductive females per year and adult survival rate (Beaudry et al., 2010; Congdon et al., 1993), we calculated fecundity to be 3.37 female eggs per female per year.

Population projections included only females, as they tend to be most important in the demography of long-lived and polygamous species (Caswell, 2001; Doak et al., 1994). Further, we focused on the effects of adult female survival on population projections because of the apparent high loss of adult females during this study (see below) and several studies suggesting female-biased mortality in freshwater turtle populations exposed to roads (Aresco 2005; Steen et al. 2006; Reid and Peery 2014, but see Congdon and Loben Sels 1991; Carstairs et al. 2019). Population viability analysis (PVA) was conducted using the R package *popbio* (Stubben et al. 2020), with populations projected deterministically over 50 years. We used probability of the population breaching a quasi-extinction threshold of 4 adult female turtles as our measure of population viability (Enneson and Litzgus, 2008; Howell and Seigel, 2019)**.** We explored the effect of anthropogenic disturbance on population projections as different road impact scenarios, by changing age-specific annual mortality rates and assessing their correspondence with observed changes in adult female turtle population size during our study (see below). Apart from our baseline model (which assumes no additional mortality), we modelled: 1) one adult female mortality per year for the first 10 years, based on the approx. number of observed adult female road-kills observed during the study (see below); 2) two adult female mortalities per year for the first 10 years, assuming 50% road mortality detection rate during road surveys, and 3) increased adult female mortality to 3 and 4 per year, in an effort to reproduce the 2010-2020 population size changes estimated from the JS model. Note that these increased mortality rates were not used to project the population further into the future. Additionally, we modelled 4) a constant reduction of adult female survival rate by 1.8% per year, which represents the mean observed number of road-kills as a proportion of the 2010 female population size, and 5) a decrease in adult female survival rate by 3.6% per year, representing 2 road mortalities proportional to the 2010 population size. 6) We explored which female survival due to female-biased road mortality could produce the observed decline in females by incrementally reducing adult female survival (compared to the baseline annual survival of 0.96) until projected population sizes were comparable to those observed during our field study. 7) To explore the maximum level of adult female mortality that would be sustainable above the quasi-extinction threshold by 2030 and 2060 (20 and 50 years after the beginning of the study, respectively), we reduced annual female survival rates incrementally until the population size was ≤4 adult females. 8) Lastly, to explore the potential consequences of habitat fragmentation on population dynamics, we conducted projections on two distinct sub-populations (northern SMH conservation forest; southern Kizell wetland) starting with estimated sub-population sizes from 2013 (the period prior to the recent development pulse). We projected sub-population dynamics with one and two female mortalities per year only in the northern sub-population and assessed adult female survival rate necessary to reproduce observed decline in the sub-population sizes. We conducted elasticity and sensitivity analyses to assess the importance of each demographic parameter to population growth rate.

Table 1**:** Demographic estimates used in a population viability analysis (PVA) of Blanding's turtles in Ottawa, Ontario, Canada. Values were taken from the literature when they could not be determined from our study.

Parameter	**Value**	**Source**
Breeding structure	polygamous	Ernst and Lovich 2009
Female age of first reproduction	14	Congdon et al. 1983, 1993; Congdon and Loben Sels 1991
Percent females at birth	50	Beaudry et al. 2008; Midwood et al. 2015
Number of eggs per clutch	11.7	Beaudry et al. 2010
Female hatchling annual survival rate	0.2610	Congdon et al. 1993
Female juvenile annual survival rate	0.7826	Congdon et al. 1993
Female adult annual survival rate	0.9600	Congdon et al. 1993
Quasi-extinction level	4 females	Enneson and Litzgus 2008
Initial adult population size	55.6 females	This study
Initial juvenile population size	17.1 females	This study
Initial adult sub-population size (SMH)	21.9 females	This study
Initial juvenile sub-population size (SMH)	5.3 females	This study
Initial adult sub-population size (Kizell)	7.1 females	This study
Initial juvenile sub-population size (Kizell)	1.0	This study
Percent adult females breeding	60	This study

Results

During 2010-2013, 92 Blanding’s turtles were captured and marked in the study area, of which 19.6% were juveniles. Among adults, 68.9% of the population was female. In contrast, during 2017-2020, we caught 36 Blanding’s turtles, of which 1.3% were juveniles and 48.6% were adult females. Thus, since the onset of intensive development in the study area (2010), the Blanding’s turtle population experienced both lower recruitment ($\chi^2{}_1 = 6.46$, p = 0.011) and an increased skew towards males ($\chi^2{}_1 = 6.75$, p = 0.009).

Habitat changes and connectivity

Compared to 2010, by 2020 development in the study area had caused a 10.0% loss in forest area, 16.8% loss in swamps, but no change in marsh area (Figure 1). Availability of Category 1 habitat decreased by 10.1% during the 10-year period. Due entirely to the creation of two artificial ponds in 2017, the study area gained 1.2% open water area. As a result of land clearing, open area covered by grassland increased by 40.5% and developed area increased by 131.4%, compared to 2010. These habitat changes occurred almost exclusively within the area occupied by Blanding’s turtles during the 2010-2013 study. Specifically, there was an 18.9% loss in forest and 34.2% loss of swamps in areas initially occupied by turtles, with a 93.6% increase in grassland. Largely due to a decrease in low-resistance wetlands (mostly swamps, Category 1 habitat) and increase in high-resistance habitat (settlement, grassland) within the central region of the study area, availability of least-cost paths linking the northern and southern wetlands declined, with the shortest paths entirely lost by 2017-2020. The single remaining corridor was 480 m (15.1%) longer than the previous least-cost path and following a more convoluted trajectory involving traversing wetland, forest, and some open field habitat, as well as roads (Figure 1).

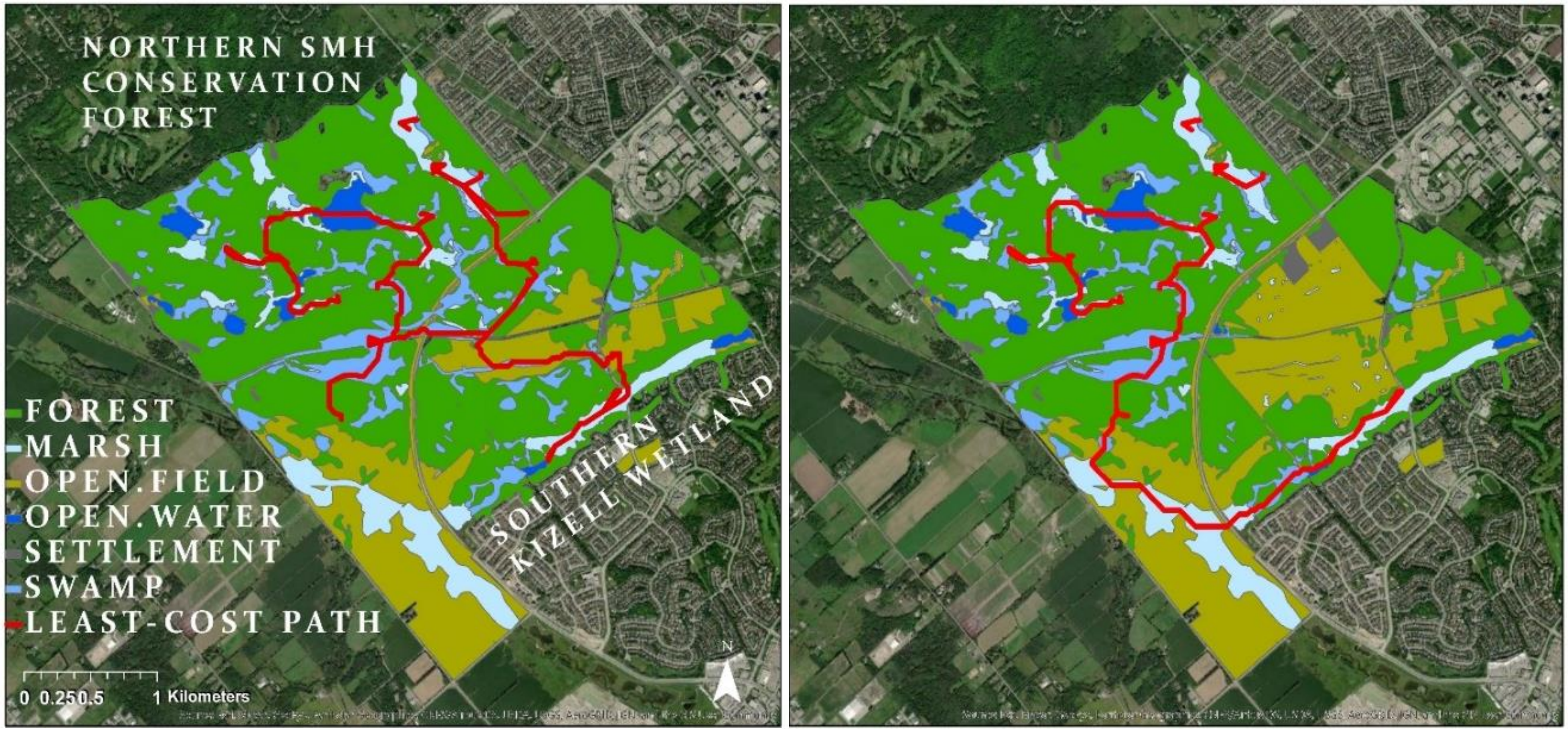

Figure 1: Blanding's turtle habitat in the study area in Ottawa, Ontario, Canada. Changes in habitat and least-cost paths (red) connecting Category 1 habitat in the northern conservation forest and southern Kizell wetlands in the study area before (left, 2010-2013) and after (right, 2017-2020) initiation of two major development projects. The South March Highland conservation area and Kizell pond sub-populations are, respectively, to the north and south of Terry Fox Drive, the main road bisecting the site.

Population size estimation

We estimated that the total adult Blanding's turtle population size was 81.0 (95% CI: 62.5-99.6) in 2010, declining to 24.4 (95% CI: 13.3-35.5) in 2020. The overall (69.9%) population decline was not consistent across sexes, with females declining >4-fold from 55.6 (95% CI: 45.6-65.6) to 11.7 (95% CI: 5.8-17.6) (79.0%), whereas males declined by half from 25.4 (95% CI: 16.9-34.0) to 12.7 (95% CI: 7.5-17.9). The greater loss of females resulted in a shift from a female-biased population in 2010 (68.6% female) to near-sex-ratio-parity (48.0% female) in 2020 (Figure 2, Table 2**Error! Reference source not found.**). The best-fit JS population estimation model had constant capture probability (ρ = 0.48; 95% CI: 0.41-0.55) and number of individuals (N_s = 8.1; 95% CI: 4.1-15.8) available to enter the population (2010 to 2020). The best-fit JS model estimated the same apparent annual survival (Φ) for both sexes, which was 0.86 (95% CI: 0.81-0.90) during 2010-2013 and 0.81 (95% CI: 0.64-0.90) during 2017-2020 (Table 2). Probability of entry into the population (p_{ent}) was very low, estimated as 0.052 (95% CI: 0.029-0.091) for males and 0.009 (95% CI: 0.001-0.080) for females (Table 2). Further, we estimated that the juvenile Blanding's turtle population decreased by 90.0% from 24.9 (95% CI: 15.4-34.3) in 2010 to 2.5 (95% CI: 0.0-5.8) in 2020, with an estimated apparent annual survival rate of 0.78 (95% CI: 0.63-0.88) and a capture probability of ρ = 0.20 (95% CI: 0.12-0.31) (Figure 2; Appendix C, Table 3).

When considering only the sub-population of adult Blanding's turtles in the northern conservation forest, we estimated a 70.4% population decline from 52.7 (95% CI: 46.1-69.4) to 15.6 (95% CI: 7.9-23.4) between 2010 and 2020. Specifically, females in this sub-population experienced a more severe decline (79.6%) than males (48.1%; Appendix C, Figure 2, Table 2). In this sub-population, adult apparent annual survival (Φ) was 0.81 (95% CI: 0.74-0.86) and probability of immigration for males (p_{ent} = 0.062; 95% CI: 0.035-0.106) was >3 times higher than that for females (Table 2). In this sub-population, estimated number of juveniles declined from 16.2 (95% CI: 6.1-26.4) in 2010 to 2.4 (95% CI: 0.0-5.6) in 2020 (Appendix C, Figure 2; Appendix C, Table 3). In contrast, the adult population model exclusive to the southern Kizell wetland revealed relatively high apparent survival (Φ = 0.94, 95% CI: 0.85-0.98), but markedly low probability of entry for both sexes (p_{ent} <0.001). In this analysis, the total adult sub-population declined by 40.2% from 17.4 (95% CI: 14.4-20.6) to 10.6 (95% CI: 5.1-16.1). In this sub-population, declines in females (39.0%) and males (39.1%) were comparable (Table 2; Appendix C, Figure 2). Juveniles in the southern Kizell sub-population were estimated to have declined from 2.3 (95% CI: 0.8-3.9) in 2010 to 0.4 (95% CI: 0.0-2.0) in 2020 (Appendix C, Figure 2; Appendix C, Table 3).

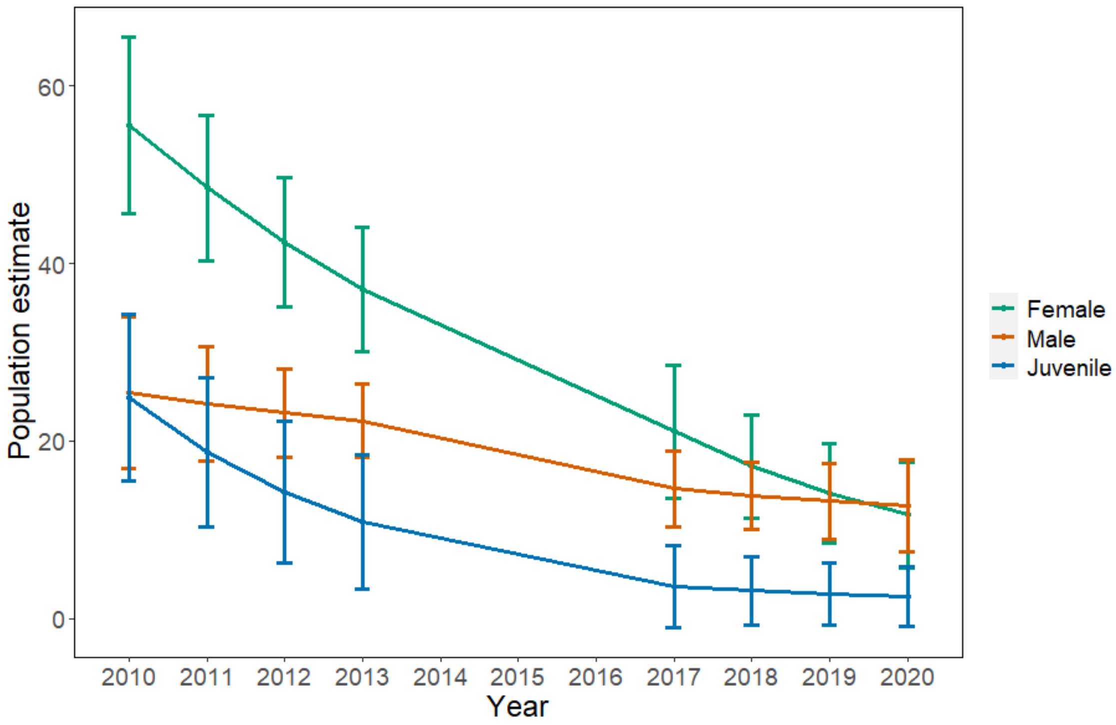

Figure 2: Estimated Blanding's turtle population size (with 95% confidence interval) in Ottawa, Ontario, Canada, including both the South March Highlands conservation area and Kizell pond sub-populations. Estimates were calculated from a Jolly-Seber population model (POPAN formulation).

Table 2: Estimated population parameters for the adult Blanding's turtle population in Ottawa, Ontario, Canada, including both the South March Highlands conservation area and Kizell pond sub-populations. Parameters were derived from Jolly-Seber estimation for the whole population and for the northern (SMH) and southern (Kizell) sub-populations separately. Sex- or study-period-specific parameters are shown where appropriate. Where only one estimate is shown, the parameter was estimated to be constant through time and for both sexes.

	Entire population			**SMH**			**Kizell**		
	Estimate	**Lower 95% CI**	**Upper 95% CI**	**Estimate**	**Lower 95% CI**	**Upper 95% CI**	**Estimate**	**Lower 95% CI**	**Upper 95% CI**
Capture probability	0.478	0.412	0.545	0.516	0.406	0.625	0.419	0.312	0.533
Superpopulation size[1]	8.1	4.1	15.8	6.3	2.8	13.9	0.3	0.0	54.5
Apparent survival									
2010-2013	0.860	0.809	0.899	0.808	0.743	0.860	0.944	0.848	0.980
2017-2020	0.805	0.643	0.904						
Probability of immigration									
Females	0.009	0.001	0.080	0.016	0.002	0.100	<0.001	<0.001	1
Males	0.052	0.029	0.091	0.062	0.035	0.106			
Female population size									
2010	55.6	45.6	65.6	37.3	27.5	47.1	8.2	6.7	9.8
2020	11.7	5.8	17.6	7.6	3.4	11.8	5.0	2.4	7.6
Male population size									
2010	25.4	16.9	34.0	15.4	8.6	22.3	9.2	7.7	10.8
2020	12.7	7.5	17.9	8.0	4.5	11.6	5.6	2.7	8.5

[1] Superpopulation = the total number of individuals available for entry into the sampled population (Schwarz and Arnason, 1996)

Home ranges and locations

Mean home range area of Blanding's turtles monitored in 2010-2013 was 19.7 ha (95% CI: 5.3-34.1) compared to 13.8 ha (95% CI: 4.6-23.02) in 2017-2020 ($F_{1,1} = 0.001$, $p = 0.98$; $n = 36$ turtles). During the 2017-2020 nesting seasons, females were found more often in close proximity to roads than males ($t_{25} = 0.68$, $p = 0.51$; $n = 27$ turtles), with 33.1% of female turtle GPS locations and 21.3% of male turtle GPS locations within 200 m of roads. On average, females were located 260.5 m (95% CI: 117.7-403.3) (or 44.3%) closer to roads than males ($t_{25} = 3.75$, $p < 0.001$; $n = 27$). Moreover, the proportion of realised GPS fixes was twice as high for females as for males ($t_{25} = 2.12$, $p = 0.043$), implying that females spent more time on land. Turtle GPS trajectories showed that 5 (4 females, 1 male) of the 35 tagged turtles in 2017-2020 crossed Terry Fox Drive, the major road that bisects the study area, at least once. However, GPS data resolution was not sufficient to determine if turtles crossed through culverts or on the road.

Mortalities

During 2010-2013, of 21 radio-tagged turtles, 9.5% died during the May-September monitoring period. A single adult female died from a vehicle collision, while the other turtle succumbed to an unknown cause. During 2017-2020, of 33 tagged turtles, a single male (2.9%) died from a vehicle collision. Based on telemetry, estimated 30-day turtle survival probability during summers 2017-2020 was 0.96 (95% CI: 0.89-1.0) and 1.0 for male and female turtles, respectively, with 4 of 33 turtles succumbing to unknown fate (and thus censored in survival estimation). Our CPH model revealed no apparent hazard ratio differences between the sexes (p = 0.99).

Untagged turtles were found dead on the road during both 2010-2013 (n = 5, only one could be identified as an adult female) and 2017-2020 (n = 3, 2 of which were identified as adult females, the other could not be sexed). Note that during 2018 and 2019, a separate research team working in the area detected an additional 4 road mortalities, 2 of which were identified as adult females and 2 as juveniles (D. Seburn, Canadian Wildlife Federation, pers. comm.). Thus, we infer that a minimum of 1 adult female Blanding's turtle per year was killed on the road, during both periods. However, we consider that because the single road mortality of a tagged turtle in 2020 would not have been detected without telemetry, and because additional road mortalities may have been removed prior to our road survey, estimated road mortality rates are likely considerably higher than our estimates. Notably, 92.9% of observed road mortalities occurred on roads immediately surrounding the northern conservation forest and 78.6% were found specifically on Terry Fox Drive (Appendix C, Figure 1) and in proximity to openings in the roadside fences (e.g., for railroad crossing and development access).

Population viability analysis

In the baseline population projection for Blanding's turtles, the population experienced a stable finite growth rate throughout the 50 years ($\lambda = 0.997$). Adult female survival was the parameter with the highest elasticity (80%), with the remaining parameters having lower contributions (all <11%; Appendix C, Table 4). When one and two additional female mortalities per year were modelled, projected adult female population size in 2020 was 37.0 and 28.2, respectively, which was considerably larger than our estimated population size of 11.7 (95% CI: 5.8-17.6) females from the JS model. When female mortality was increased to 3 and 4 per year, projected adult female population size in 2020 was 19.3 and 10.5, respectively. Thus, 4 adult female mortalities per year during 2010-2020 matches closely our estimated decline of female Blanding's turtle population size. When annual female adult survival rate was reduced proportionally by 1.8% for 50 years (representing 1 of the 56 initially estimated adult females in 2010), λ was 0.982, and estimated population size in 2020 was 38.6 adult females (Figure 3; Appendix C, Table 5). When annual female survival rate was reduced by 3.6% for the duration of the projection (representing 2 of 56 females in 2010), total population growth rate declined further (λ = 0.968), and population size in 2020 was projected as 32.5 females (Figure 3; Appendix C, Table 5). Note that both these projected 2020 adult female population sizes were 3.3 and 2.7 times larger, respectively, than our estimated population size from the JS model. In fact, we found that an adult female annual survival rate of 0.82 was needed to produce the female population size estimated by the JS model (Figure 3; Appendix C, Table 5). Note that this modelled annual survival rate is comparable to the mean apparent survival rate estimated by the JS model. With a female survival rate of 0.82, the population experienced a finite growth rate of λ = 0.922 and would likely breach the quasi-extinction threshold of 4 females before 2030 (Figure 3; Appendix C, Table 5). Likewise, annual female survival of 0.75 and 0.86 would recreate the lower (n = 5.8 females) and upper 95% confidence limit (n = 17.6 females) of the population size estimate, respectively (Appendix C, Table 5).

Lastly, to sustain a population size above the quasi-extinction threshold (n = 4 females) by 2030 and 2060, the adult female survival rate would have to be ≥0.82, or ≥0.91, respectively, starting in 2010 (Figure 3; Appendix C, Table 5).

When modelled as two sub-populations and one female road mortality per year was added to the northern sub-population (as suggested from our road mortality observations), the projected size of this sub-population in 2020 was 12.1 adult females. When two female road mortalities were added per year, the projected population size in 2020 was 5.7 adult females (Appendix C, Table 6), suggesting that between 1-2 adult females were likely killed on the road in the northern conservation forest since 2013, leading to our observed number of adult females in this sub-population (n = 7.6, 95%. CI: 3.4-11.8). An annual female survival probability of 0.84 recreated the observed decline in females in this sub-population. With this survival rate, the northern sub-population experienced a growth rate of λ = 0.904 (Appendix C, Figure 3). In contrast, in the southern Kizell wetland, adult females likely experienced a higher annual survival rate of 0.94, leading to the observed sub-population size of 5.0 (95% CI: 2.4-7.6) adult females and a population growth rate of λ = 0.977 (Appendix C, Figure 3).

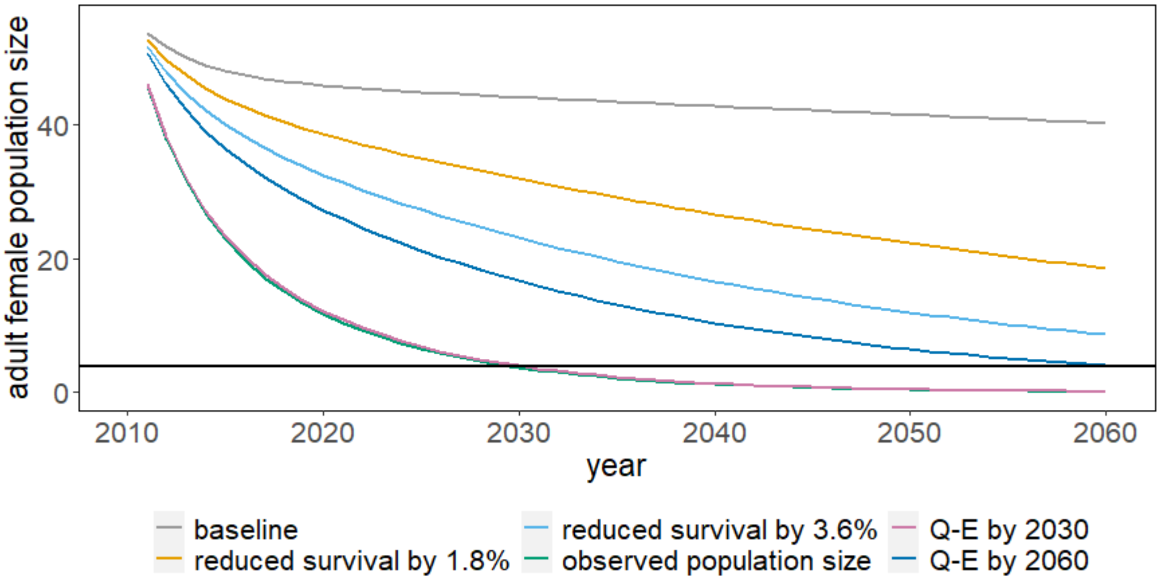

Figure 3: Population viability analysis (PVA) of the adult female Blanding's turtle population in Ottawa, Ontario, Canada, starting with the estimated female adult population size in 2010. Projected scenarios are: Baseline in the absence of road mortality; with road mortality scenarios similar to road kill observations (1.8% and 3.6% reduced female annual survival rate), with a survival rate of 0.82 that recreated observed female population size in 2020, and survival rates with which quasi-extinction (Q-E) threshold of 4 female adults were breached by 2030 and 2060 (survival rates: 0.83 and 0.91, respectively). The horizontal line represents the quasi-extinction threshold.

Discussion

Human impacts on the environment threaten wildlife worldwide (Sala et al., 2000), and knowledge about the extent of the impact of urban development on population sustainability can guide management decisions for species-at-risk. Consistent with our hypothesis, current urban development in the South March Highlands area of Ottawa, Ontario, Canada, is not compatible with Blanding's turtle population viability. Over the decade of intensive development, the study area experienced a substantial loss of turtle habitat and connectivity, likely leading to the separation of two smaller and largely distinct sub-populations of turtles. Habitat loss coincided with a severe decline in adult turtle survival and population size, which was especially pronounced in females and ultimately shifted the population's sex ratio and led to low juvenile recruitment. Turtles were killed by vehicles; females spent more time on land and were closer to roads than males. An annual survival rate for adult females of 0.82 yielded comparable changes in female population size to those observed over the last 10 years and this rate is insufficient to have a viable population over the longer term. Ultimately, our results suggest that in our study area, despite efforts to offset habitat loss and road mortality, this urban development is incompatible with the viability of this at-risk freshwater turtle population. Generally, our work suggests that development approval conditions may need to be revised to prevent population declines, and, in the long term, reduce biodiversity loss in urbanised areas.

Our study shows that urbanisation can dramatically alter animal population size and structure, primarily through reduced habitat availability and higher road mortality.

We estimated Blanding's turtle survival (or apparent survival) in two ways: using capture-mark-recapture (CMR) and telemetry-based methods. Although the two methods provided different estimates, we suspect that telemetry-based estimates were overestimates because, despite our best efforts in the field, a portion of the monitored turtles (11.4%) were not recovered and thus succumbed to unknown fate that could have included road mortality. This uncertainty reduces the precision of survival estimates (Murray, 2006; Murray and Bastille-Rousseau, 2020) and, unlike our CMR-based annual apparent survival estimates, telemetry provided survival estimates only for the May-September period during 2017-2020. Notably, apparent survival estimates derived from the JS model reflected observed changes in the total study population size, and the fact that our p_{ent} estimates were low implies that the population was functionally closed and thus that apparent survival rates were minimally influenced by turtle emigration from the study area. Further, our projection results suggest that a female adult annual survival rate similar to the mean apparent survival rates could effectively reproduce the current female population size.

Survival estimates in our urban study population were markedly lower than those observed in undisturbed Blanding's turtle populations (e.g. Congdon et al. 1993). While sex-biased road mortality is sometimes still controversial (see e.g. Carstairs et al. 2019), and often not considered in turtle management, several studies have demonstrated that roads can have dramatic and differential effects on freshwater turtles (Beaudry et al., 2010; Howell and Seigel, 2019; Howell et al., 2019). For example, Piczak et al. (2019) found a >80% decline and increased male-bias in a Snapping turtle

(*Chelydra serpentina*) population subjected to high road mortality. Likewise, our detections of road mortality combined with estimates of time spent on land and in proximity to roads (see also Aresco, 2005; Steen et al., 2006) supported that females are at higher risk of vehicle collisions (Beaudry et al., 2010; Crawford et al., 2014; Howell and Seigel, 2019). Our suspicion that road mortality has a serious impact on our study population is further reinforced by the fact that the sub-population in the northern conservation forest (which is surrounded by roads) declined more than the more isolated southern sub-population. Thus, our results demonstrate the critical impacts of roads, not only on total turtle population size, but especially on females during overland travel, such as when searching for nest sites (Ernst and Lovich, 2009; Tuberville et al., 1996), and highlights the need for careful implementation and intensive monitoring of fences and wildlife passages.

Notably, the major road bisecting the study area (Terry Fox Drive) was built just prior to our first study period and there were already indications of high road mortality and population decline at that time (Dillon Consulting Limited 2013, Hasler et al. 2015) which was supported by our JS population model results. We showed that turtle apparent survival decreased even more after the recent pulse in residential development (2017-2020), which likely spurred an increase in road traffic. Habitat loss often works in tandem with other anthropogenic disturbances, leading to aggravated impacts on wildlife populations (Paterson et al., 2021; Romero-Muñoz et al., 2020). In our case, we suspect that loss of a portion of crucial turtle habitat and reduced connectivity between sub-populations may have forced animals into the proximity of roads, where permeable fencing failed to prevent vehicle collisions. These combined effects could have aggravated and accelerated the effects of habitat change or roads alone. These results emphasize the need to consider multiple stressors when developing management plans to limit impacts on urban wildlife populations.

Coinciding with the decline of adult females in the Blanding's turtle population, we found a decrease in juvenile recruitment over the last decade. Despite lower detection probabilities of juvenile turtles compared to adults (Pike et al., 2008), we used identical capture methods in 2017-2020 and in 2010-2013, and conducted extensive visual surveys of the area. Thus, we surmise that the observed decline in juveniles is representative of demographic changes in our study population, notably the loss of reproductive females due to road mortality. Apart from road mortality, loss of juveniles could also be due to an increase in nest predation by subsidized sub-urban predators such as raccoons, which hunt for turtle eggs along road sides (Karson et al., 2018; Marchand and Litvaitis, 2004). Knowledge about recruitment rates can inform turtle management, which may consider nest-protection or head-starting programs, in addition to protecting adults (e.g. Ross et al. 2020; Campbell et al. 2020).

Our study population likely cannot sustain current rates of adult road mortality, a phenomenon seen in other systems where wildlife population sustainability has been sought in tandem with rapid urban development (e.g. Howell et al. 2019; Stokes et al. 2021; Ascensão and Desbiez 2022). Unfortunately, approval for urban development proposals rarely requires the level of pre-development baseline data that would inform, for example, robust habitat availability and population viability analyses. This implies that assessments of wildlife responses to development almost always suffer from data deficiencies, which precludes both rigorous assessment of responses and the ability to make rapid and effective adjustments to mitigation measures. In South March Highlands, the measures used to offset development impacts, including road culverts, wildlife fences, artificial turtle nest sites and hibernacula, were constructed mostly *ad hoc* and with limited surveillance and quality control (A. Auge, unpubl.). Some measures were established years after the project had been initiated and were untested. For example, although the benefits of wildlife fencing in combination with culverts have been confirmed for some freshwater turtle populations (e.g. Aresco 2005b), other mitigation measures such as artificial nest sites and hibernacula have not been evaluated. Often, newly created habitats fail to fully restore ecosystem function (Moreno-Mateos et al., 2012) or require years to become established (Vesk et al., 2008), which can prevent target species from occupying these areas and can reduce success of new habitat (Moilanen et al., 2009; Pickett et al., 2013). In principle, these measures could have worked given that creating new habitats, passages or fences can benefit a variety of wildlife species (Jarvis et al., 2019; Kiviat et al., 2000), but in other instances, such measures have not been successful (Baxter-Gilbert et al., 2015; Cunnington et al., 2014; Gilhooly et al., 2019). As a result, it is unsurprising that mitigation in our study area was insufficient to prevent population decline.

Long-lived species with delayed maturity and low natural recruitment often have a larger minimum viable population size, slower population growth rate (Wang et al., 2019), and, thus, limited ability to recover from high levels of mortality associated with anthropogenic disturbances (Hamilton et al., 2018; Norse et al., 2012; Richards et al., 2021). Further, although some effects of habitat loss can be detected over a short timespan (e.g., loss of nesting sites, increased predation), demographic consequences of habitat loss may be revealed only after an extended period and following intensive monitoring. This is especially true when long-lived species might already have been in slow decline prior to more intense disturbance, leading to challenges in evaluating the true impacts of development and merits of mitigation (Knapp and Perez-Heydrich, 2012; Pike et al., 2010).

To conclude, urban wildlife populations face a high risk of extirpation due to habitat alterations (Browne and Hecnar, 2007; Howell and Seigel, 2019; Stokes et al., 2021). Population and biodiversity protection are most successful when environmental impacts are avoided or at least minimised (Gardner et al., 2013; Marshall et al., 2020), but in the present age of widespread biodiversity loss, urban sprawl, and environmental change, the onus is on legislators and planners to devise better strategies for allowing development while ensuring protection of species at-risk. If habitat loss cannot be avoided, mitigation strategies should be demonstrated to be effective and applied correctly (Edwards et al., 2019; Ghisbain et al., 2020). We recommend that monitoring data collected before, during, and after development should be used to evaluate such strategies and to inform timely adjustments to mitigation (Maron et al., 2012; Taylor et al., 2010; Vasconcelos and Calhoun, 2006). Ultimately, these activities will be increasingly necessary to help improve the sustainability of wildlife populations in an increasingly disturbed, urbanised environment.

Chapter 5: General Discussion

Synthesis and significance

The overall objective of my thesis was to further our understanding of animal behaviour and population dynamics in response to natural and anthropogenic challenges in the environment. To achieve this, I used novel miniaturised bio-logging technologies to classify and validate activity states of free-ranging freshwater turtles; investigated how these animals navigate environments of high thermal heterogeneity near their northern range limit; and assessed their population responses to anthropogenic changes on the landscape.

Chapter 2: Accelerometer-based activity classification

In chapter 2, I developed classification models that successfully characterised and validated freshwater turtle activity states using animal-borne bio-loggers: accelerometers and water sensors. I demonstrated two approaches for using accelerometers more efficiently for behavioural studies and found the following: 1) Predictive accuracy of activity classification was unaffected by using sampling frequencies that were considerably lower than those tested in previous accelerometer studies (e.g. Halsey et al., 2009; Studd et al., 2019) – this finding implies that lower sampling frequencies can be used, at least for freshwater turtles, to benefit accelerometer battery life, deployment length, and data processing power needs; and 2) Demonstration, in one of the first studies using accelerometers to investigate freshwater turtle behaviour, that simple classification trees have high predictive accuracy and that simple classification models can be used interchangeably between closely-related species. The results of this study are more supportive of the potential cross-species transferability of accelerometer-based behavioural/activity classification, compared to previous studies (e.g. Ferdinandy et al., 2020). More generally, this chapter makes an important methodological contribution to the field of behavioural ecology by providing a framework for robust behavioural classification and by highlighting the need for similar studies to validate new bio-logging technology.

Chapter 3: Navigating the thermal landscape

In chapter 3, I investigated how two species of ectotherms select habitats in a thermal landscape near the northern edge of their range, at various spatial scales and across seasons. I showed that turtles selected warmer and more thermally homogeneous conditions compared to the available environment, but more so at finer spatial scales, which likely correspond to the scale that these relatively small and slow-moving animals perceive their surroundings. Turtle thermal sensitivity was greatest early in the year after emerging from hibernation when animals require higher temperature due to increased energy demands related to reproductive behaviour (Bouazza et al., 2016; Congdon and Tinkle, 1982; Krawchuk and Brooks, 1998).

Results from this chapter augment previous research on ectotherm habitat selection (e.g. George et al., 2017; Picard et al., 2011) and habitat thermal quality (e.g. Cadena and Tattersall, 2009; Row and Blouin-Demers, 2006) by focussing on the selection of thermal regimes, including mean temperature and thermal variability, across various environmental conditions, using fine-scale data derived from novel bio-loggers. My results highlight the importance of considering multiple factors influencing environmental properties and various spatial scales when examining habitat selection. These analyses are especially significant because they not only assess animal sensitivity to average ambient temperatures, but also the role of thermal heterogeneity on the landscape in driving behaviour. Such heterogeneity in temperatures has been shown to have comparable effects on animal behaviour in theoretical models, but has rarely been tested in wild animals (Sears and Angilletta, 2015; Sears et al., 2016b). These findings on thermal habitat selection are important because they suggest that animals may buffer environmental fluctuation in heterogeneous landscapes, which eventually will have consequences for their energy balance, physiological performance and fitness (Huey and Slatkin, 1976; Sears and Angilletta, 2015). Ultimately, this research advances our understanding of animal habitat selection in heterogeneous landscapes, and can help predict animal responses to future temperature variation in challenging and rapidly-changing environments.

Chapter 4: Urbanisation and population persistence

In chapter 4, I investigated the impact of habitat change and road development on an urban turtle population. Consistent with my prediction, I found that development in the study area over the last decade resulted in substantial turtle habitat loss and fragmentation. Moreover, I found a dramatic reduction in juvenile recruitment and adult survival, which translated to a marked decline in population size. This decline was most profound in females, which could be attributable to higher female mortality on roads given that they spent more time on land and were closer to roads than males. These findings are important as sex-biased road mortality risk is still fairly controversial in the literature (e.g. Carstairs et al., 2019). I show that road mortality in an area with reduced habitat availability and connectivity can lead to a precipitous decline in population size, even though effects of habitat loss on long-lived species can often be discerned only after a lag period (Findlay and Bourdages, 2000). In fact, I suspect that habitat loss may be the ultimate factor in this decline by forcing turtles onto roads when moving between wetlands or searching for new nesting sites. My population viability models show that with continued road mortality the local Blanding's turtle population is likely to become functionally extinct in the next decade. The results of chapter 4 are eye-opening as they challenge the long-held assumption that environmental sustainability and urban development can be compatible as long as mitigation measures are implemented (Bull et al., 2016; Maron et al., 2012). Indeed, my results imply that the application of several mitigation measures designed to protect turtles and restore their habitat in the study area was not sufficient to ensure viability of this at-risk turtle population. This point is compounded by the fact that long-term monitoring of the turtle population and adjustment of mitigation measures are not planned. More broadly, the results imply that development approval conditions should be reconsidered to require a higher level of pre- and post-development monitoring for target species, including efficacy assessment and adaptive improvements to increase the performance of mitigation measures.

Broader implications and conclusion

Species are frequently faced with a variety of natural and anthropogenic threats in the environment (Angilletta, 2001; Sala et al., 2000). My thesis adds to our understanding of the role of the thermal environment and anthropogenic land-use change in shaping animal behaviour and population dynamics. My results imply that freshwater turtles can respond behaviourally to fine-scale environmental variability in challenging environments, which likely maximises their physiological performance, survival and fitness. On the other hand, when faced with rapid and more permanent anthropogenic impacts on the environment, such as habitat loss and road mortality, populations of long-lived species are likely unable to respond quickly enough, leading to diminished long-term viability, despite measures to offset impacts on wildlife. These results have important implications for approval conditions of urban development projects, which likely need to be revised to meet environmental standards over the long term.

Future research

While I was able to show that turtles experienced warmer and less variable temperatures compared to the environment, my study did not address the mechanisms leading to animal responses to temperature variability. I suspect that animals likely used a combination of actively moving between thermally suitable locations and choosing sites that are inherently warmer and less variable (Woods et al., 2015), which could have implications for cost of thermoregulation. For example, while actively moving between preferred locations in a heterogeneous landscape can increase thermoregulatory efficiency, these benefits need to be balanced with costs related to predation risk and energy expenditure (Huey and Slatkin, 1976; Sears and Angilletta, 2015). Thus, I recommend future work to address the mechanisms of thermal habitat selection by assessing activity patterns and/or energy expenditure (using a combination of bio-loggers, including accelerometers) compared to fine-scale environmental temperature variability and distribution.

Further, my results are reflective of turtle behaviour in thermally heterogeneous environments at the northern distribution margin. I would expect that populations in regions with more benign and homogenous ambient temperatures show weaker selection of thermal locations (George et al., 2017; Sears and Angilletta, 2015). Thus, future similar work should be conducted on multiple populations, including those in more temperature regions. Several studies have addressed the relationship between ambient temperature and thermoregulation (e.g. Piasečná et al., 2015; Sears et al., 2016), and my study provides evidence that animals exhibit thermoregulatory behaviour by selecting specific microclimates. However, future work should extend my analysis by including body temperature to investigate how thermal habitat selection affects body temperature and thus, thermoregulatory efficiency and accuracy.

I suspect that habitat loss and road development worked in tandem to cause the dramatic decline in the Blanding’s turtle population. A few studies have addressed the synergistic effects of multiple threats on population viability, leading to effects that may be much stronger than each threat on its own (Jenssen et al., 2015; Paterson et al., 2021; Romero-Muñoz et al., 2020). Future studies should further investigate the effects of various disturbances, such as habitat loss, road mortality or other anthropogenic impacts, to investigate how these effects work together at various spatial scales. For example, long-term studies with a robust before-and-after-control-impact assessment (BACI) design should assess changes in movement patterns, corridor usage and survival of animals in areas undergoing development to assess to what extent individuals are forced out of their home range due to habitat loss, and what proportion of the population succumbs to immediate causes of mortality (e.g. on the road) vs. more ultimate impacts (e.g. through changes of nest site quality or predation affecting reproductive output). Ultimately, my work highlights the need to conduct rigorous environmental monitoring prior to, during, and after development, and if necessary, adopt mitigation measures that have a track record of success and that can be adjusted on the basis of monitoring results. Regardless, my study clearly shows that it may be very difficult to effectively balance urban development with environmental needs, as is so often purported by urban planning documents and development proposals (e.g. Geneletti et al., 2017; Sofeska, 2016).

Lastly, while I used accelerometers and water sensors to describe freshwater turtle activity with high accuracy, I focused on characterising simple activity states. Other studies using a combination of bio-loggers successfully described more complex behaviours in other species, such as foraging or hunting in terrestrial mammals (Studd et al., 2019b, 2021). Likewise, future work on other small or cryptic animals, or species with more complex behaviours, should aim to classify fine-scaled behaviour. For example, a combination of accelerometers and other bio-loggers could be useful for documenting nesting, mating or foraging behaviour across a range of species. Thus, adoption of these new, innovative tools could provide much deeper insight into animal time-budgets, responses to environmental variation, and the effect of natural and anthropogenic threats. Moreover, accelerometer data correlate with energy expenditure in a variety of species (e.g. Jeanniard-du-Dot et al., 2017; Ladds et al., 2018; Wilson et al., 2012), meaning that future work should calibrate these metrics for freshwater turtles and other species to gain insights into energy-time-budgets and the determinants of animal survival, fitness and population dynamics.

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Appendix A: Supplementary materials for Chapter 2

Table 1: Percent overlap of the best and second-best accelerometer summary statistic following histogram separation of terrestrial and aquatic in-motion and motionless.

Dataset	Species	Separated activities	Best summary statistic	% overlap	% improvement to second best statistic	Second best summary statistic
1 Hz sampling frequency	Blanding's	Terrestrial-in-motion vs. motionless	ΔODBA, ΔVeDBA	1.4	61.1	SDODBA
		Aquatic-in-motion vs. motionless	ΔODBA	6.7	5.6	ΔVeDBA
	Painted	Terrestrial-in-motion vs. motionless	ΔODBA, ΔVeDBA	1.1	9	TODBA
		Aquatic-in-motion vs. motionless	ΔODBA	0.5	16.7	ΔVeDBA
Cross-species comparison	Blanding's	Terrestrial-in-motion vs. motionless	ΔODBA, ΔVeDBA	1.6	38.5	TODBA
		Aquatic-in-motion vs. motionless	ΔODBA	6.2	3.1	ΔVeDBA
	Painted	Terrestrial-in-motion vs. motionless	ΔODBA, ΔVeDBA, SDVeDBA	1.1	8.3	TODBA
		Aquatic-in-motion vs. motionless	ΔODBA	0.6	14.3	ΔVeDBA

Table 2: Correlation matrix showing Pearson's correlation coefficients between different accelerometer metrics. All correlations were significant (p <0.001).

	ODBA	VeDBA	ΔODBA	ΔVeDBA	TODBA	TVeDBA	SDODBA	SDVeDBA
ODBA	1.00							
VeDBA	0.99	1.00						
ΔODBA	0.65	0.65	1.00					
ΔVeDBA	0.65	0.65	1.00	1.00				
TODBA	0.78	0.79	0.85	0.85	1.00			
TVeDBA	0.78	0.79	0.84	0.84	1.00	1.00		
SDODBA	0.64	0.63	0.81	0.81	0.70	0.69	1.00	
SDVeDBA	0.64	0.64	0.82	0.82	0.71	0.71	0.99	1.00

Table 3: State classification performance for the testing data used to classify Blanding’s turtle and Painted turtle accelerometry and water sensor data, using the other species threshold values.

			Observed			
			Motionless (aquatic)	Motionless (terrestrial)	In-motion (aquatic)	In-motion (terrestrial)
Blanding`s	Predicted	Motionless (aquatic)	35	0	0	0
		Motionless (terrestrial)	6	242	0	3
		In-motion (aquatic)	20	0	41	0
		In-motion (terrestrial)	22	1	13	465
		Sensitivity (%)	42.2	99.6	75.9	99.4
		Specificity (%)	100	98.5	97.5	90.5
		Overall accuracy (%):	92.5 (95% CI: 90.3, 94.0%)			
			Motionless (aquatic)	Motionless (terrestrial)	In-motion (aquatic)	In-motion (terrestrial)
Painted	Predicted	Motionless (aquatic)	88	233	0	0
		Motionless (terrestrial)	0	878	0	0
		In-motion (aquatic)	12	0	34	19
		In-motion (terrestrial)	0	25	0	42
		Sensitivity (%)	88.0	77.0	100	68.9
		Specificity (%)	81.1	100	97.6	98.0
		Overall accuracy (%):	78.3 (95% CI: 76.0, 80.5%)			

Table 4: Effect of sampling frequency on state classification accuracy. Best-fit smoothing window, threshold values, accuracy, sensitivity and specificity of Blanding's turtle and Painted turtle activity classification based on accelerometry data, sampled at 0.5, 0.25, 0.125 and 0.0625 Hz.

SF (Hz)	**Species**	**Separation of in-motion vs. motionless**	**SW (s)**	**Thresh-old**	**Acc. (%) (95% CI)**	**Sens. (%)**	**Spec. (%)**	Overall accuracy (%) (**95% CI)**
0.5	Blanding's	Terrestrial	90	0.7	99.2 (97.6, 99.8)	99.2	99.2	93.2 (90.3, 95.4)
		Aquatic		1.2	92.9 (84.1, 97.6)	88.1	100	
	Painted	Terrestrial	50	0.4	98.3 (97.0, 99.2)	98.3	100	79.4 (76.1, 82.4)
		Aquatic		1.5	98.5 (92.0, 1.0)	98.0	100	
0.25	Blanding's	Terrestrial	92	0.7	97.7(94.3, 99.4)	95.0	99.1	91.9 (87.4, 95.2)
		Aquatic		1.4	73.5 (55.6, 87.1)	70.0	78.6	
	Painted	Terrestrial	72	0.6	99.6 (98.1, 99.9)	100	92.6	91.4 (88.0, 94.3)
		Aquatic		2.1	85.3 (68.9, 95.1)	82.6	90.9	
0.125	Blanding's	Terrestrial	112	0.8	93.1 (85.6, 97.4)	96.7	91.2	85.8 (77.7, 91.9)
		Aquatic		1.5	73.7 (48.8, 90.9)	54.5	100	
	Painted	Terrestrial	112	1.7	96.6 (92.3, 98.9)	100	37.5	89.2 (83.4, 93.4)
		Aquatic		1.9	82.3 (56.7, 96.2)	83.3	80.0	
0.0625	Blanding's	Terrestrial	128	0.7	86.4 (72.3, 94.5)	68.8	96.4	80.4 (66.8, 90.2)
		Aquatic		5.1	42.9 (1.0, 81.6)	20.0	100	
	Painted	Terrestrial	96	0.9	97.3 (90.6, 99.7)	100	50	89.0 (80.2, 94.9)
		Aquatic		2.8	100 (63.1, 100)	100	100	

SF: sampling frequency, SW: smoothing window, Acc.: accuracy, Sens.: Sensitivity, Spec.: Specificity, CI: 95% confidence interval

Figure 1: Accelerometer (left) and VHF transmitter (right) bolted onto the rear carapace margin of a Painted turtle.

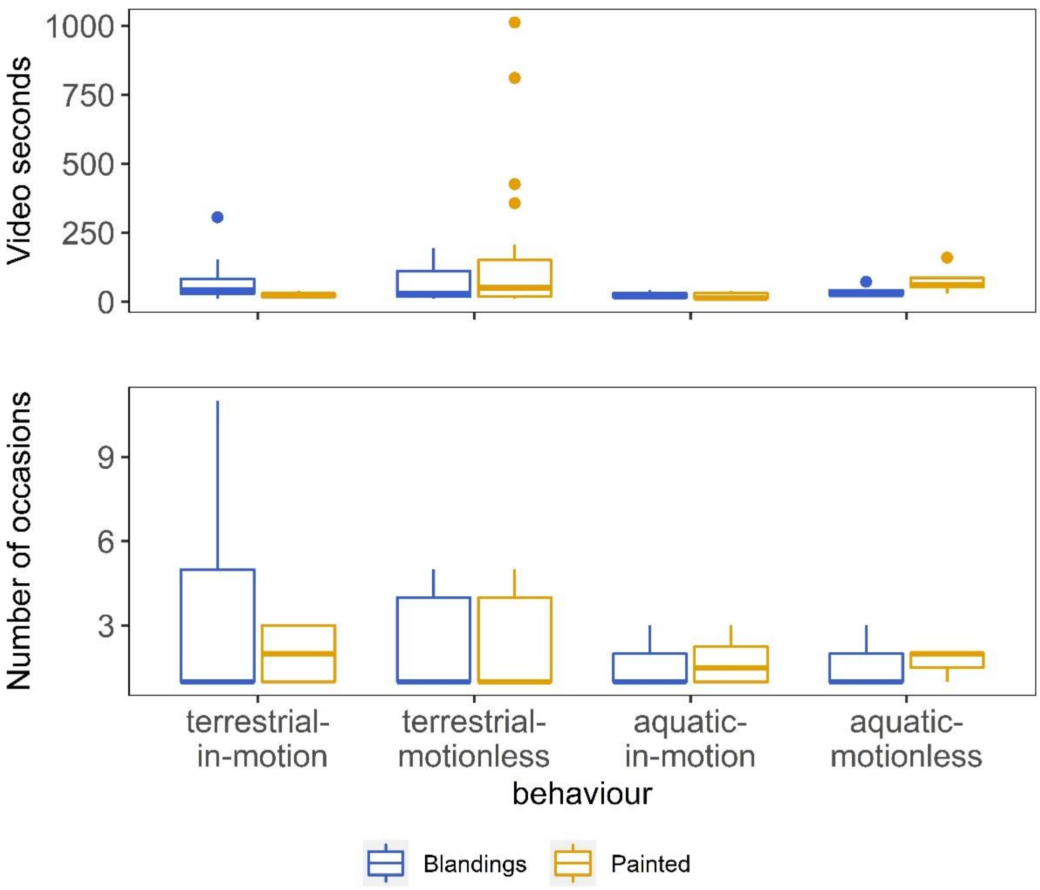


Figure 2: Boxplot of length of recorded states (top panel), and number of occasions each state was observed (bottom panel) across Blanding's (blue) and Painted turtles (orange).

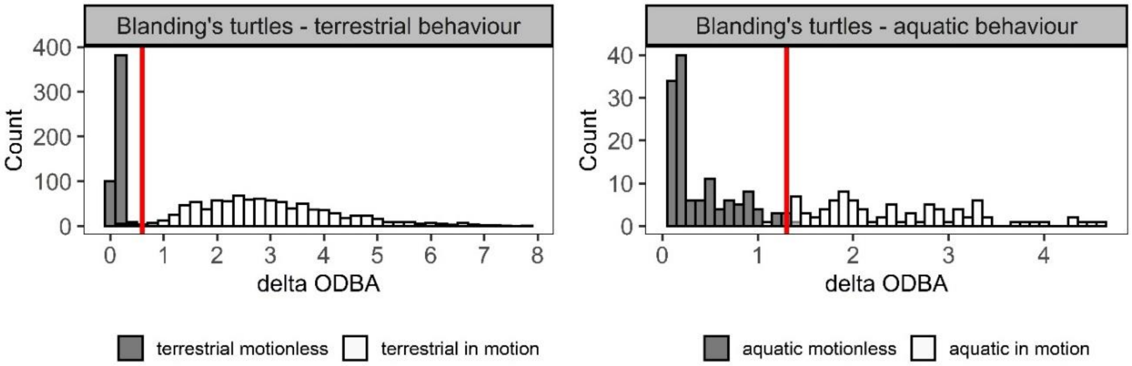


Figure 3: Sample histogram separating activity modes in Blanding's turtles: terrestrial in-motion from motionless and aquatic in-motion from motionless. The red vertical line indicates the threshold value determined after testing the accuracy of ΔODBA values within the overlapping regions. These histograms are based on data sampled at 1 Hz.

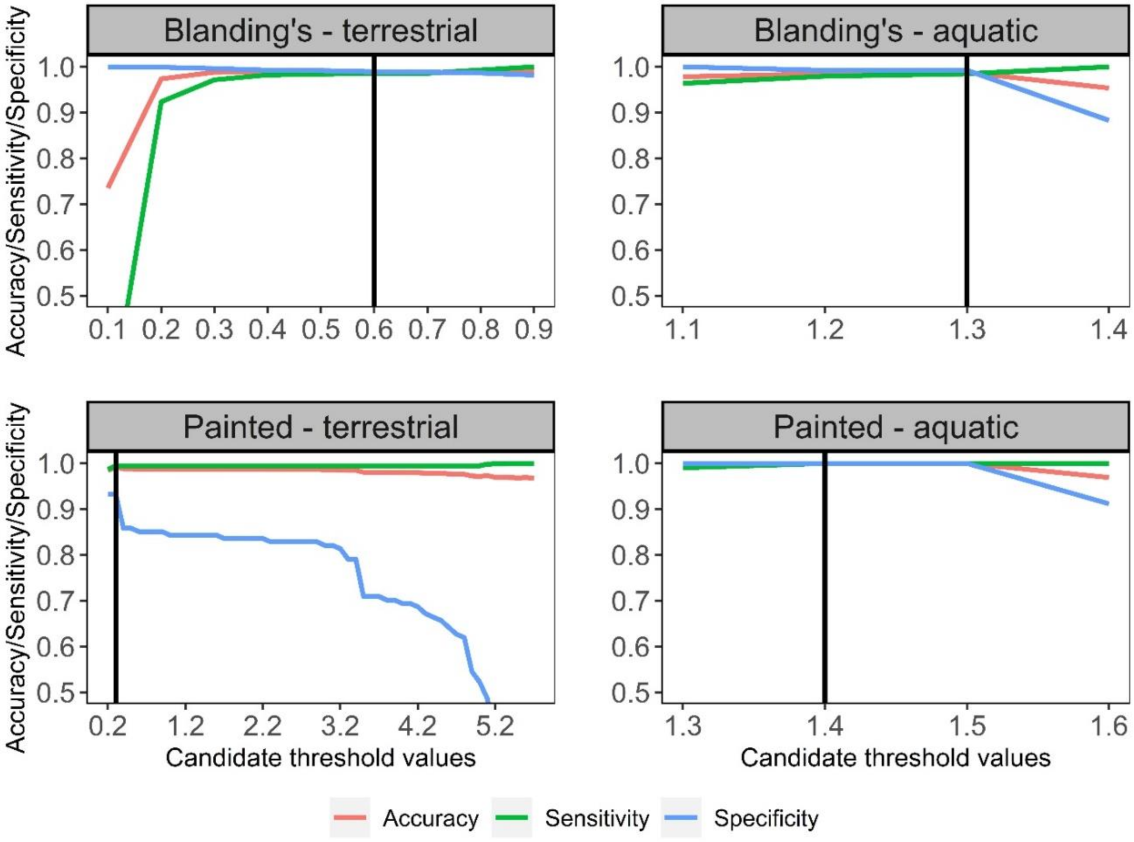
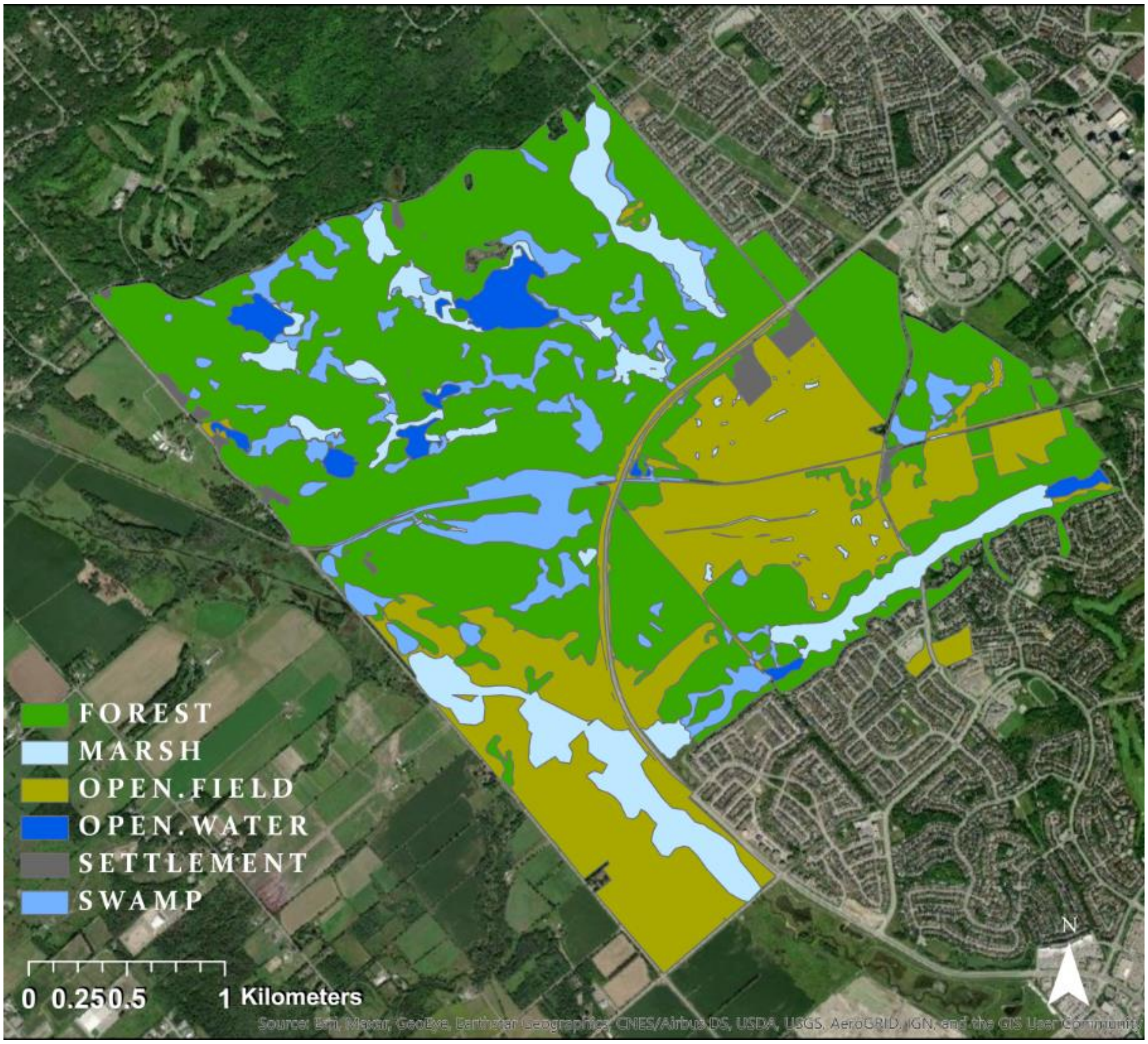


Figure 4: Optimizing the threshold value (vertical lines) relative to data accuracy, sensitivity and specificity, for Blanding's turtles and Painted turtles, using acceleration data calculated with smoothing windows of the other species.

Appendix B: Supplementary materials for Chapter 3



Source: Esri, Maxar, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

Figure 1: Blanding's and Painted turtle habitat in the study area in Southern Ontario, Canada.

Table 1: Pairwise comparison between parameter estimates from mixed effect model comparing mean environmental temperature (mean T) and mean temperature coefficient of variation (T C.V.) within selected turtle locations vs. available locations at three different spatial scales, across seasons.

Spatial scale	**Response variable**	**Random vs. selected temperature during**	**Estimate**	**95% CI**		**p-value**
				Lower	**Upper**	
Home range	Mean T	Pre-nesting season	0.253	-0.026	0.536	0.075
		Nesting season	-0.225	-0.493	0.044	0.099
		Post-nesting season	-0.372	-0.677	-0.066	0.018
	T C.V.	Pre-nesting season	0.071	0.048	0.094	<0.001
		Nesting season	0.026	0.004	0.048	0.020
		Post-nesting season	0.035	0.009	0.060	0.008
Within home ranges	Mean T	Pre-nesting season	-4.391	-4.792	-3.991	<0.001
		Nesting season	-3.947	-4.326	-3.569	<0.001
		Post-nesting season	-3.611	-4.057	-3.164	<0.001
	T C.V.	Pre-nesting season	0.081	0.045	0.118	<0.001
		Nesting season	0.043	0.007	0.079	0.020
		Post-nesting season	0.036	-0.002	0.074	0.064
Within aquatic habitats	Mean T	Pre-nesting season	-3.210	-3.642	-2.778	<0.001
		Nesting season	-3.513	-3.921	-3.104	<0.001
		Post-nesting season	-2.645	-3.120	-2.169	<0.001
	T C.V.	Pre-nesting season	-0.006	-0.021	0.008	0.390
		Nesting season	-0.006	-0.020	0.008	0.372
		Post-nesting season	0.017	0.002	0.032	0.031
Within terrestrial habitats	Mean T	Pre-nesting season	-8.941	-9.742	-8.139	<0.001
		Nesting season	-7.531	-8.287	-6.783	<0.001
		Post-nesting season	-8.061	-8.938	-7.185	<0.001
	T C.V.	Pre-nesting season	0.263	0.217	0.310	<0.001
		Nesting season	0.195	0.150	0.240	<0.001
		Post-nesting season	0.177	0.128	0.227	<0.001

Appendix C: Supplementary materials for Chapter 4

Supplementary Methods

We developed maps of development and natural habitat in the study area during 2010-2013 and 2017-2020 using existing maps, satellite images, and ground-truthing. This allowed us to quantify natural habitat loss with classified habitat types being: open water, marsh, swamp, forest, grassland, and settlement (Appendix C, Table 1 for details). Highly sensitive Category 1 habitats (MNR, 2021) include with main ponds within the SMH wetlands and 55.5% of observed turtle locations. We assigned wetlands (open water, marsh, swamp) the lowest resistance values (and increasing resistance with increasing distance to wetlands), while forest and grasslands provided intermediate, and settlement and roads the highest resistance (as derived by Mui et al. 2017) (Appendix C, Table 2).

Source: Esri, Maxar, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

Figure 1: Blanding’s turtle study area in Ottawa, Ontario, Canada, where intensive development was initiated in the early 2000’s and has continued to 2020. The study area includes the South March Highlands Conservation Forest in the North und the Kizell Wetland in the South, which is adjacent to the area being developed since 2017.

Table 1: Definitions of habitat types in the study area that were used in the habitat suitability analysis

Habitat type	Definition
Open water	Wetland with some emergent and submerged macrophytes, shallow to deep
Marsh	Wetland with cattails, willow thickets, dogwood, floating vegetation
Swamp	Bogs, fens, forested swamps with minimal open water area
Forest	Deciduous, coniferous, mixed forest; used as upland travel corridors between wetlands
Grassland/field	Open grassed field, vegetated (abandoned) developed area; possibly used for nesting
Settlement	Any developed area (e.g. residential areas, parking lots, schools); generally unsuitable

Table 2: Resistance values for variables used in the connectivity analysis. Habitat resistance values are mean Blanding's turtle specific values for spring and summer resistance reported by Mui et al. (2017) (0 = least resistance, 100 = highest resistance).

Factor	**Variable**	**Resistance value**
Habitat	Swamp	14
	Marsh	15
	Open water	0
	Grassland	46
	Forest	48
	Settlement	70
Road	0-5 m	90
	>5 m	1
Distance to water	0-10 m	0
	10-50 m	5
	50-100 m	20
	100-500 m	35
	>500 m	50

Supplementary Results

Consistent with the decrease in connectivity pathways, we observed a decline in turtles moving between north and south of the study area. During 2010-2013, 13.0% of the 23 tracked turtles were found in both populations and an additional 2 turtles observed in one area during 2010-2013 were captured in the other site during 2017-2020. In contrast, during 2017-2020 only 6.2% of tracked turtles (n = 32) were detected on both sides of the study area, indicating that loss of connectivity led to a decline in movement between the two main wetlands. During 2010-2013, 39.1% of tagged turtles used wetlands within the development zones either partially or exclusively. In contrast, during 2017-2020, only 14.3% were detected in those areas, none which used the area exclusively.

Table 3: Estimated population parameters for the juvenile Blanding's turtle population near Ottawa, Ontario, Canada, including both the South March Highlands conservation area and Kizell pond sub-populations. Parameters were derived from Jolly-Seber estimation for the whole population and for the northern (SMH) and southern (Kizell) sub-populations separately.

	Entire population			**SMH**			**Kizell**		
	Estimate	**Lower 95% CI**	**Upper 95% CI**	**Estimate**	**Lower 95% CI**	**Upper 95% CI**	**Estimate**	**Lower 95% CI**	**Upper 95% CI**
Capture probability	0.197	0.116	0.313	0.700	0.345	0.911	0.495	0.327	0.664
Super-population size	3.4	2.8	3.6	1.3	0.8	1.1	0.1	0	36.9
Apparent survival	0.777	0.631	0.877	0.123	0.014	0.578	0.832	0.287	0.984
Probability of immigration	0.017	0.006	0.057	0.109	0.080	0.148	0	0	1
Juvenile population size									
2010	24.9	15.4	34.3	16.2	6.1	26.4	2.3	0.8	3.9
2020	2.5	0	5.8	2.4	0	5.6	0.4	0	2.0

Table 4: Sensitivity and elasticity of demographic parameters used for the population viability analysis (PVA) for the female Blanding's turtle population in Ottawa, Ontario, Canada.

Parameter	**Value**	**Sensitivity**	**Elasticity**
Fecundity	3.37	0.009	0.031
Female hatchling survival	0.261	0.118	0.031
Female juvenile survival	0.7826	0.137	0.107
Female adult survival	0.96	0.832	0.801

Table 5: Population viability analysis (PVA) results for each simulated scenario of the Blanding's turtle population in Ottawa, Ontario, Canada, starting with initial population size from 2010 (n=55.6 female adults, n=17.1 female juveniles) and recreating estimated adult female population size in 2020 (n=11.7 females, 95% CI: 5.8-17.6) as estimated by the Jolly-Seber model.

Scenario	**Female adult survival rate**	**growth rate λ**	**Projected adult female population size in**		
			2020	2030	2060
Baseline	0.960	0.9969	45.8	44.1	40.2
1.8% increased in female annual mortality rate	0.942	0.982	38.6	32.0	18.7
3.6% increased in female annual mortality rate	0.924	0.968	32.5	23.1	8.6
Recreation of observed mean female population size in 2020	0.821	0.896	11.7	3.7	0.1
Recreation of lower CL of female population size in 2020	0.751	0.861	5.8	1.2	0.0
Recreation of upper CL female population size in 2020	0.862	0.922	17.6	7.6	0.7
Breaching Q-E threshold by 2030	0.825	0.898	12.2	4.0	0.2
Breaching Q-E threshold by 2060	0.906	0.954	27.2	16.7	4.0

Table 6: Population viability analysis (PVA) results for each simulated scenario of the two Blanding's turtle northern conservation forest (SMH) and in the southern Kizell sub-populations in Ottawa, Ontario, Canada, starting with initial population sizes from 2013 (SMH: n = 21.9 female adults, n = 5.3 female juveniles; Kizell: n = 7.1 female adults, n = 1.0 female juveniles) as estimated by the Jolly-Seber model, and assuming 70% females in the juvenile cohort.

Sub-population	**Scenario**	**Female adult survival rate**	**Projected adult female population size in**		
			2020	2030	2060
SMH	Baseline	0.960	18.4	17.5	15.9
	1 female road mortality / year in SMH	0.960	12.1	3.0	0.0
	2 female road mortality / year in SMH	0.960	5.7	0.0	0.0
	Recreation of observed SMH adult female population size in 2020	0.835	7.5	2.5	0.1
Kizell	Baseline	0.960	5.9	5.6	5.1
	1 female road mortality / year in Kizell	0.960	0.0	0.0	0.0
	Recreation of observed Kizell adult female population size in 2020	0.935	5.0	3.8	1.9

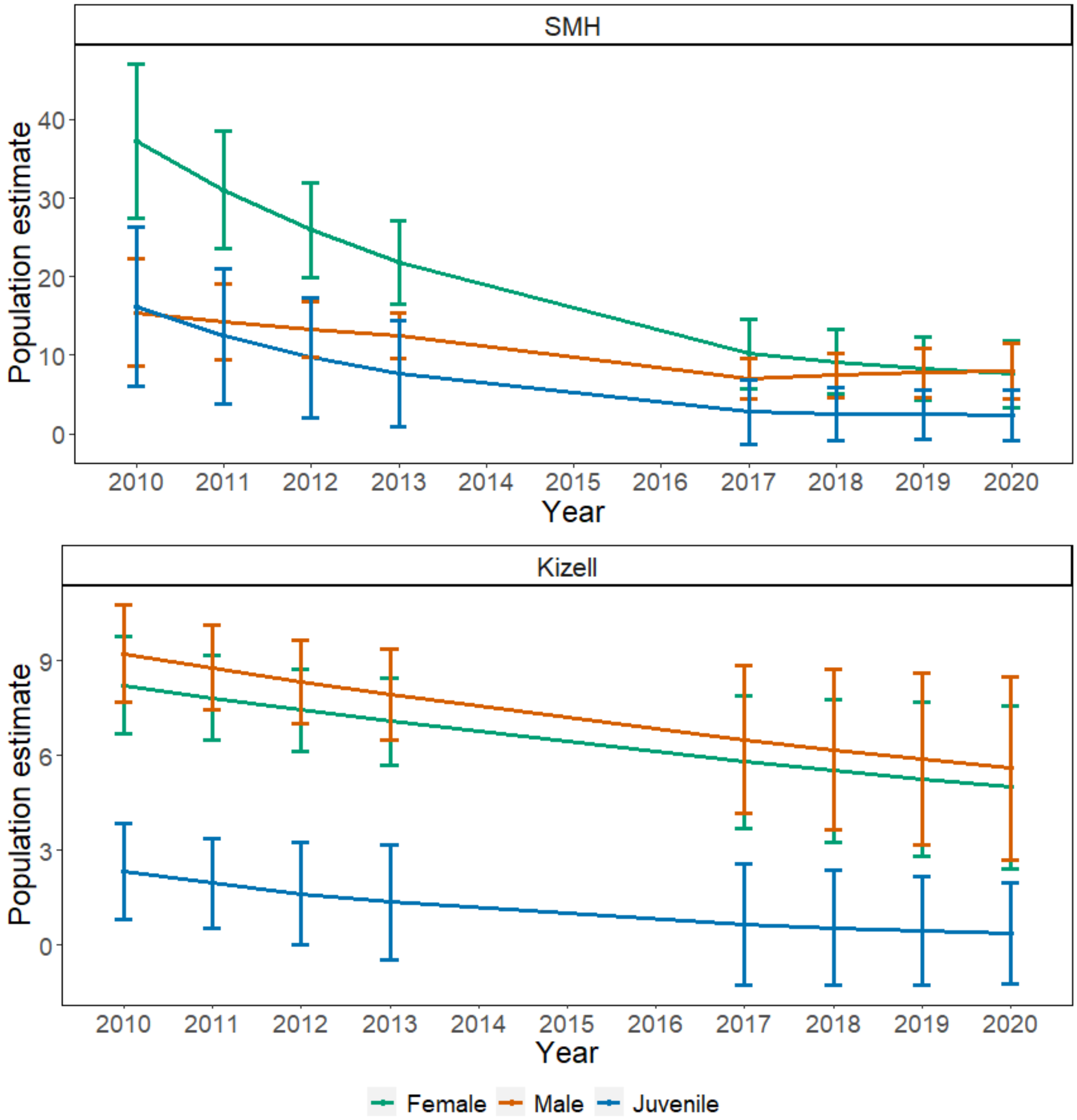


Figure 2: Estimated population size (with 95% confidence interval) of adult female and male and juvenile Blanding’s turtles in each sub-population (South March Highlands conservation forest (“SMH”) and Kizell Cell Wetland (“Kizell”) in the South March Highlands, Ottawa, between 2010 and 2020. Estimates were calculated from a Jolly-Seber population model (POPAN formulation).

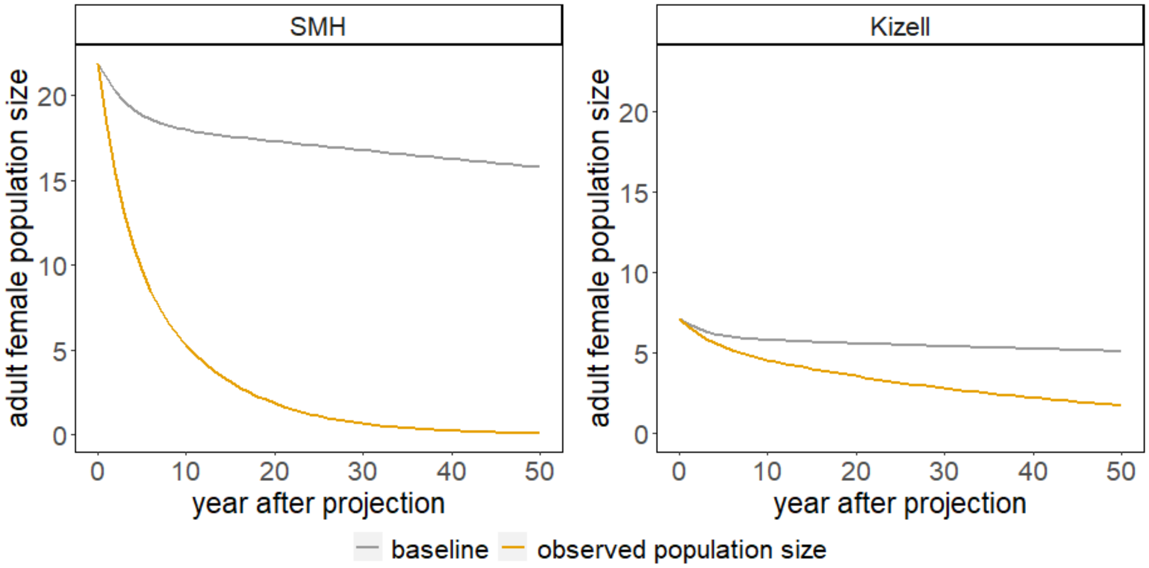


Figure 3: Population viability analysis (PVA) of the South March Highlands Blanding's turtle population treated as two distinct sub-populations, starting with estimated population sizes in SMH conservation forest and Kizell cell wetland in 2013. Shown are population projections over 50 years since 2013 for the two sub-populations, modelled with baseline conditions, and with the female adult annual survival rates necessary to recreate observed changes in the sub-populations (female survival rate in SMH: 0.84, Kizell: 0.94).