

Drone surveys reveal seasonal sex differences in painted turtle basking behaviour and advance
freshwater turtle monitoring

Lauren Dobie

A thesis submitted to the University of Ottawa in partial fulfillment of the requirements for the
Master of Science degree in Biology

Ottawa-Carleton Institute of Biology

Department of Biology

Faculty of Science

University of Ottawa

Abstract

Basking is an essential thermoregulatory behaviour in freshwater turtles, but accurately quantifying basking behaviour is challenging. Traditional survey methods can lack temporal precision, be disruptive, and have low detection probability. To address these limitations, I developed a high-frequency drone-based monitoring method that records repeated, minimally invasive video surveys of individually marked painted turtles (*Chrysemys picta*). I then applied this method to test whether basking probability varies seasonally between sexes. I predicted that females would bask more than males early and late in the active season, when reproductive energetic demands are highest, with smaller differences between sexes during mid-summer. I conducted autonomous drone surveys every 20 minutes on 13 days from June to September 2025 at a wetland on the Kenauk property in Montebello, Québec, Canada, generating 423 surveys and 127 hours of video footage. Flight initiation distance trials confirmed that surveys at a 15 m altitude did not disturb turtles. Basking probability declined over the season and was influenced by environmental conditions, peaking at intermediate temperatures and around midday, and decreasing with wind speed and cloud cover. Females basked more than males early in the season, but this difference diminished by mid-summer and did not re-emerge later. This study demonstrates that drone-based surveys enable minimally invasive behavioural monitoring at high temporal frequencies and reveal fine-scale temporal, environmental, and sex-specific patterns in freshwater turtle basking behaviour.

Résumé

Le lézardage est un comportement de thermorégulation essentiel chez les tortues d'eau douce, mais il est difficile à quantifier avec précision. Les méthodes de surveillance traditionnelles peuvent manquer de précision temporelle, être perturbatrices et présenter une faible probabilité de détection. Pour surmonter ces limites, j'ai développé une méthode de surveillance à haute fréquence par drone, permettant d'enregistrer des relevés vidéo répétés et peu invasifs de tortues peintes (*Chrysemys picta*) marquées individuellement. J'ai ensuite utilisé cette méthode pour tester si la probabilité de lézardage varie selon la saison et le sexe. J'ai prédit que les femelles lézarderaient davantage que les mâles au début et à la fin de la saison d'activité, lorsque les exigences énergétiques liées à la reproduction sont les plus élevées, avec des différences plus faibles entre les sexes au milieu de l'été. J'ai réalisé des relevés autonomes par drone toutes les 20 minutes pendant 13 jours, étalés de juin à septembre 2025, dans un milieu humide sur la propriété de Kenauk à Montebello, Québec, Canada, générant 423 relevés et 127 heures d'enregistrement vidéo. Des essais de distance de fuite ont confirmé que les relevés effectués à une altitude de 15 m ne perturbaient pas les tortues. La probabilité de lézardage a diminué au cours de la saison et a été influencée par les conditions environnementales, atteignant un maximum à des températures intermédiaires et autour de la mi-journée, et diminuant avec la vitesse du vent et la couverture nuageuse. Les femelles lézardaient davantage que les mâles au début de la saison, mais cette différence s'est atténuée au milieu de l'été et n'est pas réapparue par la suite. Cette étude montre que les relevés par drone permettent un suivi comportemental peu invasif à haute fréquence et révèlent des variations du lézardage chez les tortues d'eau douce selon le temps, l'environnement et le sexe.

Acknowledgements

I am grateful to the many people and organizations who supported me throughout my master's degree. I thank my supervisor, Dr. Gabriel Blouin-Demers, for his guidance and support throughout this project. He leads by example through fostering a healthy work-life balance, and his mentorship has shaped the type of researcher I aspire to be. I also thank my advisory committee members, Dr. Jessica Forrest and Dr. Christina Davy, for their thoughtful feedback and encouragement. I thank the volunteers from the University of Ottawa who contributed to fieldwork: Megan Byrns, Jessica Fitzgerald, and Léa Nethercott, and those who helped with video review: Lara Elmugammer, Nour Mohammad Hussein, and Eva Looper.

This research would not have been possible without the support of the Kenauk Institute and its executive director, Liane Nowell, whose mentorship over the past three years has encouraged my growth as a leader and ecologist. I thank the employees and interns at the Kenauk Institute who worked long days in the field alongside me and maintained a strong work ethic throughout: Cassandra Ciafro, Clara Coleman-Hagey, Alissa Couture, Aimee Fraser, Olivia Friesen, Grace Irwin, Roxanne Lefson, Hannah Levesque, Miriam Mills, Anne Minaki, Jessica Turgeon, and Samantha West. I thank the Dr. Marie Larocque lab at l'Université du Québec à Montréal for sharing weather station data, and Dr. Kyle Elliott at McGill University for providing supplies and introducing me to Gabriel, the Kenauk Institute, and drones. This research was funded by the Kenauk Institute, Mitacs, the Fonds de Recherche du Québec, and the Queen Elizabeth Graduate Scholarship in Science and Technology.

I also thank my amazing parents, brother, and friends for their unwavering love and support. Thank you for always celebrating my successes and for reminding me of who I am beyond this degree. Lastly, thank you to the painted turtles that made this work possible.

Table of Contents

Abstract	ii
Résumé	iii
Acknowledgements	iv
List of Tables	viii
List of Figures	x
General Introduction	xv
Chapter 1	1
Context.....	1
Abstract.....	2
Introduction.....	3
Methods	7
Study Site and Study Species.....	7
Capture and Marking	8
Drone Surveys.....	9
Data Organization.....	10
Statistical Analyses	10
Results	12
Dataset Summary	12
Predictors of Basking Presence	13

Discussion.....	13
Seasonal and Sex-Specific Patterns in Basking Behaviour	13
Environmental Drivers of Basking Probability.....	15
Individual and Morphological Drivers of Basking Probability.....	17
Drones as a Tool to Monitor Freshwater Turtles.....	18
Conclusion	19
Tables – Chapter 1.....	21
Figures – Chapter 1	22
Supplementary Information – Chapter 1	25
Supplementary Information 1: Additional Photos from the Field.....	25
Supplementary Information 2: Additional Dataset Information	29
Supplementary Information 3: Additional Model and Statistical Information	34
Supplementary Information 4: R Script.....	37
Chapter 2	70
Context.....	70
Abstract.....	71
Background.....	72
Method Details.....	73
Project Overview.....	73
Drone System and Operation Details	73

Platform Specifications	73
Takeoff and Retrieval.....	74
Flight Planning and Method of Operation	74
Payload and Data Collection.....	75
Camera Description and Data Collection Methods	75
Field Operation Details.....	76
Data Analysis	77
Permits, Regulations, Training, and Logistics	77
Method Validation.....	78
Drone Disturbance and Flight Initiation Distance.....	78
Limitations.....	79
Tables – Chapter 2.....	81
Figures – Chapter 2	82
Supplementary Information – Chapter 2	90
General Conclusion.....	91
References	93

List of Tables

Table 1-1. Parameter estimates from the final selected generalized linear mixed model predicting basking probability in painted turtles. All continuous predictors (air temperature, wind speed, cloud cover, carapace length, date, and time) were centred and scaled. Turtle identity was included as a random effect. The model used a binomial error distribution with a logit link, and estimates are on the log-odds scale. Significant effects are indicated with asterisks (***) ($p < 0.001$). Painted turtle basking patterns were surveyed via drone from June to September 2025 on the Kenauk property in Montebello, Québec, Canada.....21

Table S1-1. Summary statistics for environmental variables measured during drone-based painted turtle basking surveys and carapace length measured during turtle capture from May to September 2025 on the Kenauk property in Montebello, Québec, Canada.33

Table S1-2. Candidate generalized linear mixed models evaluated for painted turtle basking probability, showing fixed-effects structures, model degrees of freedom (df), Akaike’s Information Criterion (AIC), and Δ AIC values. All models include turtle identity as a random effect. Candidate models include combinations of environmental, biological, and temporal variables, as well as quadratic terms indicated by ² and interaction terms indicated by *. Δ AIC values are calculated relative to the model with the lowest AIC (Δ AIC = 0). Models with Δ AIC < 2 are highlighted in bold and represent the top-ranked candidate models. Painted turtle basking patterns were surveyed via drone from June to September 2025 on the Kenauk property in Montebello, Québec, Canada.....34

Table S1-3. Variance Inflation Factors (VIF) for fixed effects in the top-ranked generalized linear mixed models with $\Delta AIC < 2$. VIF values were used to assess multicollinearity among predictors during final model selection. VIF values > 5 are highlighted in bold and indicate potentially problematic collinearity. Painted turtle basking patterns were surveyed via drone from June to September 2025 on the Kenauk property in Montebello, Québec, Canada.36

Table 2-1. Dates of all drone sampling days from a study of painted turtle basking behaviour at Kenauk, Montebello, Québec, Canada. The table includes all sampling days from early June to late September 2025 and the number of completed surveys for each sampling day.81

List of Figures

Figure 1-1. Screenshots from drone video surveys of basking painted turtles. Panel (A) shows a video frame captured with a DJI Mini 4 Pro at a 15 m altitude with no zoom. Two unmarked individuals are circled in red, and one marked individual (P6) is circled in yellow. Panels (B) and (C) show post-survey digital zooms of the unmarked turtles and the marked individual (P6), respectively. Panel (D) shows the same marked individual (P6) directly after being painted while the code was drying. Painted turtle basking patterns were surveyed via drone from June to September 2025 on the Kenauk property in Montebello, Québec, Canada.22

Figure 1-2. Model-predicted basking probability in painted turtles as a function of date for male and female painted turtles. Lines represent predictions from the final generalized linear mixed model for males (blue) and females (orange), and shading around the predicted values represents 95% confidence intervals. Points show independent observed basking events for individual turtles (1 = present, 0 = absent), which represent the raw data that informed the model. Painted turtle basking patterns were surveyed via drone from June to September 2025 on the Kenauk property in Montebello, Québec, Canada (n = 55 individuals, 22,294 presence-absence observations).23

Figure 1-3. Model-predicted basking probability in painted turtles in relation to (A) time of day, (B) air temperature, (C) percent cloud cover, and (D) wind speed. Lines represent predictions from the final generalized linear mixed model, and shading around the predicted values represents 95% confidence intervals. Points show independent observed basking events for individual turtles (1 = present, 0 = absent), which represent the raw data that informed the model. Painted turtle basking patterns were surveyed via drone from June to September 2025 on the Kenauk property in Montebello, Québec, Canada (n = 55 individuals, 22,294 presence-absence observations).....24

Figure S1-1. Hoop net setup used to capture painted turtles. The nets were set parallel to the shore in tandem. The hoop nets are outlined by red rectangles, with the cod (closed) ends facing away from one another, and the mouth (open) ends facing each other. The mouth ends of the nets were joined by a lead (yellow solid lines), and each net had two wings set at approximately 45 degrees from the opening (purple dotted lines). Buoys placed in the nets created air spaces for the turtles and are visible in white (left) and orange (right) in panels (A) and (B). Panel (A) shows a practice net setup in a man-made pond used for demonstrations and field assistant training, photographed from shore. Panel (B) shows a drone image of a net setup at the study site. The hoops are collapsed in panel (B) because the image was taken during a drone survey; red rectangles show where the nets extended to when deployed. Painted turtle basking patterns were surveyed via drone from June to September 2025 on the Kenauk property in Montebello, Québec, Canada.26

Figure S1-2. Examples of secondary sexual characteristics in painted turtles. Panel (A) shows a male’s tail, which is thicker with the cloacal opening located farther down the tail. Panel (B) shows a female’s tail, which is thinner with the cloacal opening located closer to the plastron. Panel (C) shows a male’s tail (left) and a female’s tail (right). Panel (D) shows a female’s foreclaws, which are shorter. Panel (E) shows a male’s foreclaws, which are longer. Painted turtle basking patterns were surveyed via drone from June to September 2025 on the Kenauk property in Montebello, Québec, Canada.....27

Figure S1-3. Pictures of a marked painted turtle taken with a DJI Mini 4 Pro drone with no zoom from a 5 m altitude (A), a 10 m altitude (B), a 15 m altitude (C), and a 20 m altitude (D). Panel (E) is an image of the basking turtle zoomed in, showing its painted code (F7). Painted turtle basking patterns were surveyed via drone from June to September 2025 on the Kenauk property in Montebello, Québec, Canada.....28

Figure S1-4. Exploratory relationships between observed turtle basking presence and (A) turtle carapace length, (B) date, (C) time of day, (D) wind speed, (E) net radiation, (F) percent cloud cover, and (G) air temperature. Points show independent observed basking events for individual turtles (1 = present, 0 = absent), which represent the raw data. Lines represent smoothed trends fitted using generalized additive models for visualization in blue for males and orange for females. Shaded areas represent 95% confidence intervals. Painted turtle basking patterns were surveyed via drone from June to September 2025 on the Kenauk property in Montebello, Québec, Canada (n = 55 individuals, 22,294 presence-absence observations).30

Figure S1-5. Frequency distribution histogram of the number of times individual turtles were observed as present (basking) during drone surveys. Each bar represents the number of times an individual turtle was observed as present during drone surveys across the season, with males in blue and females in orange. Painted turtle basking patterns were surveyed via drone from June to September 2025 on the Kenauk property in Montebello, Québec, Canada.31

Figure S1-6. Scatterplot showing the relationship between the date individual turtles were first marked (added to the study) and the total number of times they were subsequently observed as present (basking) across the study period. Each point represents an individual turtle. Painted turtle basking patterns were surveyed via drone from June to September 2025 on the Kenauk property in Montebello, Québec, Canada.....32

Figure 2-1. Kenauk property in Montebello, Québec, Canada, where the basking behaviour of painted turtles was studied in 2025.82

Figure 2-2. A painted turtle marked with a unique alphanumeric code (F8) painted on its carapace for individual identification via drone footage in a study of basking behaviour at Kenauk, Montebello, Québec, Canada, in 2025.83

Figure 2-3. DJI Mini 4 Pro drone used to study painted turtle basking behaviour at Kenauk, Montebello, Québec, Canada, in 2025.84

Figure 2-4. Charging station used in a study of painted turtle basking behaviour at Kenauk, Montebello, Québec, Canada, in 2025. The charging station consists of a Bluetti Portable Power Station powering three individual DJI Two-Way Charging Hubs with 30 W USB-C chargers, each charging three DJI Intelligent Flight Battery Plus units, for a total of nine batteries.85

Figure 2-5. Home base setup with a workspace and charging station used in a study of painted turtle basking behaviour at Kenauk, Montebello, Québec, Canada, in 2025. The open area where the drone took off and landed, as well as the wetland, are behind the camera.86

Figure 2-6. Autonomous drone route used in a study of painted turtle basking behaviour at Kenauk, Montebello, Québec, Canada, in 2025. The drone took off from the home base, started the route at point A, took a video along the drone route, stopped the route at point Z, and landed back at the home base.....87

Figure 2-7. A Screenshot of the drone footage from a study of painted turtle basking behaviour at Kenauk, Montebello, Québec, Canada, in 2025. The screenshot shows three basking turtles: X5 and O6 circled in red, and an unmarked turtle circled in yellow. Image A is an unzoomed screenshot from the drone footage. Image B is the screenshot zoomed in, showing how the turtles can be identified in drone footage review.....88

Figure 2-8. Diagram of the method used to determine flight initiation distance with a drone in a study of painted turtle basking behaviour at Kenauk, Montebello, Québec, Canada, in 2025. I hovered the drone over a turtle at an altitude of 20 m for one minute, then descended to an altitude of 15 m and hovered for one minute, followed by 10 m for one minute and 5 m for one minute. I noted at which altitude the turtle fled, if ever, and used these data to inform the altitude at which I would fly the drone to survey turtles without altering their behaviour.89

Figure S2-1. Graphical abstract for a drone-based protocol for monitoring freshwater turtles, describing the methodological steps in a study of painted turtle basking behaviour at Kenauk, Montebello, Québec, Canada, in 2025.90

General Introduction

Thermoregulation is fundamental to animal survival because body temperature influences the rate of physiological processes and, consequently, behaviour and performance (Abram et al., 2017; Angilletta et al., 2002; Huey, 1982). Ectotherms rely primarily on external heat sources and use behavioural strategies to regulate body temperature (Abram et al., 2017; Cowles & Bogert, 1944; Huey & Slatkin, 1976). Maintaining favourable body temperatures is not without cost, however. Time and energy invested in thermoregulation can limit opportunities for other activities, such as foraging, reproduction, and predator avoidance, resulting in a trade-off between the physiological benefits of thermoregulation and the associated costs (Grant, 1990; Huey & Slatkin, 1976; Sears et al., 2016).

One of the most widespread thermoregulatory behaviours is basking, which involves exposing the body to solar radiation to elevate body temperature (Bulté & Blouin-Demers, 2010; Chessman, 2024; Harnnuengnit et al., 2024). Although commonly associated with reptiles, basking occurs across diverse taxa, including insects (Kingsolver, 1983), fish (Nordahl et al., 2020), birds (Harnnuengnit et al., 2024), and mammals (Signer et al., 2011). In freshwater turtles, basking is an important thermoregulatory behaviour, especially in those of the Emydidae family (Boyer, 1965; Peterman & Ryan, 2009). Emydids typically bask on emergent deadwood, rocks, and banks (Boyer, 1965; Peterman & Ryan, 2009). Basking in freshwater turtles can occur aquatically, by floating near the surface of the water, or atmospherically, by resting on a surface outside the water (Chessman, 2024). While the primary function of basking in freshwater turtles is thermoregulation, other purposes may exist, including ectoparasite removal (Cagle, 1950; Ibáñez et al., 2015; McAuliffe, 1977), reduction of algal and fungal growth (Boyer, 1965; Neil &

Allen, 1954), vitamin D synthesis (Acierno et al., 2006), and infection reduction (Monagas & Gatten, 1983; Wirth & Ariel, 2020).

Basking behaviour in freshwater turtles can vary across the active season and between sexes. Females of several species, including painted turtles (*Chrysemys picta*), have been observed to bask more frequently or for longer durations than males, specifically during periods associated with egg production (Bulté & Blouin-Demers, 2010; Carrière et al., 2008; Ernst, 1982; Hammond et al., 1988; Krawchuk & Brooks, 1998; Obbard & Brooks, 1979). Reproduction represents a substantial energetic cost in female turtles (Congdon et al., 1982), and because many physiological processes related to reproduction are temperature-dependent, increased basking may facilitate energy acquisition and allocation during energetically demanding periods.

Despite its ecological importance, basking behaviour in freshwater turtles remains difficult to quantify accurately. Traditional observation methods, such as shore-based surveys, canoe surveys, and wildlife cameras, can be limited by restricted fields of view, obstruction by habitat features, and the potential to disturb the turtles (Biserkov & Lukanov, 2017; Bogolin et al., 2021; Fenech, 2022). Traditional methods typically rely on relatively infrequent observations, making it difficult to capture short basking bouts. As a result, existing data may underestimate basking frequency, limiting our understanding of freshwater turtle basking behaviour.

Drones, or uncrewed aerial vehicles (UAVs), offer a promising solution to these limitations. Drones enable researchers to survey large and inaccessible areas from an aerial perspective, while minimizing disturbance to wildlife (Chabot & Bird, 2016; Floreano & Wood, 2015; Linchant et al., 2015). In many cases, drone-based observations have improved detection accuracy and expanded the spatial and temporal scale of data collection (Beaver et al., 2020; J.

C. Hodgson et al., 2018; Kelaher et al., 2020; Rees et al., 2018; Schofield et al., 2019). While drones can be powerful tools for ecological research, their use also raises concerns about potential disturbance to wildlife. Animals have been observed acting vigilantly, attempting to escape, and becoming aggressive when interacting with a drone (Weston et al., 2020). It is therefore important to evaluate and minimize disturbance when implementing drone-based surveys by ensuring that surveys do not elicit escape responses. The application of drones in freshwater turtle research remains limited to methodological development, and drones have not yet been employed to identify individual turtles reliably or to study freshwater turtle basking patterns, to my knowledge.

The painted turtle is an ideal system for addressing these gaps. It is one of the most widespread and extensively studied turtle species in North America, with a range spanning from the Atlantic to the Pacific, extending across much of the United States and southern Canada, reaching as far south as northern Mexico (Van Dijk, 2010). Its relatively high abundance, high basking frequency, and ease of capture and identification make it an ideal model species for studying freshwater turtle ecology and basking behaviour (Lovich & Ennen, 2013). Despite its widespread distribution, the painted turtle is federally designated as a species of special concern due to significant regional declines caused by habitat loss, road mortality, invasive species, and subsidized predators (COSEWIC, 2019).

Here, I use drone-based surveys to quantify basking behaviour in painted turtles and to evaluate how this behaviour varies in relation to environmental conditions, season, and sex. Chapter 1 tests the hypothesis that one of the functions of basking in painted turtles is energy acquisition and allocation by investigating seasonal and sex-specific patterns in basking probability. Chapter 2 develops and validates a standardized drone-based protocol for monitoring

freshwater turtles, including an assessment of potential disturbance from the drone. These chapters demonstrate how drones can be used to overcome methodological limitations and provide new insights into freshwater turtle basking behaviour.

Chapter 1

Drones reveal that female painted turtles bask more than males early in the active season

Context

A slightly modified version of this chapter will be submitted for publication.

Abstract

Basking is an essential thermoregulatory behaviour in freshwater turtles that may also support energy acquisition during periods of high reproductive demand. Accurately quantifying basking behaviour, however, is challenging due to the limitations of traditional survey methods. This study aimed to test whether basking probability in painted turtles (*Chrysemys picta*) varies seasonally between sexes. I predicted that females would bask more than males early and late in the active season, when reproductive energetic demands are highest, and that sex differences would be smaller during mid-summer. I tested this using high-frequency drone surveys of individually marked turtles in a wetland on the Kenauk property in Montebello, Québec, Canada. I conducted autonomous surveys every 20 minutes on 13 days from June to September 2025. Basking probability declined over the season and was influenced by environmental conditions, peaking at intermediate air temperatures and around midday, and decreasing with increasing wind speed and cloud cover. Females basked more than males early in the season, but this difference diminished by mid-summer and did not re-emerge later in the season. These results partially support the hypothesis that basking reflects reproductive energetic demands. This improved understanding of basking behaviour can inform the design and timing of future freshwater turtle monitoring efforts.

Introduction

Thermoregulation is essential to the survival of animals. The rate of metabolic reactions is influenced by body temperature, which in turn dictates animal performance and behaviour (Abram et al., 2017; Angilletta et al., 2002; Huey, 1982). Body temperature can affect an individual's locomotion velocity (Bennett, 1990; Claussen et al., 2002), cardiovascular function (Grigg & Seebacher, 1999; Hochscheid et al., 2002), and growth rate (Angilletta & Dunham, 2003). While endotherms maintain body temperatures largely through physiological means, ectotherms rely on external heat sources and commonly practice behavioural thermoregulation (Abram et al., 2017; Cowles & Bogert, 1944; Huey & Slatkin, 1976). Thermoregulation in ectotherms comes at a cost, however, as maintaining favourable body temperatures often requires substantial time investment and movement through the environment, potentially reducing time available for other essential activities, like mate searching, feeding, or predator avoidance (Grant, 1990; Huey & Slatkin, 1976). As a result, thermoregulation in ectotherms reflects a balance between physiological benefits and costs (Huey & Slatkin, 1976; Sears et al., 2016).

Ectotherms rely on external heat sources to thermoregulate and use behavioural strategies to do so (Abram et al., 2017; Cowles & Bogert, 1944; Huey & Slatkin, 1976). A common example of behavioural thermoregulation is basking, which involves exposing the body to solar radiation while staying immobile to maintain an optimal body temperature, and is used by both endotherms and ectotherms (Bulté & Blouin-Demers, 2010; Chessman, 2024; Harnnuengnit et al., 2024). Basking is the main thermoregulatory behaviour in freshwater turtles, especially those of the Emydidae family (Boyer, 1965; Peterman & Ryan, 2009). While basking is primarily used as a thermoregulatory behaviour in freshwater turtles, other functions may exist, such as ectoparasite removal (Cagle, 1950; Ibáñez et al., 2015; McAuliffe, 1977), reduction of algal and

fungal growth (Boyer, 1965; Neil & Allen, 1954), vitamin D synthesis (Acierno et al., 2006), and infection reduction (Monagas & Gatten, 1983; Wirth & Ariel, 2020). The energetic benefits of basking have been quantified in freshwater turtles, showing that basking can increase metabolic rate by 17-30% by elevating body temperature toward optimal thermal conditions for energy acquisition (Bulté & Blouin-Demers, 2010). Because basking is a voluntary behaviour that requires significant time investment, it provides insight into how turtles balance the benefits of thermoregulation with its costs.

Basking behaviour in freshwater turtles can vary temporally and by sex. For example, females can have longer basking bouts than males from May to June, early in the active season, in spotted turtles (*Clemmys guttata*) (Ernst, 1982), pond sliders (*Trachemys scripta*) (Hammond et al., 1988), common snapping turtles (*Chelydra serpentina*) (Obbard & Brooks, 1979) and painted turtles (*Chrysemys picta*) (Krawchuk & Brooks, 1998). Female painted turtles may also bask more than males later in the active season in August (Carrière et al., 2008). No significant sex differences in painted turtle basking behaviour, however, have been detected during mid-summer in July (Lefevre & Brooks, 1995). These temporal patterns suggest that sex differences in basking behaviour may be driven by seasonal variation in energetic demands. In one population of painted turtles, it has been estimated that a female's reproductive effort uses 48% of its total yearly energy, with 14% of its annual energy devoted to egg development (Congdon et al., 1982). Of the energy used for egg development, half is expended late in the active season from August to October, while the other half is used in the spring after emerging from brumation (Congdon et al., 1982).

The rate at which female turtles can acquire, mobilize, and allocate energy to follicular development is strongly temperature-dependent (Ganzhorn & Licht, 1983; Mendonça, 1987;

Rollinson & Brooks, 2007; Sarkar et al., 1996). Therefore, periods of increased basking in female painted turtles may allow individuals to maintain body temperature within an optimal range during periods of high energetic and reproductive demand. Given that, I hypothesize that one of the functions of basking in painted turtles is energy acquisition and allocation. I thus predict that individuals will invest more time in basking during periods of high energetic and reproductive demand. I expect that females will bask more than males early and late in the active season, when energy allocation to egg development in females is highest, whereas sex differences in basking will be smaller during mid-summer, when sex differences in reproductive energetic demands are lower.

Basking behaviour in freshwater turtles is typically observed from a distance using binoculars or a spotting scope, either from the shore (Krawchuk & Brooks, 1998; Lefevre & Brooks, 1995; Lindeman, 1999; Rouleau, 2020), an elevated blind (Schwarzkopf & Brooks, 1985), or a canoe (Fenech, 2022; Hill & Vodopich, 2013; Peterman & Ryan, 2009; Rouleau, 2020; Schwarzkopf & Brooks, 1985). While these are the most common methods, accessing basking areas can be challenging, and turtles are often missed when basking sites are obstructed by habitat features like emergent vegetation (Biserkov & Lukanov, 2017; Bogolin et al., 2021). Furthermore, approaching the turtles too closely could disturb them and make it challenging to estimate basking times precisely (Fenech, 2022). Basking observations using these traditional survey methods could lack accuracy due to the surveillance process taking longer and therefore occurring relatively infrequently (e.g., every hour; Krawchuk & Brooks, 1998; Lefevre & Brooks, 1995), despite the majority of painted turtle basking bouts lasting less than one hour (Lefevre & Brooks, 1995; Schwarzkopf & Brooks, 1985).

Basking behaviour has also been studied using data loggers by inferring periods of basking from differences between body and water temperature, as well as immersion and activity patterns (Auge et al., 2024; Bulté & Blouin-Demers, 2010; Dall'Antonia et al., 2001). These data loggers are surgically implanted or attached to the carapace, potentially adding logistical and ethical constraints. Wildlife cameras can also be used to observe basking behaviour, taking photos at short intervals of time (Jain-Schlaepfer et al., 2017; McKnight et al., 2021). Wildlife cameras require prior identification of basking sites, however, and have a restricted field of view that may miss turtles basking outside the camera's range. These limitations of traditional methods highlight the need for a survey tool that can be used to monitor basking behaviour over large areas at a fine temporal resolution.

Uncrewed aerial vehicles (UAVs), or drones, have recently become increasingly integrated into ecological research as tools that allow wildlife to be studied with minimal disturbance while reducing logistical constraints associated with traditional survey methods (Chabot & Bird, 2016; Floreano & Wood, 2015; Linchant et al., 2015). Drones have gained popularity in surveying wildlife that is difficult to detect or monitor using traditional methods, including species that are cryptic, highly mobile, occur in inaccessible habitats, or are sensitive to human disturbance (e.g., aerial species (Bird et al., 2024; Dobie et al., 2025), arboreal species (Wagner et al., 2025; Witt et al., 2020), and aquatic species (A. J. Hodgson et al., 2023; Sawan et al., 2023)). Despite this growing body of work, the application of drones in freshwater turtle studies remains limited, as most existing literature focuses on developing and testing preliminary drone-based surveillance methods (Biserkov & Lukanov, 2017; Bogolin et al., 2021; Daniels, 2018; Escobar et al., 2021; Fagundes et al., 2022). While one study found that traditional spotting scopes and drones are similarly effective at detecting turtle presence (Daniels, 2018),

another showed that drones may outperform traditional methods when turtles are in areas that are not visible from the shoreline (Bogolin et al., 2021). To the best of my knowledge, drones have not yet been employed to identify individual turtles reliably or to study freshwater turtle basking behaviour.

Methods

Study Site and Study Species

The painted turtle is widespread in North America, and it basks frequently. Its relatively high abundance, ease of capture and identification, and status as the most extensively studied emydid in North America make it an ideal model species for studying freshwater turtle ecology and basking behaviour (Lovich & Ennen, 2013). Despite its widespread distribution, the painted turtle is federally designated as a species of special concern due to significant regional declines caused by habitat loss, road mortality, invasive species, and subsidized predators (COSEWIC, 2019).

I conducted fieldwork on the Kenauk property in Montebello, Québec, Canada, a 26,000 ha private nature reserve that contains a high density of wetlands. I selected a ~4.4 ha wetland with a high abundance of painted turtles, as identified during a 2024 preliminary mark-recapture study and confirmed during surveys in spring 2025. The wetland contained numerous floating logs and mats of vegetation that painted turtles used as basking structures. Common snapping turtles were the only other turtle species observed in the wetland and were regularly captured, but only painted turtles were marked and included in the analyses.

Capture and Marking

I installed eight hoop nets in four sections of the wetland to capture and mark painted turtles. The nets were set in tandem parallel to the shore, with a lead connecting the two mouth ends of the nets, and wings set at a 45-degree angle from the opening (Larocque, Colotelo, et al., 2012) (Supplementary Information 1 – Figure S1-1). I checked the nets daily and placed floats in the cod ends of the nets to create air spaces and prevent anoxia in the turtles (Larocque, Cooke, et al., 2012; Ministère des Forêts, de la Faune et des Parcs, 2021). I installed the nets at the end of April and continued capturing turtles until mid-August, marking new turtles and touching up the markings on recaptured individuals (see below). I closed the hoop nets the day before each drone survey day to prevent captured turtles from impacting basking observations and to avoid entering the wetland on survey days.

When I removed a turtle from the net, I measured its plastron length with callipers and determined its sex based on size and secondary sexual characteristics, including long foreclaws and a cloacal opening located farther down the tail in males (Bayless, 1975; Cagle, 1954; House et al., 2010) (Supplementary Information 1 – Figure S1-2). I classified individuals with a plastron length greater than or equal to 13 cm without male secondary sex characteristics as female, and those with a plastron length greater than or equal to 9 cm with male secondary sex characteristics as male (Cagle, 1954). I classified those with a plastron length greater than or equal to 9 cm and less than 13 cm without male sex characteristics as juvenile females, and those with a plastron length of less than 9 cm as juveniles (Bayless, 1975; House et al., 2010). Only adults were marked and included in the study.

I painted a two-character alphanumeric code on each turtle's carapace (Carrière et al., 2008; Krawchuk & Brooks, 1998; Lefevre & Brooks, 1995; Rouleau, 2020) using fast-drying

non-toxic acrylic paint and Uni-POSCA paint markers to allow individual identification via drone (Figure 1-1). After allowing approximately 10 minutes for the paint to dry, I applied a thin layer of liquid matte acrylic mod podge to seal the paint code and allowed it to dry for another 10 minutes. I also marked turtles with notches in their marginal scutes for long-term identification and to identify turtles that have already been marked, in case the paint marking had worn off (Cagle, 1939; Ministère des Forêts, de la Faune et des Parcs, 2021). After marking the turtles, I released them back into the wetland.

Drone Surveys

The details of the drone surveys are presented in Chapter 2. Briefly, I programmed an autonomous flight route on the DJI Mini 4 Pro drone that took a video of the entire wetland in approximately 18 minutes. I conducted drone surveys on 13 days between 3 June and 26 September 2025. On each sampling day, I performed a drone survey every 20 minutes from 7:20 to 18:40, for a total of 35 surveys per day, with some surveys unsuccessful due to weather or technical issues, or intentionally skipped later in the season when turtles were no longer basking in the evening. I successfully recorded 423 surveys across the 13 sampling days, totalling approximately 7,614 minutes of drone video footage. I recorded hourly weather data from a weather station on Kenauk property located approximately 5 km from the study site, which recorded air temperature, net solar radiation, and wind speed at 2 m off the ground. I recorded cloud cover for every survey by estimating the percentage of the sky that was covered by clouds. After recording the drone footage, I reviewed the videos and recorded basking observations for each survey (Supplementary Information 1 – Figure S1-3). I watched each survey and paused whenever a turtle appeared in the frame. I then zoomed in and identified individual turtles by the painted code on their carapace. I considered a turtle to be basking when

it was stationary and at least part of its body was out of the water (Bulté & Blouin-Demers, 2010; Chessman, 2024). I only recorded basking observations from marked turtles.

Data Organization

Each basking observation represented a single individual for a single survey, with a binary variable indicating presence (1) or absence (0). Surveys that occurred before an individual was marked in the season were excluded for that turtle, so absences only reflected individuals that were part of the study at the time of the survey. Environmental data from the weather station were recorded every hour, while drone surveys were conducted every 20 minutes. To combine these datasets, I applied the environmental data from each hour to all the surveys that occurred during that hour. I removed all turtle observations where the individual was marked but could not be reliably identified in the footage. I prepared the data for modelling by converting survey times to decimal hours and survey dates to day-of-year. I centred and scaled continuous predictors to improve model convergence and to facilitate the comparison of effect sizes.

Statistical Analyses

I modelled turtle basking (binary response: present/absent) using generalized linear mixed models (GLMMs) with a binomial error distribution and logit link function, using the lme4 package (Bates et al., 2015) in R version 4.3.1 (R Core Team, 2023). To account for repeated observations of individuals, I included turtle identity as a random effect in all models. I considered quadratic terms for predictors that exhibited nonlinear relationships with basking probability in exploratory data visualizations (Supplementary Information 2 – Figure S1-4). I included sex and date, and an interaction between the two, in all models to test for sex-specific seasonal patterns in basking behaviour, which are directly related to my hypothesis.

In addition to sex and date, I also considered including several other environmental and biological predictors in the models to account for factors known to influence turtle basking behaviour. I considered air temperature during model building because basking is a thermoregulatory behaviour in freshwater turtles (Boyer, 1965), and painted turtles adjust basking behaviour in response to air temperature (Lefevre & Brooks, 1995; Schwarzkopf & Brooks, 1985). I also evaluated wind speed, cloud cover, and radiation as candidate predictors because they can impact operative environmental temperatures and warming efficiency, thereby altering basking behaviour (Boyer, 1965; Chessman, 2024; Crawford et al., 1983; Lefevre & Brooks, 1995). I considered the time of day in the models because painted turtles exhibit diel peaks in basking activity (Lefevre & Brooks, 1995; Schwarzkopf & Brooks, 1985), which may be influenced by circadian cues and not be fully explained by fluctuations in air temperature (Clavijo-Baquet & Magnone, 2017; Selman & Qualls, 2011). Finally, I considered body size, measured as carapace length, as a candidate predictor because larger animals take longer to heat up (Grigg et al., 1979), which can impact thermoregulatory behaviour and result in larger turtles basking for longer (Bulté & Blouin-Demers, 2010; Carrière et al., 2008; Schwarzkopf & Brooks, 1985).

I performed model selection to identify the most parsimonious model while minimizing multicollinearity and overfitting. I compared candidate models using Akaike's Information Criterion (AIC), and models within 2 AIC units of one another were considered equally supported (Burnham & Anderson, 2002). When multiple models were equally supported by AIC, I excluded the models exhibiting problematic collinearity, assessed using variance inflation factors (VIF), with VIF values greater than 5 considered unacceptable (James et al., 2013) (Supplementary Information 3 – Table S1-3). I retained sex, date, and their interaction in all

models because they are directly related to my hypothesis, whereas all other candidate predictors were included or excluded based on AIC and VIF diagnostics. I evaluated the final model fit through diagnostic DHARMA plots (Hartig, 2026). All candidate models and model selection diagnostics are provided in Supplementary Material 3 Table S1-2, and the full R script used for statistical analyses is provided in Supplementary Information 4.

Results

Dataset Summary

I captured and marked 62 individual painted turtles. Seven of those marked turtles, three of which were females and four of which were males, were never observed during the drone surveys. Those seven individuals were therefore removed from the analyses, resulting in 55 painted turtles included (Supplementary Information 1 – Figure S1-5). Of the 55 turtles for which I had data, 36 were male, and 19 were female. The first nesting painted turtle of the season was observed on 2 June 2026. A total of 22,294 observations were recorded from the drone footage. An observation is defined as an individual turtle identified as present or absent during a particular drone survey. Of the 22,294 observations, 2,050 were present and identified (approximately 10%), and the rest (approximately 90%) were absent. Of the 20,244 observations marked as absent, 222 (approximately 1%) were present turtles whose identity could not be determined unambiguously from the drone footage. Each individual turtle was observed basking between 1 and 114 times across the season, with a mean of 37 and a median of 31 (Supplementary Information 1 – Figure S1-6). During surveys, air temperature ranged from 10.2 to 31.4 °C, cloud cover from 0 to 100%, net radiation from -54 to 664 W/m², and wind speed from 0.07 to 1.02 m/s (Supplementary Information 2 – Table S1-1).

Predictors of Basking Presence

The final selected model explaining basking presence included air temperature, air temperature², wind speed, cloud cover, carapace length, time, time², and a sex x date interaction as fixed effects, with turtle identity included as a random effect. Significant predictors of basking probability were air temperature and air temperature², wind speed, cloud cover, date, time and time², and the sex x date interaction (Table 1-1). Carapace length and sex alone were not significant predictors. The probability of basking declined over the season, and this effect differed by sex, as indicated by a significant sex x date interaction. In particular, the seasonal decline in basking probability was weaker in males than in females (Figure 1-2). Basking probability showed a negative quadratic relationship with air temperature and time of day, peaking at approximately 20.5 °C and 12:33, respectively, and decreasing at higher and lower values (Figure 1-3). Turtles were also less likely to bask on cloudy and windy days (Figure 1-3). Turtle identity accounted for substantial between-individual variation in basking patterns (Table 1-1).

Discussion

Seasonal and Sex-Specific Patterns in Basking Behaviour

I used drone surveys to test whether basking probability in painted turtles varies seasonally and between sexes. I found that females basked more than males early in the active season, but this difference diminished by mid-summer and did not re-emerge later in the season. Basking probability declined over the season for both sexes, and this decline was significantly steeper in females than in males. These findings partially support the hypothesis that one of the functions of basking is energy acquisition and allocation. As predicted, females basked more than

males early in the season in June, consistent with previous findings in painted turtles (Krawchuk & Brooks, 1998). The sex difference diminished by mid-summer, aligning with prior work showing no difference in basking duration between sexes mid-summer in July (Lefevre & Brooks, 1995). Elevated basking in females early in the season likely reflects the temperature sensitivity and energetic demands of egg development shortly following emergence from brumation.

Contrary to my prediction, females did not bask more than males late in the active season in August and September. This contrasts with Carrière et al. (2008), who reported longer female basking bouts in August. One explanation for this difference may be that my late-season sampling occurred on four non-consecutive days in August and September and may not have captured a potential short peak in female basking late in the summer. It would have been beneficial to have more sampling days in late summer to capture this potential short peak. It is also possible that energetic investment into reproduction was mostly complete by late summer, reducing sex-specific thermoregulatory behaviour.

Another explanation as to why there was no significant difference in basking occurrence between males and females later in the season is that both sexes may experience overlapping thermoregulatory requirements during this time. In painted turtles, spermatogenesis occurs primarily during the summer, with peak spermatogenic activity reported in August (Ganzhorn & Licht, 1983). Spermatogenesis in painted turtles is facilitated by elevated body temperatures above 17 °C, and males may bask during the late summer to support this process (Ganzhorn & Licht, 1983). As a result, both sexes may bask a similar amount during this period in the late summer, despite investing in different reproductive processes. We would still expect a peak in basking activity in both sexes towards the end of the active season if reproductive

thermoregulatory demands were driving basking late in the season, but no increase in basking was observed in August or September for either sex. This suggests that reproductive timing alone does not cause a peak in basking behaviour late in the season.

It would have also been beneficial to start the drone surveys earlier in the spring to capture basking behaviour throughout the entire active season, from the spring when turtles emerge from brumation and start basking to the fall when basking slows down before re-entering brumation. Since surveys began in early June after marking individuals, early basking behaviour in the spring immediately following emergence from brumation was not captured, which would have potentially revealed an even larger peak in basking behaviour earlier in the season. Future studies could capture and paint turtles in the fall and begin drone surveys immediately following spring emergence, allowing sampling across the full season.

Environmental Drivers of Basking Probability

Basking probability showed a negative quadratic relationship with air temperature, with the model-predicted peak occurring at 20.5 °C. This model-predicted peak closely aligned with raw observations, where the highest mean basking probability occurred at 21.3 °C, with similarly high values from approximately 19-23 °C. This peak temperature closely matches the optimum activity temperature of 20.5 °C (Ernst, 1972) and the preferred body temperature of 21.3 °C - 25.0 °C reported for painted turtles (Edwards & Blouin-Demers, 2007). A similar pattern is shown in previous work, where the number of basking painted turtles peaked at 21.5 °C and decreased at higher and lower temperatures (Schwarzkopf & Brooks, 1985). Another study supports this temperature range and found that pond sliders basked the longest when they were acclimated to 20 °C, although temperature comparisons were limited by the use of widely spaced temperature treatments (10, 20, 30, and 35 °C; Hammond et al., 1988). Future studies could

investigate the effect of water temperature on basking probability and whether the difference between air temperature and water temperature may be a stronger predictor of basking occurrence, as the turtles exit the water to bask atmospherically. Investigating the difference in air and water temperature may also explain why there was no peak in basking later in the active season, as the water was likely much warmer than it was in the spring, making it more beneficial to invest time in basking in the spring when the air is much warmer than the water.

Basking probability showed a negative quadratic relationship with the time of day, with the model-predicted peak basking time occurring at 12:33. This estimate was consistent with raw observations, where mean basking probability was highest at approximately 11:42, with similarly high values observed between 11:00 and 12:40. This pattern aligns with previous studies of painted turtle basking behaviour. For example, one study found that basking observations in painted turtles peaked between 10:00 and 11:59, with basking decreasing at earlier and later times of the day (Lefevre & Brooks, 1995). Another study identified a peak in the mean number of turtles basking at 10:25, with daily peaks ranging from 9:30 to 13:00 (Schwarzkopf & Brooks, 1985). Although the peak basking time of 12:33 occurs slightly later than reported previously, it still falls within the late-morning to early-afternoon basking window described in the literature.

Basking probability decreased with increasing wind speed. This result is consistent with previous work showing that operative environmental temperature decreases as wind speed increases (Crawford et al., 1983) and that basking is most effective under conditions that promote body warming, including low wind speeds (Chessman, 2024). These findings are also supported by field observations reporting fewer basking pond sliders during windy conditions (Boyer, 1965). Since drone surveys were conducted only under light wind conditions to ensure safe flights, the range of wind speed throughout the surveys was narrow, with a maximum of

1 m/s measured 2 m above the ground. As a result, the estimated effect of wind speed on basking probability may be conservative, and stronger effects could occur under windier conditions than those sampled in this study. Basking probability also decreased with increasing cloud cover. This result aligns with the literature showing that operative environmental temperature decreases when it is cloudy (Crawford et al., 1983) and that the majority of basking in painted turtles occurs when cloud cover is less than 25% (Lefevre & Brooks, 1995).

Individual and Morphological Drivers of Basking Probability

Turtle identity accounted for significant variation in basking patterns. This indicates that there are differences between individuals in basking probability that were not fully explained by measured environmental conditions, sex, or body size. This variation could reflect individual differences in thermal preference or personality, with bolder individuals potentially basking more than shy ones. Individuals can consistently differ in behaviour over time and across situations, known as animal personality (McDougall et al., 2006; Réale et al., 2007). For example, risk-taking behaviour in painted turtles has been shown to differ consistently among individuals (Turcotte et al., 2023), which may explain differences in basking patterns among individuals. Investigating this individual variation in basking behaviour would be a valuable direction for future research to determine the role of personality and thermal preference in shaping thermoregulatory behaviour. Carapace length was not a significant predictor of basking probability, despite body size being known to impact thermoregulatory behaviour and, in some species, result in larger turtles basking for longer (Bulté & Blouin-Demers, 2010; Carrière et al., 2008; Schwarzkopf & Brooks, 1985). Since all turtles in this study were adults, limited size variation among sampled individuals may have reduced the power to detect size-based

thermoregulatory differences. Nonetheless, our results are consistent with field observations that found no correlation between the time spent basking and size in pond sliders (Boyer, 1965).

Drones as a Tool to Monitor Freshwater Turtles

While prior studies using drones to survey freshwater turtles have focused on method validation, my study was the first to use drones to quantify basking behaviour and test a specific ecological hypothesis. Surveying the wetland from an aerial perspective covered areas that were inaccessible by foot or visually obstructed by vegetation when observing from the shore. Drones allowed for repeated, non-invasive observations of individually identifiable painted turtles. Surveys occurred at a fine temporal resolution of every 20 minutes throughout the day, which made it possible to observe basking behaviour very frequently and reduced the likelihood of missing shorter basking bouts. The drone method also eliminated the need to identify specific basking locations within the wetland before the surveys and allowed turtles to be monitored without initiating flight responses. Additionally, pre-programmed autonomous flights standardized the sampling effort across surveys and days, which improved comparability across surveys. These advantages of the drone method overcome important spatial, visual, and disturbance-related limitations of traditional basking survey methods.

Although the drone method of monitoring painted turtles was successful, there were some limitations. For example, drone surveys were strongly dependent on weather conditions and could not occur in the rain or heavy wind. The capacity of the drone batteries and the portable power source charging them on the field were also limiting factors and would have made it a challenge to survey a larger wetland at the same temporal frequency. Future improvements in drone battery capacity, however, will likely minimize this limitation. The manual review of drone videos was also time-consuming, with the potential for human error, despite standardized

reviewer training. This training involved guided practice using example footage and clear criteria for identifying basking turtles. Additionally, 222 of the 22,294 observations were of marked turtles that could not be individually identified from the drone footage. This could have been due to glare or motion blur from the drone footage, or from issues with the paint code (e.g., chipped paint). These unidentified observations could have been minimized by programming the autonomous flight at a lower altitude, slower speed, or by adjusting the paint type or increasing paint drying time. These adjustments, however, would have implications for survey frequency, as flying the drone at a lower altitude or slower speed would make the survey take longer, potentially requiring multiple drone flights to complete the route due to limited battery capacity. Furthermore, such changes could have implications for animal ethics, as more durable paint may not be approved for use on animals or in natural water bodies, and longer drying times may exceed the approved handling time of turtles.

Conclusion

This drone-based surveillance method has broader potential for freshwater turtle monitoring beyond investigating basking patterns. Drones offer a fast and minimally invasive method of surveying wetlands to assess turtle presence, species composition, and approximate abundance before committing to more intensive field methods, such as trapping, marking, or telemetry. This is particularly valuable in systems that are difficult to access or are visually obstructed by vegetation. Drone surveys could be used as an initial surveillance tool to identify sites with a species of interest, estimate abundance before trapping, and guide the placement of traps or cameras, thereby improving sampling efficiency and reducing disturbance.

For preliminary surveys, I recommend surveying in May and June in the late morning or early afternoon, in conditions with minimal wind and low cloud cover, and air temperature

around 20 °C. I recommend testing the flight initiation distance (see Chapter 2) of the species of interest before conducting drone surveys to ensure that the surveillance has a minimal impact on the turtles' behaviour. Additionally, determining the maximum altitude required to differentiate species that look alike and are both present in the survey area (e.g., painted turtles and Blanding's turtles (*Emydoidea blandingii*)), before the drone surveys, is important for accurate identification.

Because drone surveys can be pre-programmed to be standardized and repeatable, they could facilitate long-term monitoring programs surveying populations over many years. As drone technology continues to improve, its application in freshwater turtle monitoring is likely to become a promising method for detecting species of interest, selecting study sites, and supporting long-term population monitoring.

Tables – Chapter 1

Table 1-1. Parameter estimates from the final selected generalized linear mixed model predicting basking probability in painted turtles. All continuous predictors (air temperature, wind speed, cloud cover, carapace length, date, and time) were centred and scaled. Turtle identity was included as a random effect. The model used a binomial error distribution with a logit link, and estimates are on the log-odds scale. Significant effects are indicated with asterisks (***) $p < 0.001$). Painted turtle basking patterns were surveyed via drone from June to September 2025 on the Kenauk property in Montebello, Québec, Canada.

Parameter	Estimate	Standard error	z-value	p-value	
(Intercept)	-1.780	0.321	-5.550	<0.001	***
Air temperature	-0.382	0.039	-9.722	<0.001	***
Air temperature ²	-0.526	0.036	-14.651	<0.001	***
Wind speed	-0.134	0.033	-4.040	<0.001	***
Cloud cover	-0.467	0.035	-13.236	<0.001	***
Sex (male)	-0.310	0.400	-0.775	0.438	
Date	-1.555	0.079	-19.578	<0.001	***
Time	-0.333	0.038	-8.688	<0.001	***
Time ²	-0.952	0.043	-21.896	<0.001	***
Carapace length	-0.195	0.187	-1.043	0.297	
Sex : date	0.538	0.089	6.032	<0.001	***

Figures – Chapter 1

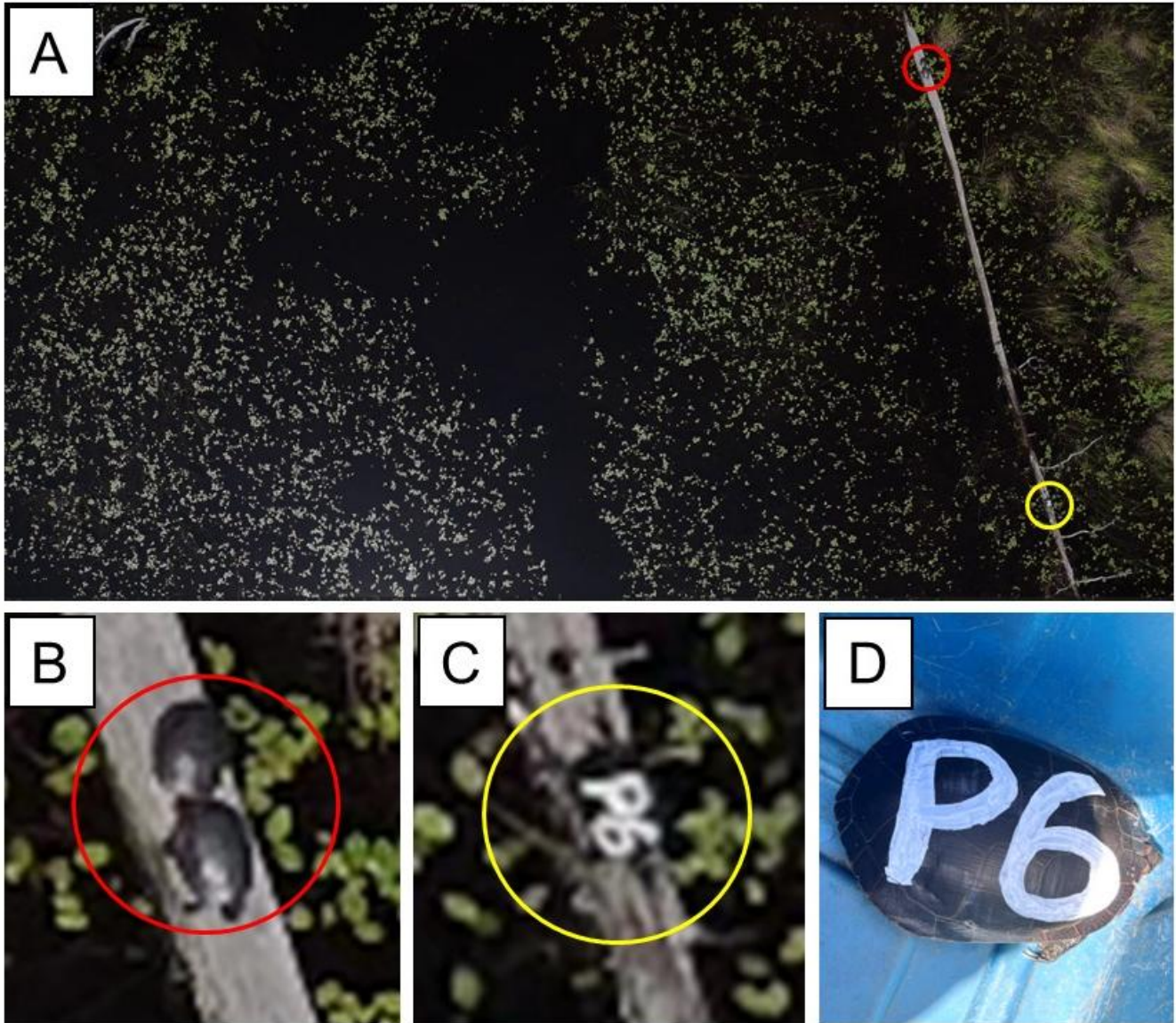


Figure 1-1. Screenshots from drone video surveys of basking painted turtles. Panel (A) shows a video frame captured with a DJI Mini 4 Pro at a 15 m altitude with no zoom. Two unmarked individuals are circled in red, and one marked individual (P6) is circled in yellow. Panels (B) and (C) show post-survey digital zooms of the unmarked turtles and the marked individual (P6), respectively. Panel (D) shows the same marked individual (P6) directly after being painted while the code was drying. Painted turtle basking patterns were surveyed via drone from June to September 2025 on the Kenauk property in Montebello, Québec, Canada.

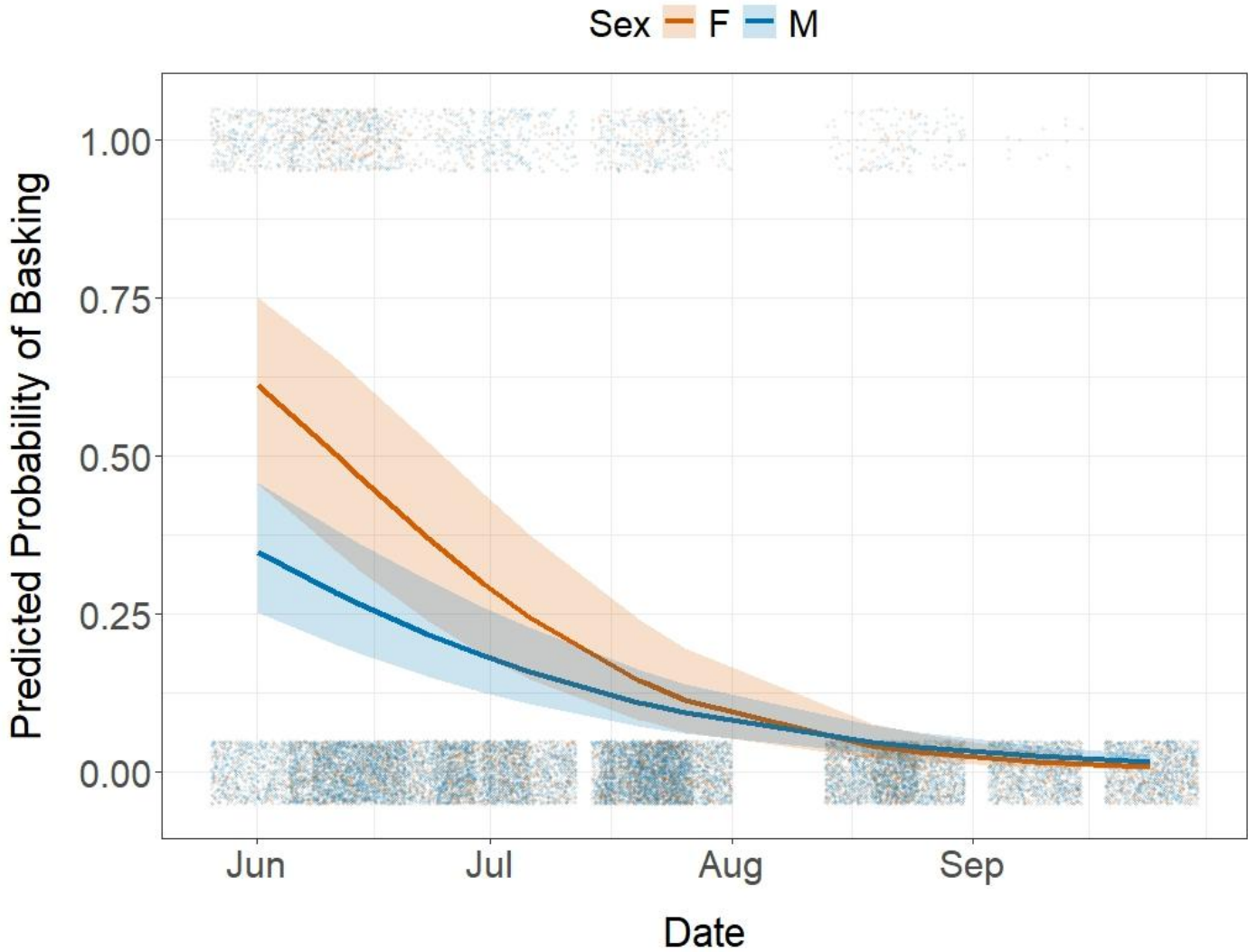


Figure 1-2. Model-predicted basking probability in painted turtles as a function of date for male and female painted turtles. Lines represent predictions from the final generalized linear mixed model for males (blue) and females (orange), and shading around the predicted values represents 95% confidence intervals. Points show independent observed basking events for individual turtles (1 = present, 0 = absent), which represent the raw data that informed the model. Painted turtle basking patterns were surveyed via drone from June to September 2025 on the Kenauk property in Montebello, Québec, Canada (n = 55 individuals, 22,294 presence-absence observations).

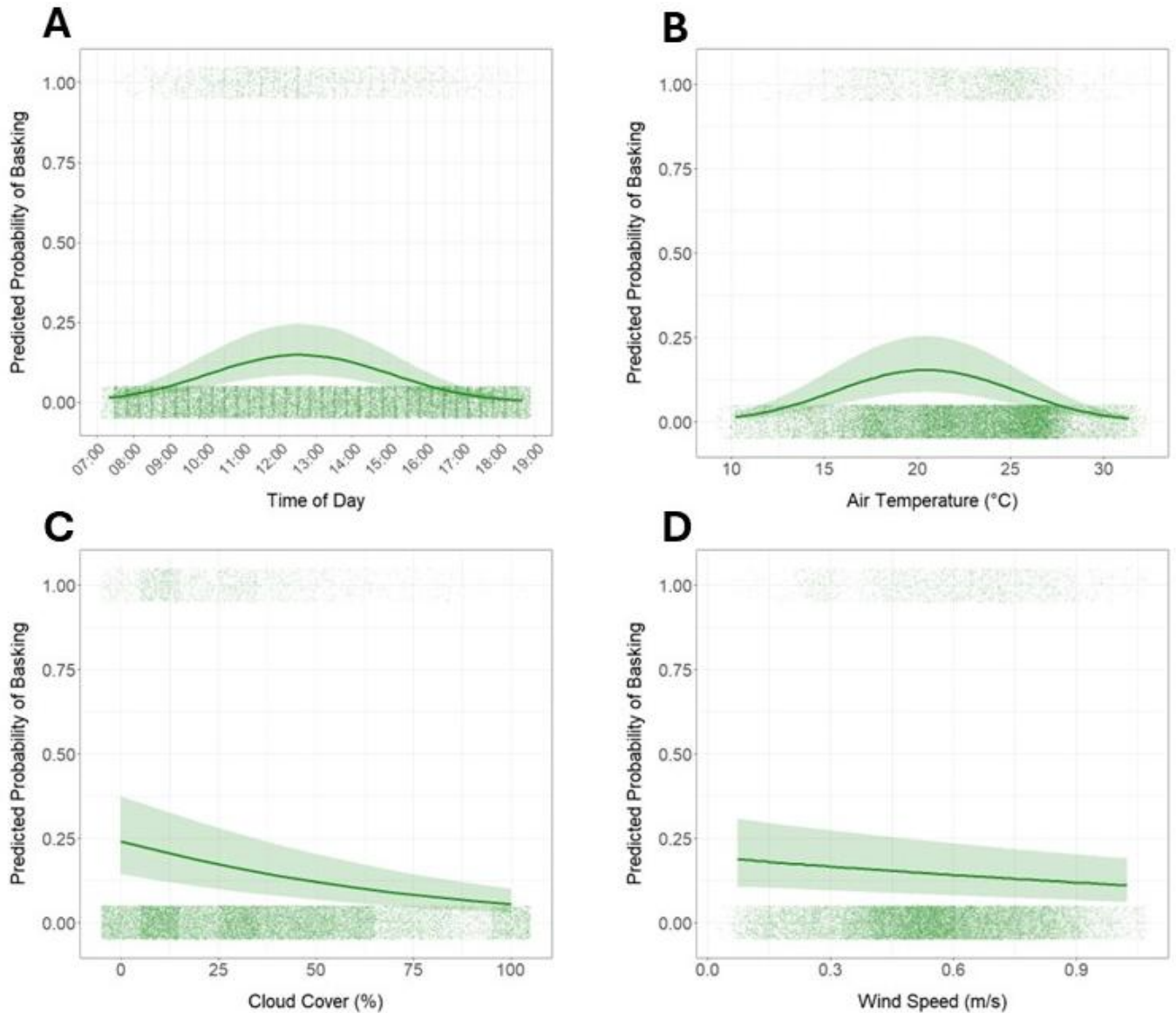


Figure 1-3. Model-predicted basking probability in painted turtles in relation to (A) time of day, (B) air temperature, (C) percent cloud cover, and (D) wind speed. Lines represent predictions from the final generalized linear mixed model, and shading around the predicted values represents 95% confidence intervals. Points show independent observed basking events for individual turtles (1 = present, 0 = absent), which represent the raw data that informed the model. Painted turtle basking patterns were surveyed via drone from June to September 2025 on the Kenauk property in Montebello, Québec, Canada (n = 55 individuals, 22,294 presence-absence observations).

Supplementary Information – Chapter 1

Supplementary Information 1: Additional Photos from the Field

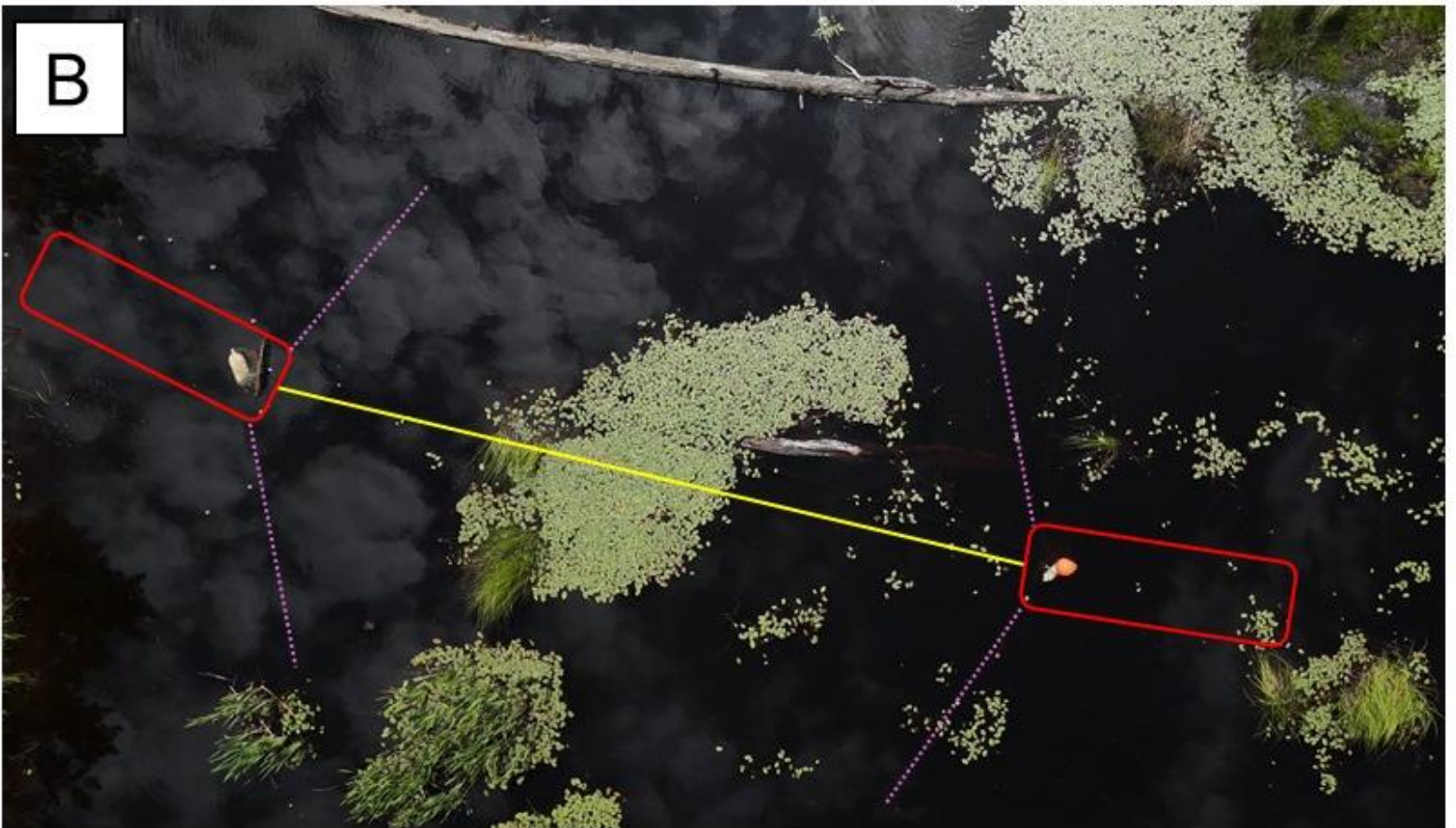


Figure S1-1. Hoop net setup used to capture painted turtles. The nets were set parallel to the shore in tandem. The hoop nets are outlined by red rectangles, with the cod (closed) ends facing away from one another, and the mouth (open) ends facing each other. The mouth ends of the nets were joined by a lead (yellow solid lines), and each net had two wings set at approximately 45 degrees from the opening (purple dotted lines). Buoys placed in the nets created air spaces for the turtles and are visible in white (left) and orange (right) in panels (A) and (B). Panel (A) shows a practice net setup in a man-made pond used for demonstrations and field assistant training, photographed from shore. Panel (B) shows a drone image of a net setup at the study site. The hoops are collapsed in panel (B) because the image was taken during a drone survey; red rectangles show where the nets extended to when deployed. Painted turtle basking patterns were surveyed via drone from June to September 2025 on the Kenauk property in Montebello, Québec, Canada.

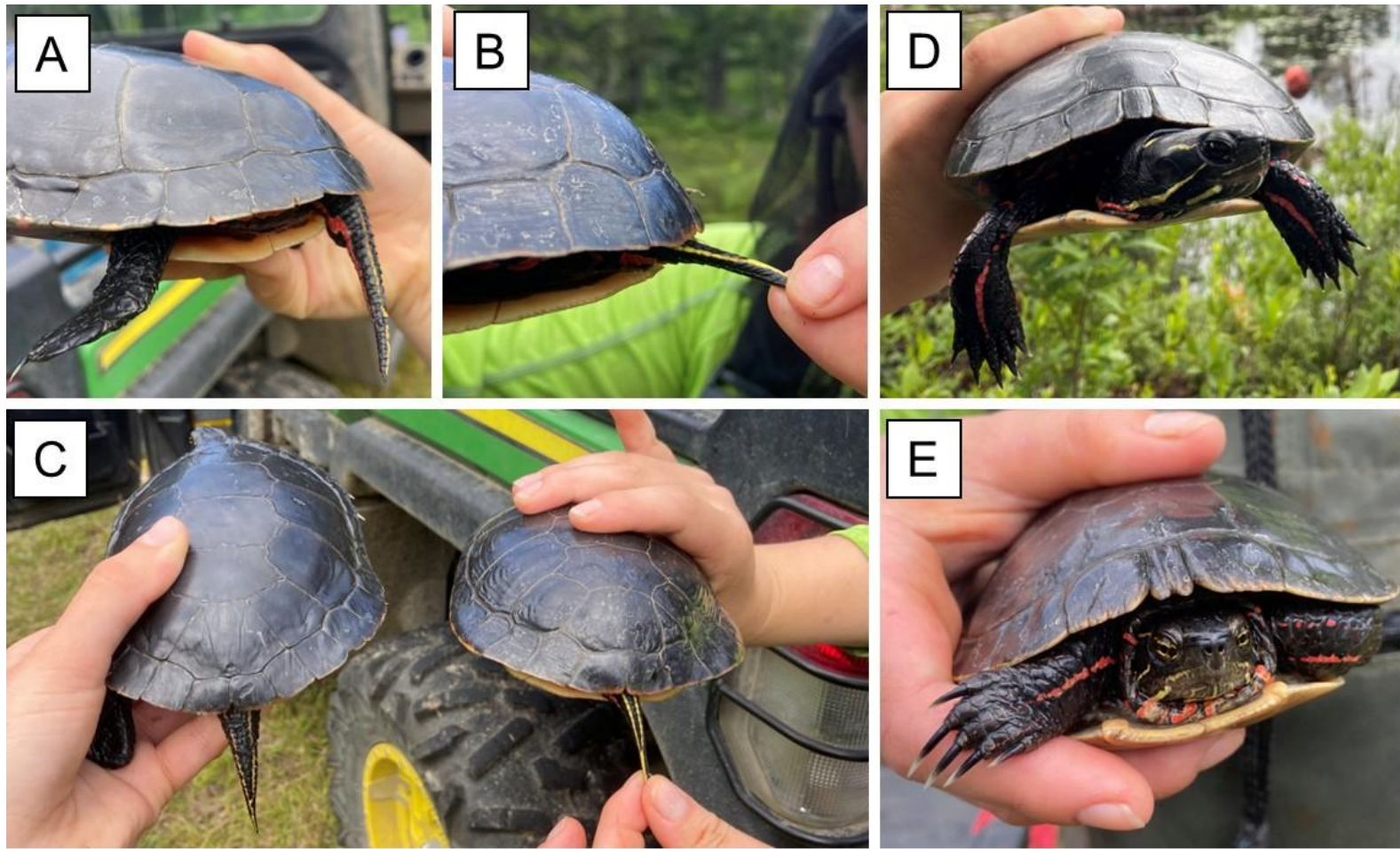


Figure S1-2. Examples of secondary sexual characteristics in painted turtles. Panel (A) shows a male's tail, which is thicker with the cloacal opening located farther down the tail. Panel (B) shows a female's tail, which is thinner with the cloacal opening located closer to the plastron. Panel (C) shows a male's tail (left) and a female's tail (right). Panel (D) shows a female's foreclaws, which are shorter. Panel (E) shows a male's foreclaws, which are longer. Painted turtle basking patterns were surveyed via drone from June to September 2025 on the Kenauk property in Montebello, Québec, Canada.

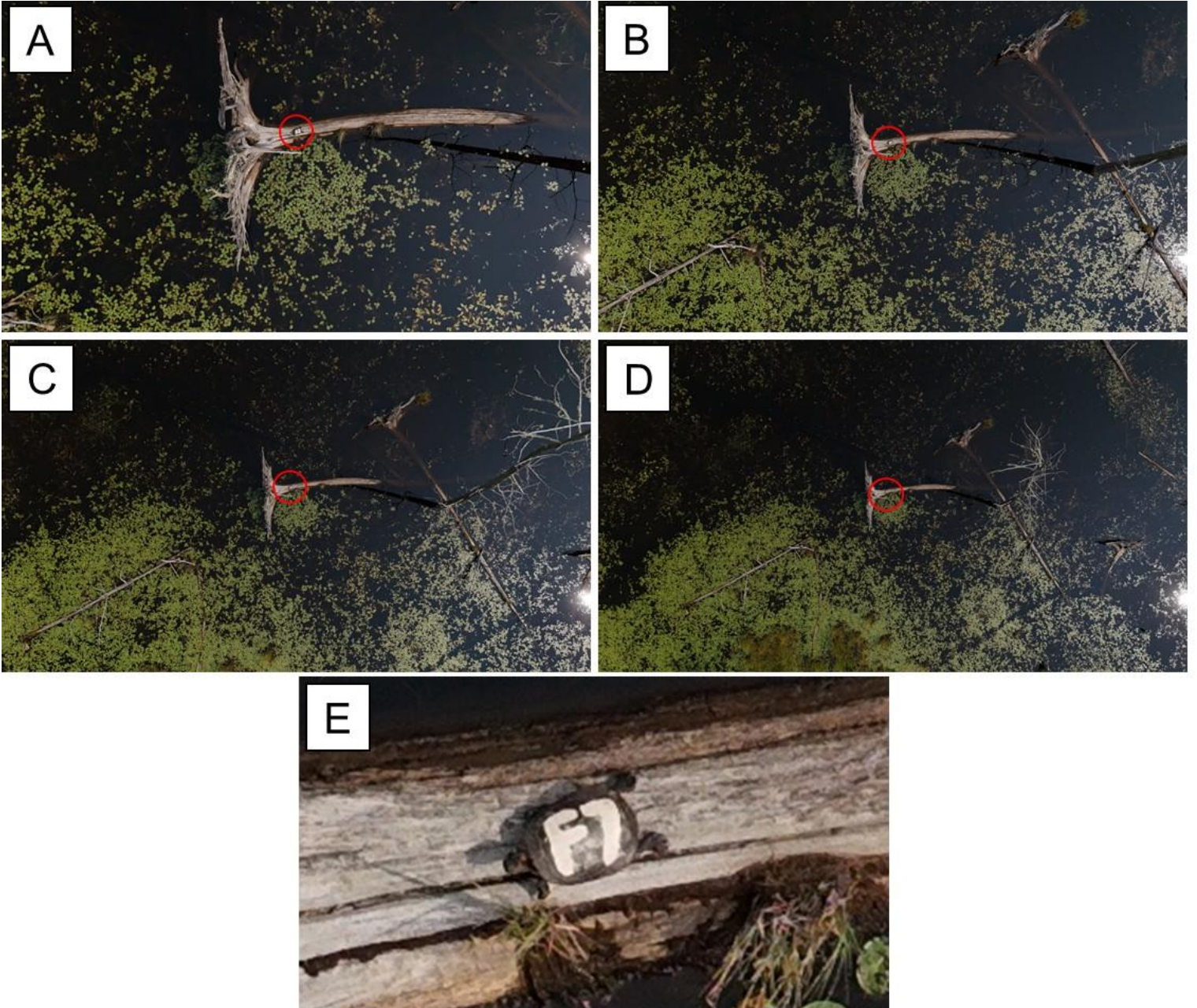


Figure S1-3. Pictures of a marked painted turtle taken with a DJI Mini 4 Pro drone with no zoom from a 5 m altitude (A), a 10 m altitude (B), a 15 m altitude (C), and a 20 m altitude (D). Panel (E) is an image of the basking turtle zoomed in, showing its painted code (F7). Painted turtle basking patterns were surveyed via drone from June to September 2025 on the Kenauk property in Montebello, Québec, Canada.

Supplementary Information 2: Additional Dataset Information

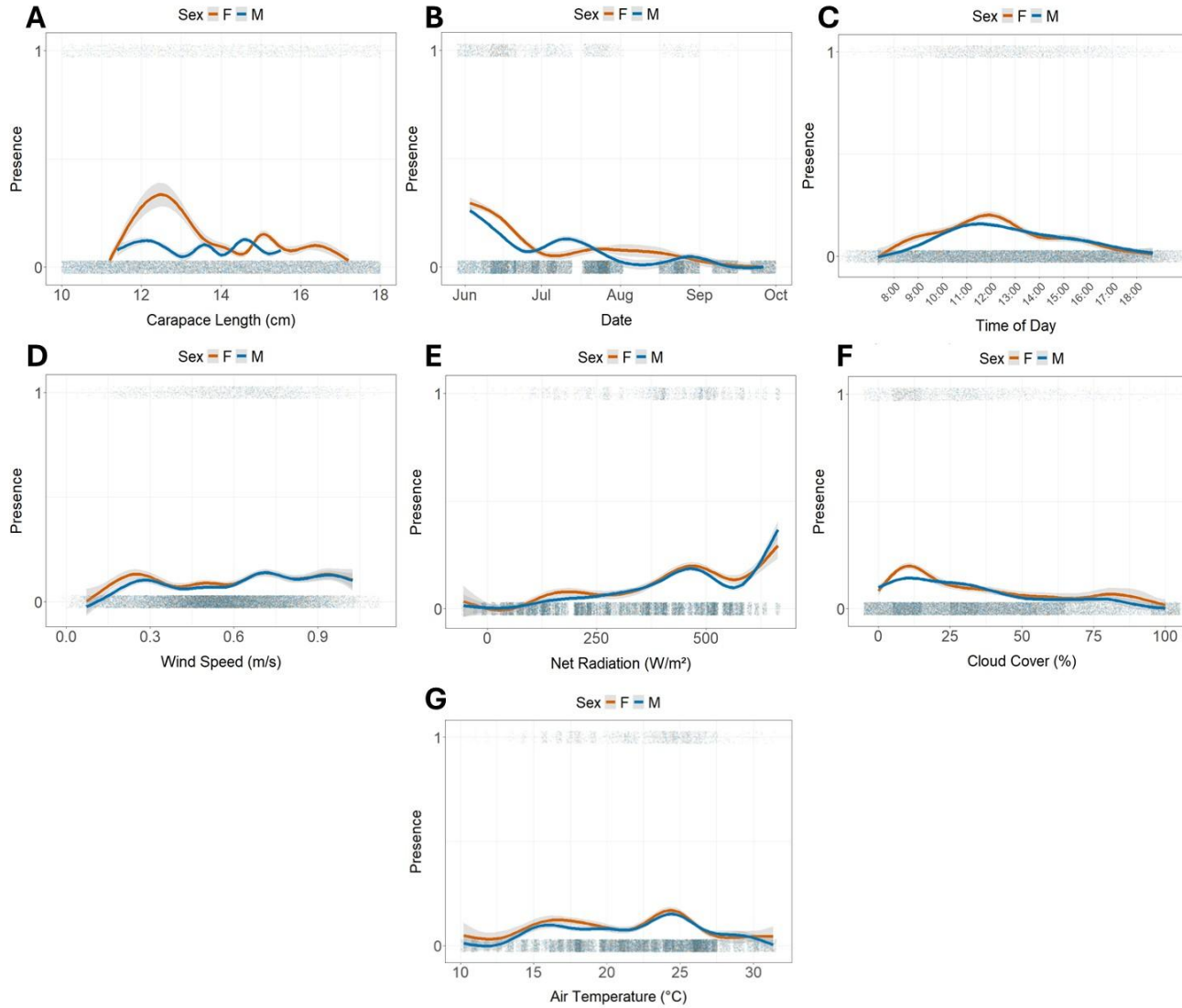


Figure S1-4. Exploratory relationships between observed turtle basking presence and (A) turtle carapace length, (B) date, (C) time of day, (D) wind speed, (E) net radiation, (F) percent cloud cover, and (G) air temperature. Points show independent observed basking events for individual turtles (1 = present, 0 = absent), which represent the raw data. Lines represent smoothed trends fitted using generalized additive models for visualization in blue for males and orange for females. Shaded areas represent 95% confidence intervals. Painted turtle basking patterns were surveyed via drone from June to September 2025 on the Kenauk property in Montebello, Québec, Canada (n = 55 individuals, 22,294 presence-absence observations).

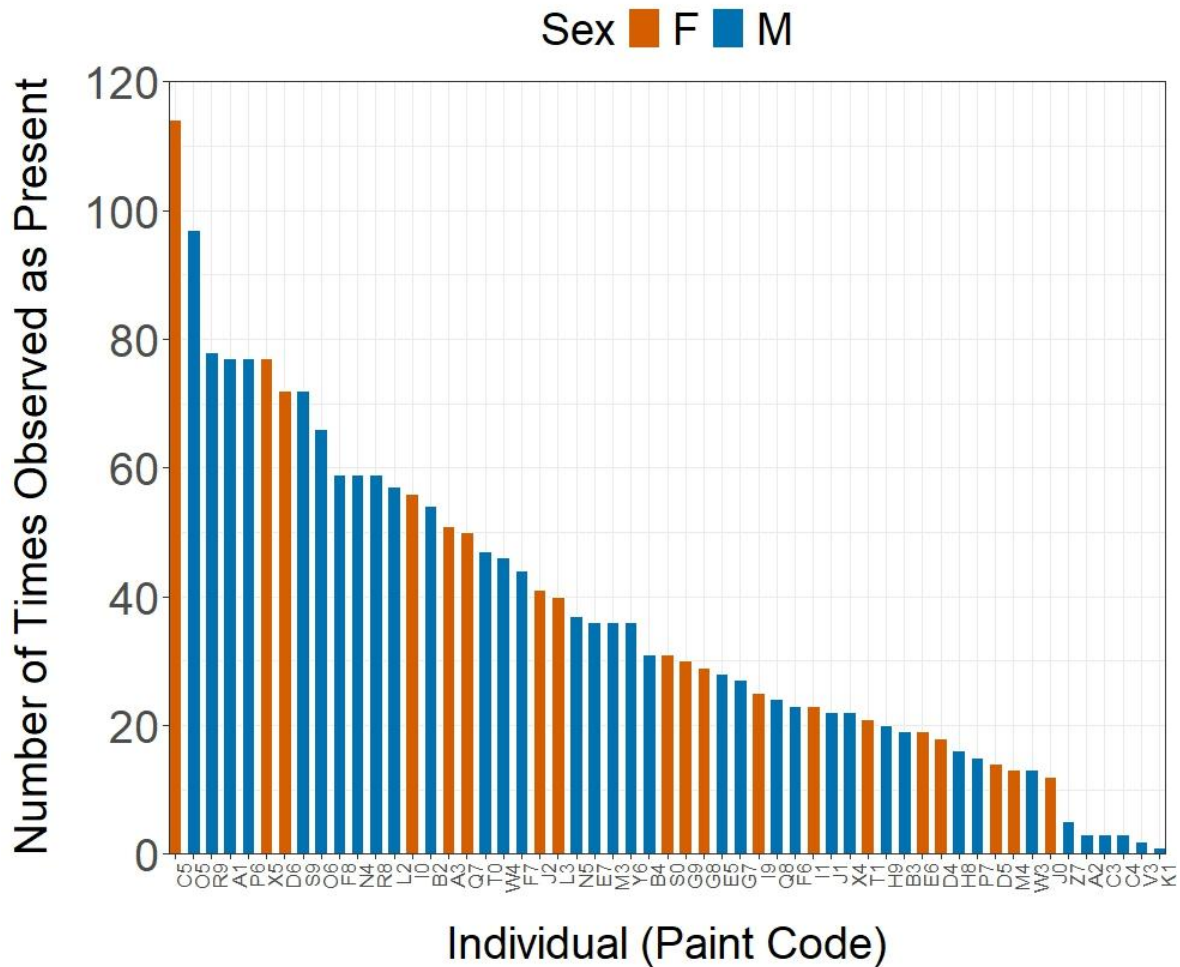


Figure S1-5. Frequency distribution histogram of the number of times individual turtles were observed as present (basking) during drone surveys. Each bar represents the number of times an individual turtle was observed as present during drone surveys across the season, with males in blue and females in orange. Painted turtle basking patterns were surveyed via drone from June to September 2025 on the Kenauk property in Montebello, Québec, Canada.

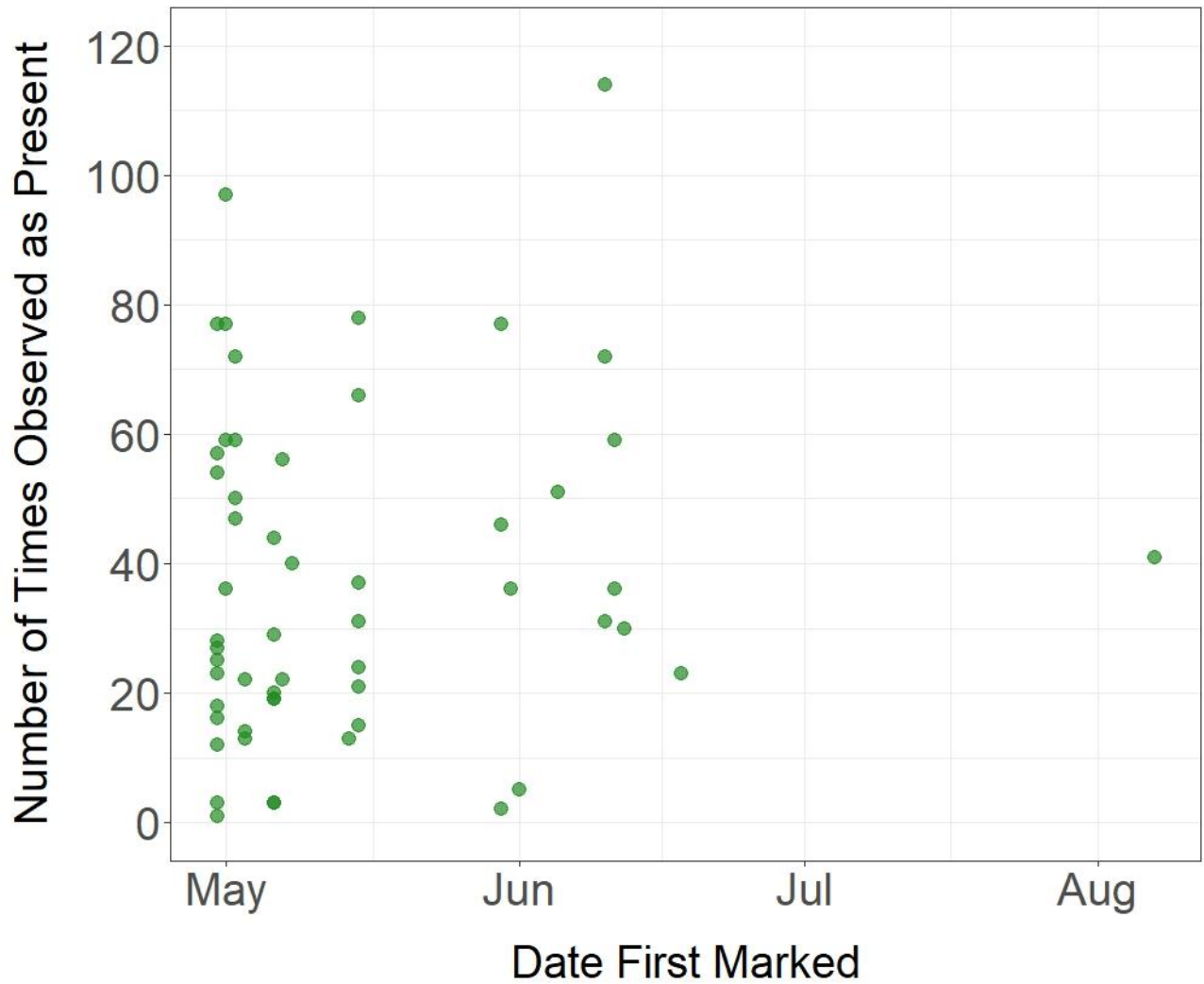


Figure S1-6. Scatterplot showing the relationship between the date individual turtles were first marked (added to the study) and the total number of times they were subsequently observed as present (basking) across the study period. Each point represents an individual turtle. Painted turtle basking patterns were surveyed via drone from June to September 2025 on the Kenauk property in Montebello, Québec, Canada.

Table S1-1. Summary statistics for environmental variables measured during drone-based painted turtle basking surveys and carapace length measured during turtle capture from May to September 2025 on the Kenauk property in Montebello, Québec, Canada.

Variable	Minimum	Maximum	Mean	Standard Deviation
Air temperature (°C)	10.2	31.4	22.1	4.6
Wind speed (m/s)	0.07	1.02	0.56	0.21
Cloud cover (%)	0	100	37.4	27.6
Net radiation (W/m ²)	-54.2	664.1	308.5	177.1
Carapace length (cm)	11.2	17.2	14.2	1.2

Supplementary Information 3: Additional Model and Statistical Information

Table S1-2. Candidate generalized linear mixed models evaluated for painted turtle basking probability, showing fixed-effects structures, model degrees of freedom (df), Akaike's Information Criterion (AIC), and Δ AIC values. All models include turtle identity as a random effect. Candidate models include combinations of environmental, biological, and temporal variables, as well as quadratic terms indicated by ² and interaction terms indicated by *. Δ AIC values are calculated relative to the model with the lowest AIC (Δ AIC = 0). Models with Δ AIC < 2 are highlighted in bold and represent the top-ranked candidate models. Painted turtle basking patterns were surveyed via drone from June to September 2025 on the Kenauk property in Montebello, Québec, Canada.

Model ID	Fixed effects	df	AIC	Δ AIC
MFull	Temp + Wind + Cloud + Radiation + Sex + Length + Date + Time	10	10111.481	540.547
M1	Temp + Wind + Cloud + Radiation + Length + Time + Sex * Date	11	10078.387	507.453
M2	Temp + Wind + Cloud + Radiation + Length + Time + Time ² + Sex * (Date + Date ²)	14	9855.558	284.624
M3	Temp + Wind + Cloud + Radiation + Length + Time + Time ² + Sex * Date	12	9852.159	281.225
M4	Temp + Wind + Cloud + Radiation + Length + Time + Sex * (Date + Date ²)	13	10048.365	477.431
M5	Temp + Cloud + Radiation + Length + Time + Time ² + Sex * Date	11	9870.826	299.892
M6	Temp + Temp ² + Wind + Cloud + Radiation + Length + Time + Time ² + Sex * Date	13	9574.032	3.098
M7	Temp + Temp² + Wind + Cloud + Length + Time + Time² + Sex * Date	12	9572.217	1.283
M8	Temp + Temp ² + Cloud + Radiation + Length + Time + Time ² + Sex * Date	12	9588.408	17.474
M9	Temp + Temp² + Wind + Cloud + Radiation + Radiation² + Length + Time + Time² + Sex * Date	14	9570.934	0
M10	Temp + Temp ² + Wind + Cloud + Radiation + Time + Time ² + Sex * Date + Sex * Length	14	9575.905	4.971
M11	Temp + Temp ² + Wind + Cloud + Time + Time ² + Sex * Date	11	9983.505	412.571
M12	Wind + Cloud + Length + Time + Time ² + Sex * Date	10	9887.414	316.480
M13	Temp + Temp ² + Wind + Cloud + Length + Sex * Date	10	10333.837	762.903
M14	Wind + Cloud + Radiation + Radiation ² + Length + Sex * Date + Time + Time ²	12	9875.235	304.301

Table S1-3. Variance Inflation Factors (VIF) for fixed effects in the top-ranked generalized linear mixed models with $\Delta AIC < 2$. VIF values were used to assess multicollinearity among predictors during final model selection. VIF values > 5 are highlighted in bold and indicate potentially problematic collinearity. Painted turtle basking patterns were surveyed via drone from June to September 2025 on the Kenauk property in Montebello, Québec, Canada.

Predictor	Model VIF	
	M7	M9
Air temperature	1.46	1.62
Air temperature ²	1.21	1.25
Wind speed	1.45	1.55
Cloud	1.14	1.28
Radiation	NA	7.38
Radiation ²	NA	2.02
Date	4.44	4.49
Time	1.27	1.48
Time ²	1.36	5.18
Length	1.12	1.12
Sex	1.14	1.14
Sex * Date	4.33	4.32

Supplementary Information 4: R Script

```
# -----  
# SETUP  
# -----  
  
# Clearing environment  
rm(list=ls())  
  
# Installing packages  
install.packages("readr")  
install.packages("dplyr")  
install.packages("lubridate")  
install.packages("tidyverse")  
install.packages("lme4")  
install.packages("ggplot2")  
install.packages("DHARMA")  
install.packages("car")  
install.packages("ggeffects")  
install.packages("performance")  
install.packages("broom")  
install.packages("purrr")  
  
# Adding packages to library  
library(readr)  
library(dplyr)  
library(lubridate)  
library(tidyverse)  
library(lme4)  
library(ggplot2)
```

```

library(DHARMA)
library(car)
library(ggeffects)
library(performance)
library(broom)
library(purrr)

# Loading data
dronedat <- read_csv("drone_data.csv")
weatherdat <- read_csv("weather_station_data.csv")
individualsdat <- read_csv("individuals_data.csv")

# -----
# ORGANIZING THE DATA
# -----

# MERGING WEATHER AND DRONE DATA

# Creating timestamp column in dronedat
dronedat <- dronedat %>%
  mutate(
    timestamp = mdy_hm(paste(date, substr(time, 1, 5)))
  )

# Converting weather timestamp
weatherdat <- weatherdat %>%
  mutate(timestamp = ymd_hm(timestamp))

# Flooring timestamps to the hour
dronedat <- dronedat %>% mutate(timestamp_hour = floor_date(timestamp, "hour"))

```

```

weatherdat <- weatherdat %>% mutate(timestamp_hour = floor_date(timestamp, "hour"))

# Merging datasets by hour
dronedat_merged <- left_join(dronedat, weatherdat, by = "timestamp_hour")

# Removing duplicate timestamp columns
dronedat_merged <- dronedat_merged %>% select(-timestamp.y, -timestamp_hour)

# REMOVING UNIDENTIFIED TURTLES

# Counting how many rows will be removed
removed_rows <- dronedat_merged %>%
  filter(presence == "yes" & is.na(paint_id)) %>%
  nrow()
removed_rows

# Keeping all rows except when a turtle was observed but ID was undetermined
dronedat_marked <- dronedat_merged %>%
  filter(!(presence == "yes" & is.na(paint_id)))

# CREATING MASTER SURVEY LIST

# Removing surveys that did not occur (when presence is NA)
# Extracting one row per survey with environmental variables
all_surveys <- dronedat_marked %>%
  filter(!is.na(presence)) %>% # remove surveys that did not occur
  select(survey_id, date, time, cloud, timestamp.x, AirTemp_Avg, WindSpeed_Avg_ms_2m,
NetRadiation_Avg) %>%
  distinct()

```

```

# Convert date columns to Date so simplify comparisons
all_surveys <- all_surveys %>% mutate(date = mdy(date))
individualsdat <- individualsdat %>% mutate(date_marked = mdy(date_marked))

# CREATING INDIVIDUAL X SURVEY GRID

# Creating all combinations of surveys and individual turtles
complete_data <- expand_grid(
  survey_id = all_surveys$survey_id,
  paint_id = individualsdat$paint_id
) %>%
  left_join(
    dronedat_marked %>% select(survey_id, paint_id, presence),
    by = c("survey_id", "paint_id")
  )

# MERGING INDIVIDUAL AND ENVIRONMENTAL SURVEY DATA
complete_data <- complete_data %>%
  left_join(individualsdat, by = "paint_id") %>%
  left_join(all_surveys, by = "survey_id")

# FILTERING OUT SURVEYS BEFORE INDIVIDUAL WAS MARKED
complete_data <- complete_data %>%
  filter(date >= date_marked)

# CREATING BINARY PRESENCE COLUMN
complete_data <- complete_data %>%
  mutate(present = case_when(
    presence == "yes" ~ 1,
    presence == "no" ~ 0,
  ))

```

```

    TRUE           ~ 0
  )) %>%
  select(-presence)

# REMOVING INDIVIDUALS THAT WERE NEVER OBSERVED BASKING

# Identifying individuals that were never seen
never_seen <- complete_data %>%
  group_by(paint_id) %>%
  summarize(total_present = sum(present)) %>%
  filter(total_present == 0) %>%
  pull(paint_id)
never_seen

# Removing individuals never seen from the dataset
complete_data <- complete_data %>%
  filter(!paint_id %in% never_seen)

# Checking how many times each individual was observed
seen_counts <- complete_data %>%
  group_by(paint_id) %>%
  summarize(times_seen = sum(present, na.rm = TRUE)) %>%
  arrange(desc(times_seen))
view(seen_counts)
summary(seen_counts$times_seen)

# PLOT OF HOW MANY TIMES EAH INDIVIDUAL WAS OBSERVED
seen_counts <- complete_data %>%
  group_by(paint_id, sex) %>%
  summarize(times_seen = sum(present, na.rm = TRUE), .groups = "drop") %>%

```

```

    arrange(desc(times_seen))
ggplot(seen_counts,
       aes(x = reorder(paint_id, -times_seen),
           y = times_seen,
           fill = sex)) +
geom_col(
  width = 0.7,
  color = "white",
  linewidth = 0.5
) +
labs(
  x = "Individual (Paint Code)",
  y = "Number of Times Observed as Present",
  fill = "Sex"
) +
scale_fill_manual(
  values = c(
    "F" = "#D55E00",
    "M" = "#0072B2"
  )
) +
scale_x_discrete(
  expand = expansion(mult = c(0, 0))
) +
scale_y_continuous(
  breaks = seq(0, 120, by = 20),
  limits = c(0, 120),
  expand = expansion(mult = c(0, 0))
) +
theme_bw() +

```

```

theme(
  legend.position = "top",
  axis.title.x = element_text(size = 22, margin = margin(t = 15)),
  axis.title.y = element_text(size = 22, margin = margin(r = 15)),
  axis.text.x = element_text(size = 10, angle = 90, hjust = 1),
  axis.text.y = element_text(size = 22),
  legend.title = element_text(size = 22),
  legend.text = element_text(size = 22)
)

# PLOT OF NUMBER OF TIMES SEEN AND DATE FIRST MARKED
individualsdat <- individualsdat %>%
  mutate(date_marked = as.Date(date_marked))
seen_with_dates <- seen_counts %>%
  left_join(individualsdat, by = "paint_id")
ggplot(seen_with_dates, aes(x = date_marked, y = times_seen)) +
  geom_point(color = "#228B22", size = 3, alpha = 0.7) +
  labs(
    x = "Date First Marked",
    y = "Number of Times Observed as Present"
  ) +
  scale_y_continuous(
    limits = c(0, 120),
    breaks = seq(0, 120, by = 20)
  ) +
  theme_bw() +
  theme(
    legend.position = "top",
    axis.title.x = element_text(size = 22, margin = margin(t = 15)),
    axis.title.y = element_text(size = 22, margin = margin(r = 15)),

```

```

    axis.text = element_text(size = 22),
    legend.title = element_text(size = 22),
    legend.text = element_text(size = 22)
  )

# COUNTING MALES VS FEMALES
count_unique_individuals <- complete_data[!duplicated(complete_data$paint_id), ]
table(count_unique_individuals$sex)

# FINAL DATA IS COMPLETE
view(complete_data)

# CALCULATING PRESENT VS ABSENT OBSERVATIONS
table(complete_data$present)
prop.table(table(complete_data$present))

# CALCULATING HOW MANY TIMES EACH INDIVIDUAL WAS OBSERVED BASKING
table_1 <- table(complete_data$paint_id, complete_data$present)
table_1

# -----
# DATA EXPLORATION
# -----

# SETTING VARIABLE TYPES

# Sex and individual as factors
complete_data <- complete_data %>%
  mutate(
    sex = factor(sex),

```

```

    paint_id = factor(paint_id)
  )
levels(complete_data$sex)
levels(complete_data$paint_id)

# Checking continuous variables
str(complete_data %>% select(length, AirTemp_Avg, WindSpeed_Avg_ms_2m, cloud,
NetRadiation_Avg, time, date))
complete_data <- complete_data %>%

# Converting time to decimal hours
mutate(time_dec = hour(time) + minute(time)/60 + second(time)/3600,

# Converting date to day-of-year
      day_of_year = yday(date)) %>%

# Scaling continuous predictors
mutate(length_s = scale(length),
      AirTemp_s = scale(AirTemp_Avg),
      WindSpeed_s = scale(WindSpeed_Avg_ms_2m),
      cloud_s = scale(cloud),
      time_s = scale(time_dec),
      Radiation_s = scale(NetRadiation_Avg),
      date_s = scale(day_of_year))

# Checking scaled variables
summary(complete_data %>% select(length_s, AirTemp_s, WindSpeed_s, cloud_s, time_s,
Radiation_s, date_s))

# Making sure response is numeric 0/1
complete_data$present <- as.integer(complete_data$present)

```

```

view(complete_data)

summary(complete_data)

# DATA EXPLORATION PLOTS

# Date by sex
complete_data <- complete_data %>%
  mutate(time_f = factor(format(time, "%H:%M")))
time_breaks <- c("07:00:00", "08:00:00", "09:00:00", "10:00:00",
                "11:00:00", "12:00:00", "13:00:00", "14:00:00",
                "15:00:00", "16:00:00", "17:00:00", "18:00:00", "19:00:00")
time_labels <- sub("^0?([0-9]{1,2}):([0-9]{2}):00$", "\\1:\\2", time_breaks)
p_date <- ggplot(complete_data, aes(x = date, y = present)) +
  geom_jitter(aes(color = sex), height = 0.03, width = 5, alpha = 0.07, size = 0.5) +
  geom_smooth(aes(color = sex, group = sex), method = "gam", formula = y ~ s(x), se =
TRUE, linewidth = 2, alpha = 0.3) +
  theme_bw() +
  labs(
    x = "Date",
    y = "Presence",
    color = "Sex",
    title = "Basking vs Date by Sex"
  ) +
  scale_color_manual(values = c("#D55E00", "#0072B2")) +
  scale_y_continuous(breaks = c(0, 1)) +
  theme(
    legend.position = "top",
    axis.title.x = element_text(size = 22, margin = margin(t = 15)),
    axis.title.y = element_text(size = 22, margin = margin(r = 15)),
    axis.text = element_text(size = 22),

```

```

    legend.title = element_text(size = 22),
    legend.text = element_text(size = 22)
)

# Time of Day by Sex
p_time <- ggplot(complete_data, aes(x = time_f, y = present)) +
  geom_jitter(aes(color = sex), height = 0.03, width = 5, alpha = 0.07, size = 0.5) +
  geom_smooth(aes(color = sex, group = sex), method = "gam", formula = y ~
s(as.numeric(x)), se = TRUE, linewidth = 2, alpha = 0.3) +
  theme_bw() +
  labs(
    x = "Time of Day",
    y = "Presence",
    color = "Sex",
    title = "Basking vs Time of Day by Sex"
) +
  scale_color_manual(values = c("#D55E00", "#0072B2")) +
  scale_x_discrete(breaks = time_breaks, labels = time_labels) +
  scale_y_continuous(breaks = c(0, 1)) +
  theme(
    legend.position = "top",
    axis.title.x = element_text(size = 22, margin = margin(t = 15)),
    axis.title.y = element_text(size = 22, margin = margin(r = 15)),
    axis.text.x = element_text(size = 16, angle = 45, hjust = 1),
    axis.text.y = element_text(size = 22),
    legend.title = element_text(size = 22),
    legend.text = element_text(size = 22)
)

# Cloud Cover by Sex

```

```

p_cloud <- ggplot(complete_data, aes(x = cloud, y = present)) +
  geom_jitter(aes(color = sex), height = 0.03, width = 5, alpha = 0.07, size = 0.5) +
  geom_smooth(aes(color = sex, group = sex), method = "gam", formula = y ~ s(x), se =
TRUE, linewidth = 2, alpha = 0.3) +
  theme_bw() +
  labs(
    x = "Cloud Cover (%)",
    y = "Presence",
    color = "Sex",
    title = "Basking vs Cloud Cover by Sex"
  ) +
  scale_color_manual(values = c("#D55E00", "#0072B2")) +
  scale_y_continuous(breaks = c(0, 1)) +
  theme(
    legend.position = "top",
    axis.title.x = element_text(size = 22, margin = margin(t = 15)),
    axis.title.y = element_text(size = 22, margin = margin(r = 15)),
    axis.text = element_text(size = 22),
    legend.title = element_text(size = 22),
    legend.text = element_text(size = 22)
  )

```

```
# Wind Speed by Sex
```

```

p_wind <- ggplot(complete_data, aes(x = WindSpeed_Avg_ms_2m, y = present)) +
  geom_jitter(aes(color = sex), height = 0.03, width = 0.1, alpha = 0.07, size = 0.5)
+
  geom_smooth(aes(color = sex, group = sex), method = "gam", formula = y ~ s(x), se =
TRUE, linewidth = 2, alpha = 0.3) +
  theme_bw() +
  labs(
    x = "Wind Speed (m/s)",

```

```

    y = "Presence",
    color = "Sex",
    title = "Basking vs Wind Speed by Sex"
  ) +
  scale_color_manual(values = c("#D55E00", "#0072B2")) +
  scale_y_continuous(breaks = c(0, 1)) +
  theme(
    legend.position = "top",
    axis.title.x = element_text(size = 22, margin = margin(t = 15)),
    axis.title.y = element_text(size = 22, margin = margin(r = 15)),
    axis.text = element_text(size = 22),
    legend.title = element_text(size = 22),
    legend.text = element_text(size = 22)
  )

# Air Temperature by Sex
p_temp <- ggplot(complete_data, aes(x = AirTemp_Avg, y = present)) +
  geom_jitter(aes(color = sex), height = 0.03, width = 0.2, alpha = 0.07, size = 0.5)
+
  geom_smooth(aes(color = sex, group = sex), method = "gam", formula = y ~ s(x), se =
TRUE, linewidth = 2, alpha = 0.3) +
  theme_bw() +
  labs(
    x = "Air Temperature (°C)",
    y = "Presence",
    color = "Sex",
    title = "Basking vs Air Temperature by Sex"
  ) +
  scale_color_manual(values = c("#D55E00", "#0072B2")) +
  scale_y_continuous(breaks = c(0, 1)) +
  theme(

```

```

    legend.position = "top",
    axis.title.x = element_text(size = 22, margin = margin(t = 15)),
    axis.title.y = element_text(size = 22, margin = margin(r = 15)),
    axis.text = element_text(size = 22),
    legend.title = element_text(size = 22),
    legend.text = element_text(size = 22)
)

# Net Radiation by Sex
p_radiation <- ggplot(complete_data, aes(x = NetRadiation_Avg, y = present)) +
  geom_jitter(aes(color = sex), height = 0.03, width = 5, alpha = 0.07, size = 0.5) +
  geom_smooth(aes(color = sex, group = sex), method = "gam", formula = y ~ s(x), se =
TRUE, linewidth = 2, alpha = 0.3) +
  theme_bw() +
  labs(
    x = "Net Radiation (W/m2)",
    y = "Presence",
    color = "Sex",
    title = "Basking vs Radiation by Sex"
) +
  scale_color_manual(values = c("#D55E00", "#0072B2")) +
  scale_y_continuous(breaks = c(0, 1)) +
  theme(
    legend.position = "top",
    axis.title.x = element_text(size = 22, margin = margin(t = 15)),
    axis.title.y = element_text(size = 22, margin = margin(r = 15)),
    axis.text = element_text(size = 22),
    legend.title = element_text(size = 22),
    legend.text = element_text(size = 22)
)

```

```

# Carapace Length by Sex
p_length <- ggplot(complete_data, aes(x = length, y = present)) +
  geom_jitter(aes(color = sex), height = 0.03, width = 5, alpha = 0.07, size = 0.5) +
  geom_smooth(aes(color = sex, group = sex), method = "gam", formula = y ~ s(x), se =
TRUE, linewidth = 2, alpha = 0.3) +
  theme_bw() +
  labs(
    x = "Carapace Length (cm)",
    y = "Presence",
    color = "Sex",
    title = "Basking vs Carapace Length by Sex"
  ) +
  scale_color_manual(values = c("#D55E00", "#0072B2")) +
  scale_y_continuous(breaks = c(0, 1)) +
  scale_x_continuous(limits = c(10, 18)) +
  theme(
    legend.position = "top",
    axis.title.x = element_text(size = 22, margin = margin(t = 15)),
    axis.title.y = element_text(size = 22, margin = margin(r = 15)),
    axis.text = element_text(size = 22),
    legend.title = element_text(size = 22),
    legend.text = element_text(size = 22)
  )

p_date
p_time
p_cloud
p_wind
p_temp

```

```

p_radiation
p_length

# -----
# MODEL BUILDING
# -----

# MODFULL
mod_full <- glmer(
  present ~ AirTemp_s + WindSpeed_s + cloud_s + sex + length_s + date_s + time_s +
  Radiation_s +
    (1 | paint_id),
  data = complete_data,
  family = binomial,
  control = glmerControl(optimizer = "bobyqa")
)
summary(mod_full)

# MOD1
mod_1 <- glmer(
  present ~ AirTemp_s + WindSpeed_s + cloud_s + Radiation_s + time_s + sex * date_s +
  length_s +
    (1 | paint_id),
  data = complete_data,
  family = binomial,
  control = glmerControl(optimizer = "bobyqa")
)
summary(mod_1)

# MOD2
mod_2 <- glmer(

```

```

present ~ AirTemp_s + WindSpeed_s + cloud_s + Radiation_s +
  sex * (date_s + I(date_s^2)) +
  time_s + I(time_s^2) +
  length_s +
  (1 | paint_id),
data = complete_data,
family = binomial,
control = glmerControl(optimizer = "bobyqa")
)
summary(mod_2)

```

```
# MOD3
```

```

mod_3 <- glmer(
  present ~ AirTemp_s + WindSpeed_s + cloud_s + Radiation_s +
    sex * date_s +
    time_s + I(time_s^2) +
    length_s +
    (1 | paint_id),
data = complete_data,
family = binomial,
control = glmerControl(optimizer = "bobyqa")
)
summary(mod_3)

```

```
# MOD4
```

```

mod_4 <- glmer(
  present ~ AirTemp_s + WindSpeed_s + cloud_s + Radiation_s +
    sex * (date_s + I(date_s^2)) +
    time_s +
    length_s +

```

```

    (1 | paint_id),
  data = complete_data,
  family = binomial,
  control = glmerControl(optimizer = "bobyqa")
)
summary(mod_4)

```

```
# MOD5
```

```

mod_5 <- glmer(
  present ~ AirTemp_s + cloud_s + Radiation_s +
    sex * date_s +
    time_s + I(time_s^2) +
    length_s +
    (1 | paint_id),
  data = complete_data,
  family = binomial,
  control = glmerControl(optimizer = "bobyqa")
)
summary(mod_5)

```

```
# MOD6
```

```

mod_6 <- glmer(
  present ~ AirTemp_s + I(AirTemp_s^2) + WindSpeed_s + cloud_s + Radiation_s +
    sex * date_s +
    time_s + I(time_s^2) +
    length_s +
    (1 | paint_id),
  data = complete_data,
  family = binomial,
  control = glmerControl(optimizer = "bobyqa")
)

```

```

)
summary(mod_6)

# MOD7
mod_7 <- glmer(
  present ~ AirTemp_s + I(AirTemp_s^2) + WindSpeed_s + cloud_s +
    sex * date_s +
    time_s + I(time_s^2) +
    length_s +
    (1 | paint_id),
  data = complete_data,
  family = binomial,
  control = glmerControl(optimizer = "bobyqa")
)
summary(mod_7)

# MOD8
mod_8 <- glmer(
  present ~ AirTemp_s + I(AirTemp_s^2) + cloud_s + Radiation_s +
    sex * date_s +
    time_s + I(time_s^2) +
    length_s +
    (1 | paint_id),
  data = complete_data,
  family = binomial,
  control = glmerControl(optimizer = "bobyqa")
)
summary(mod_8)

# MOD9

```

```

mod_9 <- glmer(
  present ~ AirTemp_s + I(AirTemp_s^2) + WindSpeed_s + cloud_s + Radiation_s +
  I(Radiation_s^2) +
    sex * date_s +
    time_s + I(time_s^2) +
    length_s +
    (1 | paint_id),
  data = complete_data,
  family = binomial,
  control = glmerControl(optimizer = "bobyqa")
)
summary(mod_9)

```

```
# MOD10
```

```

mod_10 <- glmer(
  present ~ AirTemp_s + I(AirTemp_s^2) + WindSpeed_s + cloud_s + Radiation_s +
    sex * date_s +
    time_s + I(time_s^2) +
    sex * length_s +
    (1 | paint_id),
  data = complete_data,
  family = binomial,
  control = glmerControl(optimizer = "bobyqa")
)
summary(mod_10)

```

```
# MOD11
```

```

mod_11 <- glmer(
  present ~ AirTemp_s + I(AirTemp_s^2) + WindSpeed_s + cloud_s +
    sex * date_s +

```

```

    time_s + I(time_s^2) +
    (1 | paint_id),
data = complete_data,
family = binomial,
control = glmerControl(optimizer = "bobyqa")
)
summary(mod_11)

```

```
# MOD 12
```

```

mod_12 <- glmer(
  present ~ WindSpeed_s + cloud_s +
    sex * date_s +
    time_s + I(time_s^2) +
    length_s +
    (1 | paint_id),
data = complete_data,
family = binomial,
control = glmerControl(optimizer = "bobyqa")
)
summary(mod_12)

```

```
#MOD 13
```

```

mod_13 <- glmer(
  present ~ AirTemp_s + I(AirTemp_s^2) + WindSpeed_s + cloud_s +
    sex * date_s +
    length_s +
    (1 | paint_id),
data = complete_data,
family = binomial,
control = glmerControl(optimizer = "bobyqa")
)

```

```

)
summary(mod_13)

#MOD14
mod_14 <- glmer(
  present ~ WindSpeed_s + cloud_s + Radiation_s + I(Radiation_s^2) +
    sex * date_s +
    time_s + I(time_s^2) +
    length_s +
    (1 | paint_id),
  data = complete_data,
  family = binomial,
  control = glmerControl(optimizer = "bobyqa")
)
summary(mod_14)

# -----
# COMPARING MODELS
# -----

AIC(mod_full, mod_1, mod_2, mod_3, mod_4, mod_5, mod_6, mod_7, mod_8, mod_9, mod_10,
mod_12, mod_13, mod_14)

AIC(mod_11)

# -----
# CHECKING MODEL FIT
# -----

# CHECKING FOR COLLINEARILY
check_collinearity(mod_7)

```

```

check_collinearity(mod_9)
check_collinearity(mod_6)

# MOD7
mod_7_glm <- glm(
  present ~ AirTemp_s + I(AirTemp_s^2) + WindSpeed_s + cloud_s +
    sex * date_s +
    time_s + I(time_s^2) +
    length_s,
  data = complete_data,
  family = binomial
)
vif(mod_7_glm, type="predictor")

# MOD 9
mod_9_glm <- glm(
  present ~ AirTemp_s + I(AirTemp_s^2) + WindSpeed_s + cloud_s + Radiation_s +
  I(Radiation_s^2) +
    sex * date_s +
    time_s + I(time_s^2) +
    length_s,
  data = complete_data,
  family = binomial
)
vif(mod_9_glm, type="predictor")

sim_mod_9 <- simulateResiduals(mod_9)
plot(sim_mod_9)
sim_mod_7 <- simulateResiduals(mod_7)
plot(sim_mod_7)

```

```
#DHARMA TESTS
```

```
# Simulate residuals
```

```
res_7 <- simulateResiduals(  
  fittedModel = mod_7,  
  n = 1000  
)
```

```
# Basic diagnostic plots
```

```
plot(res_7)
```

```
# Test for uniformity (overall model fit)
```

```
testUniformity(res_7)
```

```
# Test for dispersion
```

```
testDispersion(res_7)
```

```
# Test for zero-inflation
```

```
testZeroInflation(res_7)
```

```
# _____
```

```
# SUMMARY STATS FROM MODEL 7
```

```
# _____
```

```
# CALCULATING PEAKS IN TEMP AND TIME
```

```
coef_mod7 <- fixef(mod_7)
```

```
coef_mod7
```

```
# Air temperature peak
```

```

peak_airtemp_s <- -coef_mod7["AirTemp_s"] / (2 * coef_mod7["I(AirTemp_s^2)"])
peak_airtemp_s

# Time peak
peak_time_s <- -coef_mod7["time_s"] / (2 * coef_mod7["I(time_s^2)"])
peak_time_s

# Replacing with actual mean and SD
mean_airtemp <- mean(complete_data$AirTemp_Avg)
sd_airtemp <- sd(complete_data$AirTemp_Avg)
mean_time <- mean(complete_data$time)
sd_time <- sd(complete_data$time)

# Converting to original scale
peak_airtemp <- peak_airtemp_s * sd_airtemp + mean_airtemp
peak_time <- peak_time_s * sd_time + mean_time
peak_airtemp
peak_time

# CHECKING RANGE OF ENVIRONMENTAL AND BIOLOGICAL PREDICTORS
range(complete_data$AirTemp_Avg, na.rm = TRUE)
range(complete_data$WindSpeed_Avg_ms_2m, na.rm = TRUE)
range(complete_data$cloud, na.rm = TRUE)
range(complete_data$length, na.rm = TRUE)
range(complete_data$NetRadiation_Avg, na.rm = TRUE)

# OTHER SUMMARY STATS
env_summary <- complete_data %>%
  summarise(
    across(

```

```

.cols = c(
  AirTemp_Avg,
  WindSpeed_Avg_ms_2m,
  cloud,
  length,
  NetRadiation_Avg
),
.fns = list(
  Mean = ~mean(.x, na.rm = TRUE),
  SD   = ~sd(.x, na.rm = TRUE),
  Min  = ~min(.x, na.rm = TRUE),
  Max  = ~max(.x, na.rm = TRUE),
  n    = ~sum(!is.na(.x))
),
.names = "{.col}_{.fn}"
)
) %>%
pivot_longer(
  everything(),
  names_to = c("Variable", "Statistic"),
  names_sep = "_(?=[^_]+$)"
) %>%
pivot_wider(
  names_from = Statistic,
  values_from = value
)
env_summary
as.data.frame(env_summary)

```

#

```

# PLOTTING MODEL RESULTS USING MOD7

# -----

# MODEL PREDICTED DATE
pred_date <- ggpredict(mod_7, terms = c("date_s [all]", "sex"))
mean_date <- mean(as.numeric(complete_data$date), na.rm = TRUE)
sd_date <- sd(as.numeric(complete_data$date), na.rm = TRUE)
pred_date$date <- as.Date(pred_date$x * sd_date + mean_date, origin = "1970-01-01")
all_months <- seq(min(pred_date$date), max(pred_date$date), by = "1 month")
months_to_show <- all_months[month(all_months) %in% c(1:9, 11, 12)]
ggplot() +
  geom_jitter(
    data = complete_data,
    aes(x = date, y = present, color = sex),
    width = 4, height = 0.05,
    alpha = 0.08, size = 0.6
  ) +
  geom_line(
    data = pred_date,
    aes(x = date, y = predicted, color = group),
    size = 1.3
  ) +
  geom_ribbon(
    data = pred_date,
    aes(x = date, ymin = conf.low, ymax = conf.high, fill = group),
    alpha = 0.2,
    color = NA
  ) +
  labs(
    x = "Date",

```

```

    y = "Predicted Probability of Basking",
    color = "Sex",
    fill = "Sex",
  ) +
  scale_color_manual(values = c(
    "M" = "#0072B2",
    "F" = "#D55E00"
  )) +

  scale_fill_manual(values = c(
    "M" = "#0072B2",
    "F" = "#D55E00"
  )) +
  scale_x_date(
    breaks = months_to_show,
    date_labels = "%b"
  ) +
  theme_bw() +
  theme(
    legend.position = "top",
    axis.title.x = element_text(size = 20, margin = margin(t = 15)),
    axis.title.y = element_text(size = 20, margin = margin(r = 15)),
    axis.text = element_text(size = 18),
    legend.title = element_text(size = 18),
    legend.text = element_text(size = 18)
  )

# MODEL PREDICTED TEMP
pred_temp <- ggpredict(mod_7, terms = "AirTemp_s [all]")
mean_temp <- mean(complete_data$AirTemp_Avg, na.rm = TRUE)

```

```

sd_temp <- sd(complete_data$AirTemp_Avg, na.rm = TRUE)
pred_temp$AirTemp_Avg <- pred_temp$x * sd_temp + mean_temp
ggplot() +
  geom_jitter(data = complete_data, aes(x = AirTemp_Avg, y = present),
             width = 1, height = 0.05, alpha = 0.1, size = 0.6, color = "#228B22") +
  geom_line(data = pred_temp, aes(x = AirTemp_Avg, y = predicted),
           color = "#228B22", size = 1.3) +
  geom_ribbon(data = pred_temp, aes(x = AirTemp_Avg, ymin = conf.low, ymax =
conf.high),
           alpha = 0.2, fill = "#228B22", color = NA) +
  theme_bw() +
  labs(x = "Air Temperature (°C)", y = "Predicted Probability of Basking") +
  theme_bw() +
  theme(
    legend.position = "top",
    axis.title.x = element_text(size = 20, margin = margin(t = 15)),
    axis.title.y = element_text(size = 20, margin = margin(r = 15)),
    axis.text = element_text(size = 18),
    legend.title = element_text(size = 18),
    legend.text = element_text(size = 18)
  )

# MODEL PREDICTED WIND
pred_wind <- ggpredict(mod_7, terms = "WindSpeed_s [all]")
mean_wind <- mean(complete_data$WindSpeed_Avg_ms_2m, na.rm = TRUE)
sd_wind <- sd(complete_data$WindSpeed_Avg_ms_2m, na.rm = TRUE)
pred_wind$WindSpeed <- pred_wind$x * sd_wind + mean_wind
ggplot(pred_wind, aes(x = WindSpeed, y = predicted)) +
  geom_line(size = 1.2, color = "#228B22") +
  geom_ribbon(aes(ymin = conf.low, ymax = conf.high), alpha = 0.2, fill = "#228B22",
color = NA) +

```

```

theme_bw() +
labs(
  x = "Wind Speed (m/s)",
  y = "Predicted Probability of Basking",
) +
theme(
  legend.position = "none",
  axis.title.x = element_text(size = 16, margin = margin(t = 15)),
  axis.title.y = element_text(size = 16, margin = margin(r = 15)),
  axis.text = element_text(size = 14)
)
ggplot() +
  geom_jitter(data = complete_data, aes(x = WindSpeed_Avg_ms_2m, y = present),
    width = 0.05, height = 0.05, alpha = 0.08, size = 0.6, color =
"#228B22") +
  geom_line(data = pred_wind, aes(x = WindSpeed, y = predicted),
    color = "#228B22", size = 1.3) +
  geom_ribbon(data = pred_wind, aes(x = WindSpeed, ymin = conf.low, ymax =
conf.high),
    alpha = 0.2, fill = "#228B22", color = NA) +
  theme_bw() +
  labs(x = "Wind Speed (m/s)", y = "Predicted Probability of Basking") +
  theme_bw() +
  theme(
    legend.position = "top",
    axis.title.x = element_text(size = 20, margin = margin(t = 15)),
    axis.title.y = element_text(size = 20, margin = margin(r = 15)),
    axis.text = element_text(size = 18),
    legend.title = element_text(size = 18),
    legend.text = element_text(size = 18)
  )

```

```

# MODEL PREDICTED CLOUD
pred_cloud <- ggpredict(mod_7, terms = "cloud_s [all]")
mean_cloud <- mean(complete_data$cloud, na.rm = TRUE)
sd_cloud <- sd(complete_data$cloud, na.rm = TRUE)
pred_cloud$Cloud <- pred_cloud$x * sd_cloud + mean_cloud
ggplot(pred_cloud, aes(x = Cloud, y = predicted)) +
  geom_line(size = 1.2, color = "#228B22") +
  geom_ribbon(aes(ymin = conf.low, ymax = conf.high), alpha = 0.2, fill = "#228B22",
color = NA) +
  theme_bw() +
  labs(
    x = "Cloud Cover (%)",
    y = "Predicted Probability of Basking",
  ) +
  theme(
    legend.position = "none",
    axis.title.x = element_text(size = 16, margin = margin(t = 15)),
    axis.title.y = element_text(size = 16, margin = margin(r = 15)),
    axis.text = element_text(size = 14)
  )
ggplot() +
  geom_jitter(data = complete_data,
    aes(x = cloud, y = present),
    width = 5, height = 0.05,
    alpha = 0.08, size = 0.6, color = "#228B22") +
  geom_line(data = pred_cloud, aes(x = Cloud, y = predicted),
    size = 1.3, color = "#228B22") +
  geom_ribbon(data = pred_cloud, aes(x = Cloud, ymin = conf.low, ymax = conf.high),
    alpha = 0.2, fill = "#228B22", color = NA) +

```

```

theme_bw() +
labs(
  x = "Cloud Cover (%)",
  y = "Predicted Probability of Basking",
) +
theme_bw() +
theme(
  legend.position = "top",
  axis.title.x = element_text(size = 20, margin = margin(t = 15)),
  axis.title.y = element_text(size = 20, margin = margin(r = 15)),
  axis.text = element_text(size = 18),
  legend.title = element_text(size = 18),
  legend.text = element_text(size = 18)
)

# MODEL PREDICTED TIME OF DAY
pred_time <- ggpredict(mod_7, terms = "time_s [all]")
mean_time <- mean(complete_data$time_dec, na.rm = TRUE)
sd_time <- sd(complete_data$time_dec, na.rm = TRUE)
pred_time$TimeHours <- pred_time$x * sd_time + mean_time
ggplot() +
  geom_jitter(
    data = complete_data,
    aes(x = time_dec, y = present),
    width = 0.2, height = 0.05, alpha = 0.1, size = 0.6, color = "#228B22"
  ) +
  geom_line(
    data = pred_time,
    aes(x = TimeHours, y = predicted),
    color = "#228B22", size = 1.3
  )

```

```

) +
geom_ribbon(
  data = pred_time,
  aes(x = TimeHours, ymin = conf.low, ymax = conf.high),
  alpha = 0.2, fill = "#228B22", color = NA
) +
scale_x_continuous(
  breaks = seq(6, 20, by = 1),
  labels = sprintf("%02d:00", seq(6, 20, by = 1))
) +
scale_y_continuous(
  breaks = seq(0, 1, by = 0.25)
) +
labs(x = "Time of Day", y = "Predicted Probability of Basking") +
theme_bw() +
theme(
  legend.position = "top",
  axis.title.x = element_text(size = 20, margin = margin(t = 15)),
  axis.title.y = element_text(size = 20, margin = margin(r = 15)),
  axis.text.x = element_text(size = 16, angle = 45, hjust = 1),
  axis.text.y = element_text(size = 18),
  legend.title = element_text(size = 18),
  legend.text = element_text(size = 18)
)

```

Chapter 2

A standardized drone-based protocol for monitoring freshwater turtles

Context

This chapter is a slightly modified version of the manuscript published in *MethodsX*:

Dobie, L., & Blouin-Demers, G. (2026). A standardized drone-based protocol for monitoring freshwater turtles. *MethodsX*, 16, 103791. <https://doi.org/10.1016/j.mex.2026.103791>

Abstract

Basking is an essential thermoregulatory behaviour for freshwater turtles, but accurately monitoring basking occurrence is challenging due to the limitations of traditional survey methods. Traditional methods afford low detection probabilities, are often disruptive, and lack precision due to infrequent sampling. To address these limitations, I developed a high-frequency drone-based monitoring method that records repeated, minimally invasive video surveys of individually marked painted turtles (*Chrysemys picta*). The method involves three main elements:

- Programming an autonomous drone route at fixed, short intervals covering the entire study area
- Recording drone videos to document turtles basking without altering their behaviour
- Manually reviewing video footage to quantify basking occurrence

I implemented this method at a wetland on the Kenauk property in Montebello, Québec, Canada. I monitored 62 painted turtles from June to September 2025. A DJI Mini 4 Pro drone performed an autonomous survey of the wetland every 20 min, producing 423 surveys and 127 h of video over 13 days. Flight initiation distance trials confirmed that surveys conducted at an altitude of 15 m did not initiate escape responses in painted turtles. Drone surveys allow for quantification of individual basking behaviour with unprecedented frequency and without being invasive.

Background

Basking is an essential thermoregulatory behaviour in most reptiles, including freshwater turtles, that facilitates physiological processes and, hence, affects fitness (Abram et al., 2017; Angilletta et al., 2002; Huey, 1982). Accurately estimating basking occurrence in freshwater turtles, however, is challenging. Traditional methods used to monitor basking behaviour include shore-based or canoe surveys, but both methods have shortcomings. For example, in shore-based observations, turtles can be obstructed by habitat features like emergent vegetation (Biserkov & Lukanov, 2017; Bogolin et al., 2021), and canoe surveys can disturb turtles, thus artificially shortening basking duration (Fenech, 2022). Wildlife cameras, on the other hand, require prior identification of basking sites for proper camera placement and have a restricted field of view, allowing some turtles to avoid detection. Basking observations using traditional survey methods could also lack precision due to the surveillance process taking longer and, therefore, occurring relatively infrequently (e.g., every hour; (Krawchuk & Brooks, 1998; Lefevre & Brooks, 1995)).

Uncrewed Aerial Vehicles (UAVs), or drones, are increasingly used in ecological research, providing a safe, efficient, and minimally disruptive method for monitoring wildlife (Chabot & Bird, 2016; Floreano & Wood, 2015; Linchant et al., 2015). Despite their growing use in wildlife research, drone-based methods for studying freshwater turtles remain limited and have not yet been used to identify individual turtles reliably or to quantify basking behaviour (Biserkov & Lukanov, 2017; Bogolin et al., 2021; Daniels, 2018; Escobar et al., 2021; Fagundes et al., 2022). This methodological gap restricts the ability to study basking behaviour from an aerial perspective and at high temporal frequencies. To address these limitations, I developed a drone-based method for repeatedly surveying freshwater turtles at a high temporal frequency to obtain individual-level records of basking occurrence.

Method Details

Project Overview

Fieldwork took place at a wetland on the Kenauk property in Montebello, Québec, Canada (Figure 2-1). I trapped 62 painted turtles with hoop nets and marked them with unique alphanumeric codes painted on their carapace (Figure 2-2). After the turtles were marked, I performed drone surveys to monitor their basking behaviour from early June until late September 2025 (13 days). I programmed an autonomous route on the DJI Mini 4 Pro to run every 20 min throughout the day, capturing nadir-oriented RGB video used to detect and identify individual turtles in the wetland (Supplementary Information Figure S2-1). Each survey generated continuous video footage that I later reviewed to determine which individuals were basking when. The methodological details presented here follow a standardized reporting protocol for drone-based wildlife research (Barnas et al., 2020).

Drone System and Operation Details

Platform Specifications. I used two identical DJI Mini 4 Pro drones (Figure 2-3), each with its own DJI RC Pro 2 controller. These four-rotor quadcopters were equipped with the DJI Intelligent Flight Battery Plus. Each drone weighed 292 g with the battery installed and measured $148 \times 94 \times 64$ mm when folded without propellers and $298 \times 373 \times 101$ mm when unfolded with propellers. The maximum flight time reported by DJI under controlled conditions is 45 min. In the field with light winds, however, with obstacle avoidance enabled, and landing at ~25% battery, the maximum safe flight duration was ~30 min. DJI reports a maximum hovering time of 39 min under controlled conditions, but I did not measure this in the field. The drones have a maximum wind resistance of 10 m/s and no rain tolerance.

The Intelligent Flight Battery Plus is a 3850 mAh lithium-ion battery and requires ~78 min to charge fully using a 30 W USB-C charger and DJI Two-Way Charging Hub. A high-capacity charging station powered by a Bluetti AC180P 1440 Wh Portable Power Station supplied three DJI Mini 4 Pro Two-Way Charging Hubs, each capable of charging three batteries simultaneously, for a total of nine batteries (Figure 2-4). The station was fully charged before fieldwork and provided sufficient power to maintain a fully charged battery for all the surveys while also powering the two drone remote controllers, a laptop computer, and a smartphone throughout the day.

Takeoff and Retrieval. All flights originated from a designated “home base” located ~20 m from the shoreline, approximately equidistant from the start and end points of the autonomous route (see section below). The area was flat and in an opening of the canopy with clear visibility that allowed us to maintain a visual line-of-sight with the drone throughout the flight. I set up a small base area with a shaded workspace and the charging station (Figure 2-5). No specialized takeoff equipment was required. To prevent rotor damage from vegetation, I used a plastic storage bin lid as a takeoff and landing platform. After each flight, I returned the drones manually to the home base to land and charge the batteries, and to download video files occasionally from the microSD cards onto a hard drive.

Flight Planning and Method of Operation. I preprogrammed an autonomous flight route using WaypointMap, an online tool for waypoint-based photogrammetry and mapping (Figure 2-6). The area of the wetland being surveyed was ~44,345 m². I programmed and visualized the autonomous flight on a PC to optimize wetland coverage and minimize survey duration. The .KMZ file generated by WaypointMap was installed on the DJI RC Pro 2 controllers via a placeholder route created in DJI Fly. At the field site, I tested the programmed

route and made minor adjustments to avoid the drone approaching trees too closely. This required several rounds of iterative testing: running the route on site, returning to a location with internet access to modify the route on a PC, downloading the updated file onto the controller, and retesting in the field. I also tried using DJI Fly for flight programming, but it was unsuitable in this situation because routes could not be edited on a PC. DJI Fly's requirement to program routes during flight prevented the precise waypoint placement that was needed to cover the entire wetland without gaps or excessive overlap.

I programmed the flight with an altitude of 15 m, the maximum altitude that I found to allow consistent identification of individual turtles from nadir video footage (Supplementary Information Figure S2-1). I set the drone speed to 2.5 m/s and the gimbal angle to -90° for direct overhead imaging. The video started recording at the beginning of the route and stopped at the end of the route. The autonomous flight lasted approximately 18 min. We were typically two people operating the system: the pilot would operate the drone, take off and land the drone, and initiate the autonomous route, and the assistant would manage the charging station and retrieve the drones once they landed.

Payload and Data Collection

Camera Description and Data Collection Methods. I captured all video recordings using the integrated RGB camera of the DJI Mini 4 Pro. The camera has a 1/1.3-inch type CMOS sensor with 48 MP effective pixels and a fixed lens with a field of view of 82.1° and a 24 mm equivalent focal length. The aperture is $f/1.7$, and the focus range is 1 m to infinity. I recorded video at 4 K resolution (3840×2160) at 60 frames per second using H.264/H.265 encoding. I set EV to -3.0 , and all other settings (white balance, ISO, shutter speed) were left on auto. I stored videos on microSD cards in the drones (Lexar V30 1066x A2 128 GB and

Kingston CanvasGo Plus V30 A2 256 GB). Each sampling day produced approximately 600 GB of video footage. I downloaded video files periodically throughout the day to two redundant external drives: a SanDisk Extreme Portable solid-state drive and a Western Digital My Passport Portable hard-disk drive, ensuring two separate copies of all data to minimize the risk of loss.

Field Operation Details

I conducted drone surveys on 13 days between 3 June and 26 September 2025. Each sampling day was designed to generate an 18-minute survey every 20 min from 7:20 to 18:40, producing up to 35 surveys per day. Some surveys were unsuccessful due to weather conditions (e.g., heavy wind or rain) or technical issues (e.g., the autonomous route failing to load correctly, obstacle-avoidance halting the mission, or microSD cards reaching capacity). Some surveys were also skipped intentionally later in the season, during the evening when turtles were no longer basking. After accounting for unsuccessful or skipped surveys, I completed 423 surveys across the 13 sampling days, totalling approximately 7614 min (127 h) of usable drone video footage (Table 2-1).

Two identical DJI Mini 4 Pro drones alternated surveys throughout the day to prevent motor fatigue and overheating, each equipped with its own DJI RC Pro 2 controller. The drone that was not flying and the spare batteries were kept in a shaded area to cool down between flights. Two minutes prior to each survey, I flew the drone manually from the home base to the start point of the autonomous route. I then initiated the autonomous flight through the DJI Fly application on the drone controller, and the drone completed the route. Upon completion, I returned the drone to the home base manually to land it, swap batteries, and recharge. I repeated this procedure for every survey throughout the day. Obstacle avoidance remained enabled for all surveys, and flight altitude was consistently 15 m above the ground. Air temperature during

surveys ranged from 11 to 31 °C, and wind speeds measured 2 m above the ground ranged from 0 to 1 m/s.

Data Analysis

I did not perform post-processing on the raw video data. All analyses were conducted directly from the nadir-oriented RGC videos produced by the DJI Mini 4 Pro. No photogrammetric processing or automated detection algorithms were applied. The video files retained their original spatial resolution throughout analysis, and the spatial resolution of the videos analyzed was identical to that of the raw 4 K imagery originally recorded.

During post-survey analysis, I watched each video at 1x speed and paused whenever a turtle appeared in the frame. This allowed me to zoom in and identify individual turtles based on their unique carapace paint markings (Figure 2-7). A turtle was considered to be basking when it was stationary and at least part of its body was out of the water (Bulté & Blouin-Demers, 2010; Chessman, 2024). Turtles could sometimes be seen swimming in the drone footage, but only basking turtle observations were recorded.

Permits, Regulations, Training, and Logistics

Drone operations were conducted by a pilot (Lauren Dobie) holding a Small Remotely Piloted Aircraft Basic Operations Certificate issued by Transport Canada (PC2311825878). Research was conducted on the private property of Kenauk with the permission of the Kenauk Institute.

Method Validation

Drone Disturbance and Flight Initiation Distance

To validate that our drone survey method did not disturb painted turtles or alter their behaviour, I assessed their flight initiation distance (FID). FID is the distance between an approaching threat and an animal at which the animal initiates a behavioural escape response (Blumstein, 2003; Cooper, 2008; Ydenberg & Dill, 1986). In this case, the drone acted as the perceived threat and the escape response was defined as the turtle leaving the basking site and entering the water. The goal was to identify a survey altitude above the FID to ensure that I did not alter turtle behaviour during the drone surveys.

I conducted FID tests using the DJI Mini 4 Pro, the same platform used for all surveys. I flew the drone above the wetland at an altitude of >20 m until I located a basking turtle. Once a turtle was located, I hovered the drone directly above it at 20 m for 60 s. If the turtle did not flee, I reduced the altitude to 15 m, and the drone hovered for 60 s. This process was repeated at 10 m and finally at 5 m, hovering for 60 s at each altitude (Figure 2-8). If the turtle fled at any point, I recorded the drone altitude at the moment of fleeing as the FID and the test was terminated. A trial where the turtle that did not flee at any altitude was assigned an FID < 5 m. Tests were conducted between May and August, between 10:00 and 15:30.

I performed 50 FID tests. Of these, 34 tests were on marked turtles that I could identify, corresponding to 24 unique individuals, as some marked individuals were tested more than once, but on different days. The remaining 16 tests were on unmarked turtles. I observed turtles flee in only 4 of the 50 tests (8 %). All four of the escape responses occurred at 5 m, the lowest altitude tested. The four turtles that fled included one unmarked individual, two males, and one female,

and all were basking alone. Although all individuals that fled were basking alone, 31 of the 50 turtles tested were also basking alone, indicating that solitary basking was not a reliable predictor of escape behaviour. Because 46 of the 50 turtles did not flee at any tested altitude ≥ 5 m, I concluded that their FID was < 5 m. Because the highest observed FID was 5 m, and because the majority of turtles tolerated drone presence at even lower altitudes, our monitoring protocol using a survey altitude of 15 m did not initiate an escape response and did not reduce the number of basking turtles during drone surveys. I recommend that similar FID tests be conducted by researchers implementing drone-based turtle surveys, as species differences, environmental conditions, and the drone model used may influence FID and should be considered when selecting an appropriate survey altitude.

Limitations

While this drone-based method for surveying freshwater turtle basking behaviour was overall successful, there are some limitations. The DJI Mini 4 Pro is not rain-tolerant and can only withstand wind speeds up to 10 m/s. Because our design involved continuous surveys over ~ 12 -hour periods at 20-minute intervals, data collection was strongly dependent on stable weather conditions. Survey days had to be selected such that there would be no rain or high winds for almost the entire day, not just during a short sampling window. In regions with frequent storms, high winds, or rapid weather changes, the requirement of stable weather conditions could reduce the number of sampling days.

Under realistic field conditions, I identified a safe flight duration of ~ 30 min per fully charged battery. This was sufficient to survey a $\sim 44,345$ m² wetland on a single programmed route. Surveying much larger areas, however, would require battery swaps mid-route or multiple flight plans. This would demand more batteries, additional charging capacity in the portable

power source, and likely reduced sampling frequency if the survey duration exceeded the desired survey interval. Future technological improvements in battery capacity may partially reduce this constraint.

This drone-based survey method generates many hours of continuously recorded video, which is time-consuming to review manually. A single 18-minute survey could take up to one hour to review and extract the data when many turtles were present. Manual analysis also introduces the possibility of human error, as turtles may be missed or misidentified despite standardized reviewer training. Although occasional missed detections are unlikely to affect results meaningfully with such high sample sizes, automated detection and identification tools (e.g., machine learning) could substantially reduce processing time in future applications.

Finally, although the carapace paint markings were generally identifiable, some recordings were obscured by glare or motion blur, preventing the identification of certain individuals. In these cases, I logged a partial identification (e.g., known letter, but not number of the alphanumeric code) and revisited the identification during the next survey. The high temporal resolution (every 20 min) made retroactive correction feasible, as many turtles were still basking at the same location in the following survey, where they could be identified properly. If surveys were conducted at lower frequencies, however, or if the species of turtle being surveyed basked for shorter intervals, unidentifiable turtles could accumulate and reduce the precision of individual-level data.

Tables – Chapter 2

Table 2-1. Dates of all drone sampling days from a study of painted turtle basking behaviour at Kenauk, Montebello, Québec, Canada. The table includes all sampling days from early June to late September 2025 and the number of completed surveys for each sampling day.

Sampling day	Date	Number of completed surveys
1	3 June 2025	33
2	13 June 2025	35
3	16 June 2025	35
4	25 June 2025	34
5	2 July 2025	27
6	8 July 2025	30
7	22 July 2025	33
8	23 July 2025	34
9	28 July 2025	34
10	21 August 2025	34
11	27 August 2025	34
12	11 September 2025	31
13	26 September 2025	29

Figures – Chapter 2

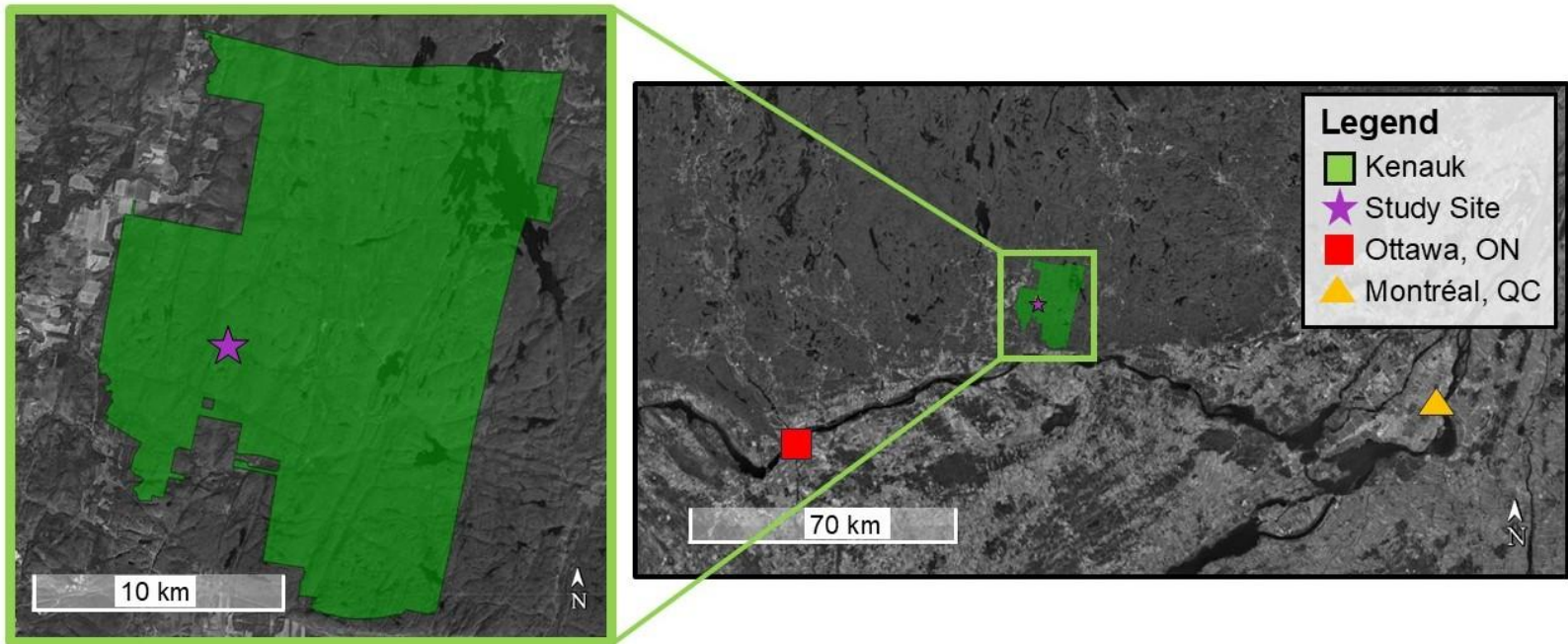


Figure 2-1. Kenauk property in Montebello, Québec, Canada, where the basking behaviour of painted turtles was studied in 2025.



Figure 2-2. A painted turtle marked with a unique alphanumeric code (F8) painted on its carapace for individual identification via drone footage in a study of basking behaviour at Kenauk, Montebello, Québec, Canada, in 2025.



Figure 2-3. DJI Mini 4 Pro drone used to study painted turtle basking behaviour at Kenauk, Montebello, Québec, Canada, in 2025.



Figure 2-4. Charging station used in a study of painted turtle basking behaviour at Kenauk, Montebello, Québec, Canada, in 2025. The charging station consists of a Bluetti Portable Power Station powering three individual DJI Two-Way Charging Hubs with 30 W USB-C chargers, each charging three DJI Intelligent Flight Battery Plus units, for a total of nine batteries.



Figure 2-5. Home base setup with a workspace and charging station used in a study of painted turtle basking behaviour at Kenauk, Montebello, Québec, Canada, in 2025. The open area where the drone took off and landed, as well as the wetland, are behind the camera.

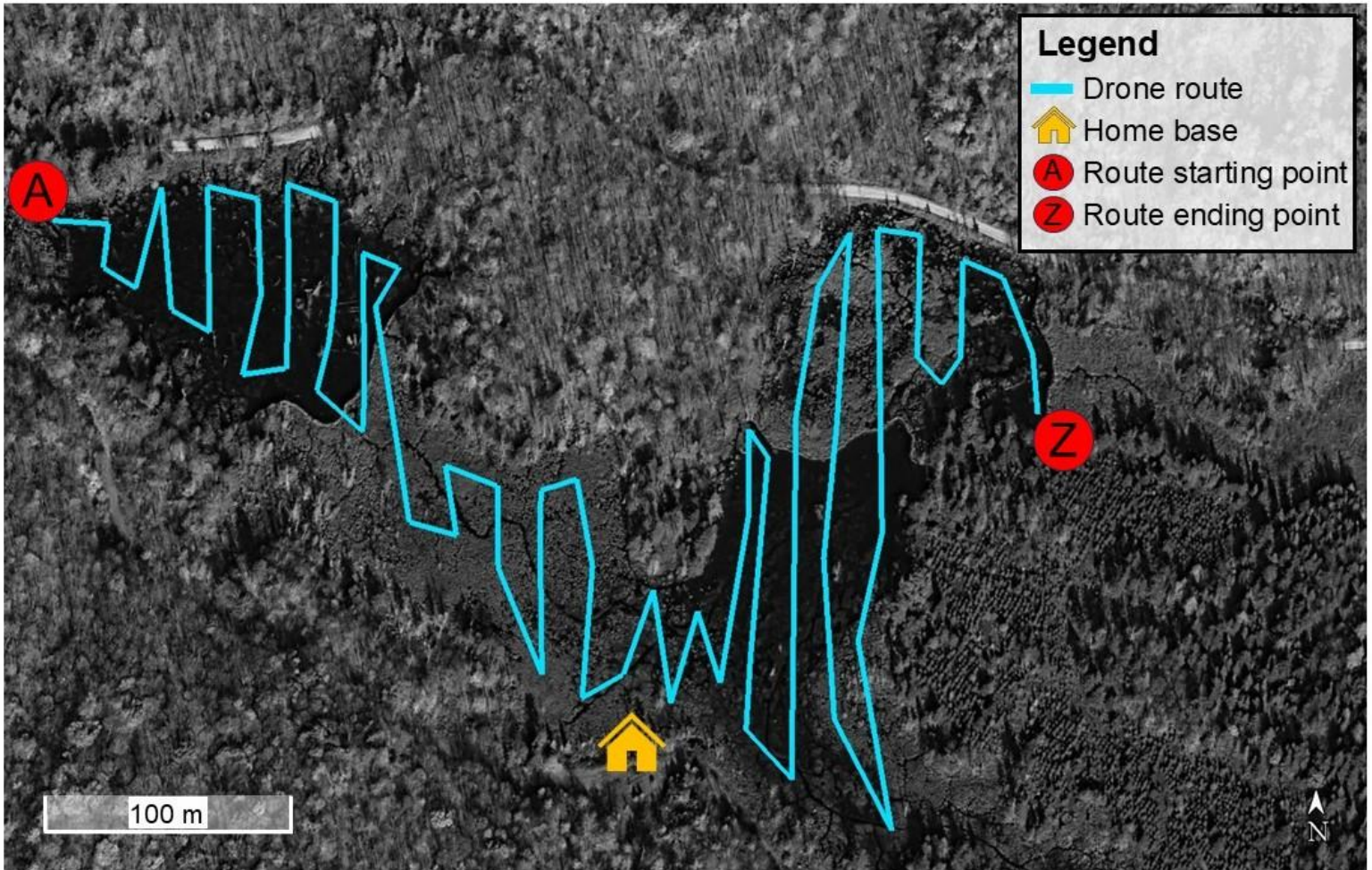


Figure 2-6. Autonomous drone route used in a study of painted turtle basking behaviour at Kenauk, Montebello, Québec, Canada, in 2025. The drone took off from the home base, started the route at point A, took a video along the drone route, stopped the route at point Z, and landed back at the home base.

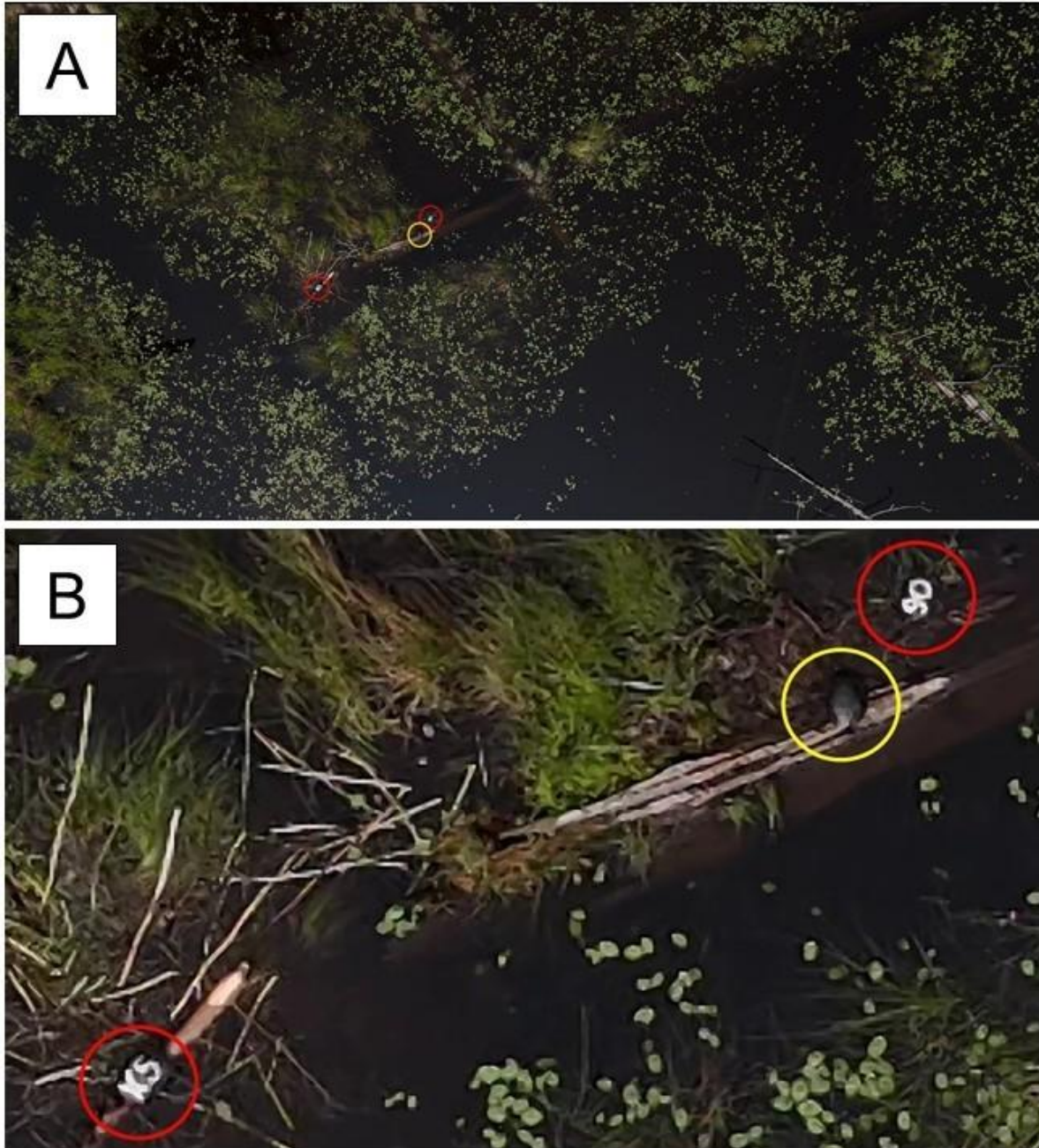


Figure 2-7. A Screenshot of the drone footage from a study of painted turtle basking behaviour at Kenauk, Montebello, Québec, Canada, in 2025. The screenshot shows three basking turtles: X5 and O6 circled in red, and an unmarked turtle circled in yellow. Image A is an unzoomed screenshot from the drone footage. Image B is the screenshot zoomed in, showing how the turtles can be identified in drone footage review.

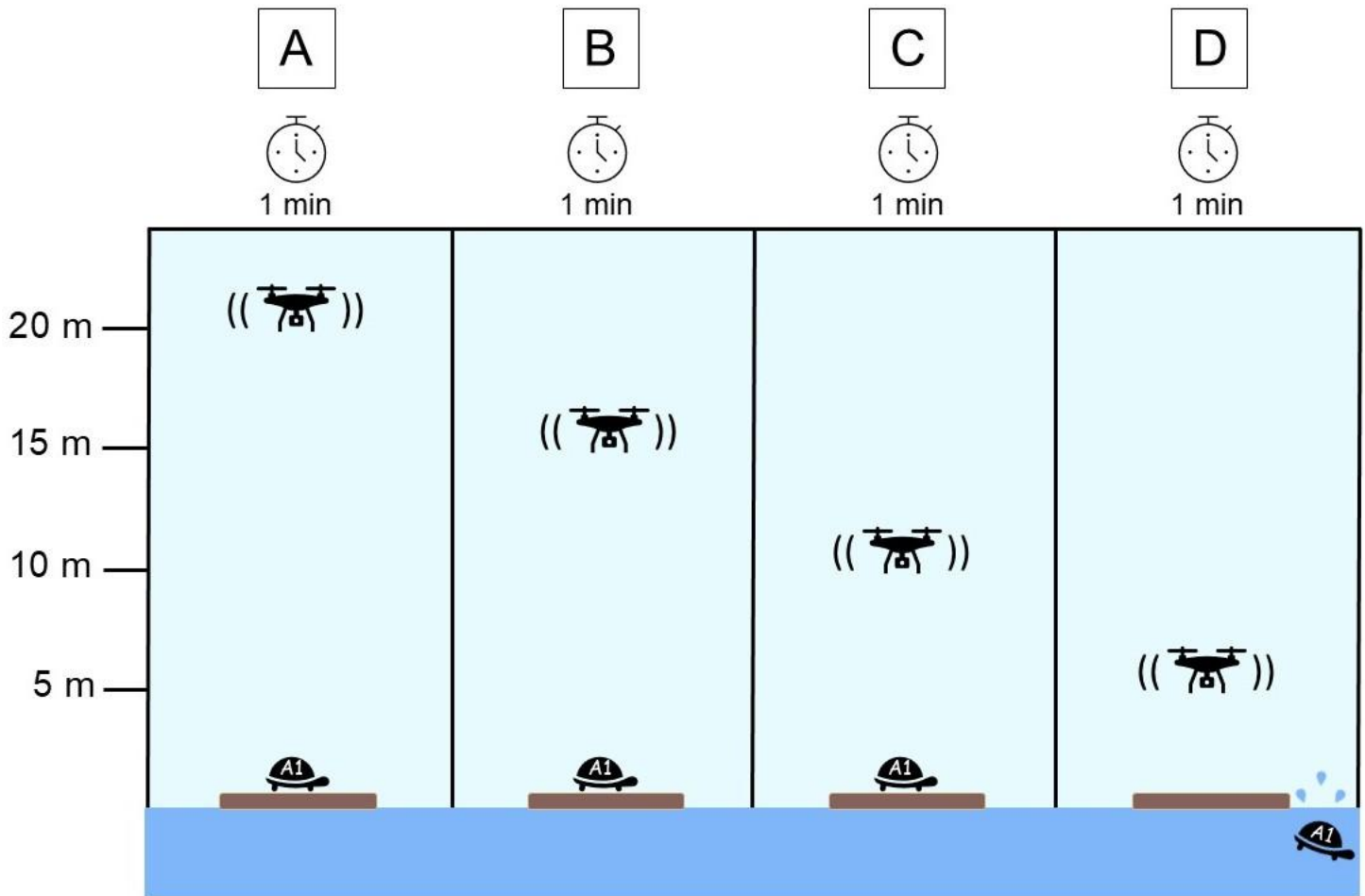


Figure 2-8. Diagram of the method used to determine flight initiation distance with a drone in a study of painted turtle basking behaviour at Kenauk, Montebello, Québec, Canada, in 2025. I hovered the drone over a turtle at an altitude of 20 m for one minute, then descended to an altitude of 15 m and hovered for one minute, followed by 10 m for one minute and 5 m for one minute. I noted at which altitude the turtle fled, if ever, and used these data to inform the altitude at which I would fly the drone to survey turtles without altering their behaviour.

A drone-based protocol for monitoring freshwater turtles

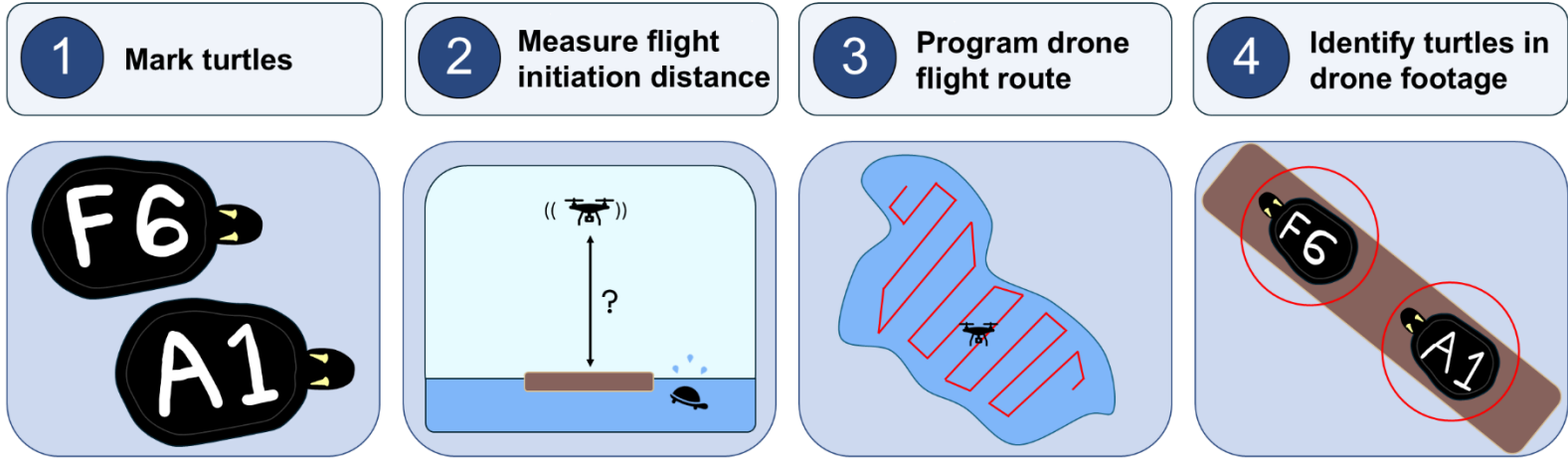


Figure S2-1. Graphical abstract for a drone-based protocol for monitoring freshwater turtles, describing the methodological steps in a study of painted turtle basking behaviour at Kenauk, Montebello, Québec, Canada, in 2025.

General Conclusion

I investigated basking behaviour in painted turtles and evaluated the use of drone-based surveys as a tool to survey freshwater turtles. My findings highlight the ecological drivers of basking behaviour and the importance of methodological approaches that allow it to be quantified accurately. This work demonstrates how integrating emerging technologies with ecological questions can improve our understanding of animal behaviour.

I show that basking behaviour varies across the active season between sexes, supporting the idea that it is influenced by changing energetic demands and environmental conditions. Higher basking probability in females early in the active season is consistent with the energetic requirements of reproduction following emergence from brumation. The absence of increased female basking later in the season, however, suggests that the relationship between basking and reproductive investment is not constant across time. These findings reinforce the idea that thermoregulatory behaviour reflects a balance between physiological needs and ecological constraints.

The drone-based monitoring approach developed here enabled repeated, minimally invasive observations of individually identifiable turtles across an entire wetland. This allowed for the detection of fine-scale temporal patterns that would likely be missed using traditional observation methods. Drone-based surveys offer a rapid and minimally invasive method for assessing turtle behaviour and habitat use, which could improve monitoring efficiency in future monitoring efforts. This work also demonstrated the need to evaluate potential disturbance when using drones in wildlife research. By assessing flight initiation distance, I showed that surveys conducted at appropriate altitudes did not elicit escape responses in painted turtles, supporting the use of drones as a non-invasive monitoring tool for this system.

Overall, this work shows that basking behaviour in painted turtles is impacted by a combination of physiological and environmental factors, and that drone-based monitoring is a valuable method for observing these patterns. By investigating an ecological question with a novel method, this work contributes to a more comprehensive understanding of freshwater turtle behaviour and highlights the benefits of integrating emerging technologies in ecological research and monitoring.

References

- Abram, P. K., Boivin, G., Moiroux, J., & Brodeur, J. (2017). Behavioural effects of temperature on ectothermic animals: Unifying thermal physiology and behavioural plasticity. *Biological Reviews*, 92(4), 1859–1876. <https://doi.org/10.1111/brv.12312>
- Acierno, M. J., Mitchell, M. A., Roundtree, M. K., & Zachariah, T. T. (2006). Effects of ultraviolet radiation on 25-hydroxyvitamin D3 synthesis in red-eared slider turtles (*Trachemys scripta elegans*). *American Journal of Veterinary Research*, 67(12), 2046–2049. <https://doi.org/10.2460/ajvr.67.12.2046>
- Angilletta, M. J., & Dunham, A. E. (2003). The temperature-size rule in ectotherms: Simple evolutionary explanations may not be general. *The American Naturalist*, 162(3), 332–342. <https://doi.org/10.1086/377187>
- Angilletta, M. J., Niewiarowski, P. H., & Navas, C. A. (2002). The evolution of thermal physiology in ectotherms. *Journal of Thermal Biology*, 27(4), 249–268. [https://doi.org/10.1016/S0306-4565\(01\)00094-8](https://doi.org/10.1016/S0306-4565(01)00094-8)
- Auge, A.-C., Blouin-Demers, G., & Murray, D. L. (2024). Differences in activity between reproductive and non-reproductive freshwater turtles during the nesting season. *Herpetology Notes*, 17, 153–159.
- Barnas, A. F., Chabot, D., Hodgson, A. J., Johnston, D. W., Bird, D. M., & Ellis-Felege, S. N. (2020). A standardized protocol for reporting methods when using drones for wildlife research. *Journal of Unmanned Vehicle Systems*, 8(2), 89–98. <https://doi.org/10.1139/juvs-2019-0011>
- Bates, D., M, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1), 1–48. <https://doi.org/10.18637/jss.v067.i01>

- Bayless, L. E. (1975). Population parameters for *Chrysemys picta* in a New York pond. *The American Midland Naturalist*, 93(1), 168–176. <https://doi.org/10.2307/2424115>
- Beaver, J. T., Baldwin, R. W., Messinger, M., Newbolt, C. H., Ditchkoff, S. S., & Silman, M. R. (2020). Evaluating the use of drones equipped with thermal sensors as an effective method for estimating wildlife. *Wildlife Society Bulletin*, 44(2), 434–443. <https://doi.org/10.1002/wsb.1090>
- Bennett, A. F. (1990). Thermal dependence of locomotor capacity. *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology*, 259(2), 253–258. <https://doi.org/10.1152/ajpregu.1990.259.2.R253>
- Bird, D. M., Petalas, C., Pace, P., & Elliott, K. H. (2024). Using drones to measure the status of cavity-nesting raptors. *Drone Systems and Applications*, 12, 1–7. <https://doi.org/10.1139/dsa-2023-0121>
- Biserkov, V. Y., & Lukanov, S. P. (2017). Unmanned aerial vehicles (UAVs) for surveying freshwater turtle populations: Methodology adjustment. *Acta Zoologica Bulgaria*, 161–163.
- Blumstein, D. T. (2003). Flight-initiation distance in birds is dependent on intruder starting distance. *The Journal of Wildlife Management*, 67(4), 852–857. <https://doi.org/10.2307/3802692>
- Bogolin, A. P., Davis, D. R., Kline, R. J., & Rahman, A. F. (2021). A drone-based survey for large, basking freshwater turtle species. *PLOS ONE*, 16(10), e0257720. <https://doi.org/10.1371/journal.pone.0257720>
- Boyer, D. R. (1965). Ecology of the basking habit in turtles. *Ecology*, 46(1–2), 99–118. <https://doi.org/10.2307/1935262>

- Bulté, G., & Blouin-Demers, G. (2010). Estimating the energetic significance of basking behaviour in a temperate-zone turtle. *Écoscience*, 17(4), 387–393.
<https://doi.org/10.2980/17-4-3377>
- Burnham, K. P., & Anderson, D. R. (Eds.). (2002). Information and likelihood theory: A basis for model selection and inference. In *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach* (pp. 49–97). Springer. https://doi.org/10.1007/978-0-387-22456-5_2
- Cagle, F. R. (1939). A system of marking turtles for future identification. *Copeia*, 1939(3), 170–173. <https://doi.org/10.2307/1436818>
- Cagle, F. R. (1950). The life history of the slider turtle, *Pseudemys scripta troostii*. *Ecological Monographs*, 20(1), 31–54. <https://doi.org/10.2307/1943522>
- Cagle, F. R. (1954). Observations on the life cycles of painted turtles (*Chrysemys picta*). *The American Midland Naturalist*, 52(1), 225–235. <https://doi.org/10.2307/2422060>
- Carrière, M.-A., Rollinson, N., Suley, A. N., & Brooks, R. J. (2008). Thermoregulation when the growing season is short: Sex-biased basking patterns in a northern population of painted turtles (*Chrysemys picta*). *Journal of Herpetology*, 42(1), 206–209.
- Chabot, D., & Bird, D. M. (2016). Wildlife research and management methods in the 21st century: Where do unmanned aircraft fit in? *Journal of Unmanned Vehicle Systems Virtual Issue*, 01(01), 137–155. <https://doi.org/10.1139/juvs-2015-0021@juvs-vi.2016.01.issue-1>
- Chessman, B. C. (2024). The conundrum of turtle and tortoise basking: A critical review. *Journal of Zoology*, 323(4), 263–283. <https://doi.org/10.1111/jzo.13175>

- Claussen, D. L., Lim, R., Kurz, M., & Wren, K. (2002). Effects of slope, substrate, and temperature on the locomotion of the ornate box turtle, *Terrapene ornata*. *Copeia*, 2002(2), 411–418.
- Clavijo-Baquet, S., & Magnone, L. (2017). Daily and seasonal basking behavior in two South American freshwater turtles, *Trachemys dorbigni* and *Phrynops hilarii*. *Chelonian Conservation and Biology*, 16(1), 62–69. <https://doi.org/10.2744/CCB-1201.1>
- Congdon, J. D., Dunham, A. E., & Tinkle, D. W. (1982). Energy budgets and life histories of reptiles. *Biology of the Reptilia*, 13, 233–271.
- Cooper, W. E. (2008). Strong artifactual effect of starting distance on flight initiation distance in the actively foraging lizard *Aspidoscelis exsanguis*. *Herpetologica*, 64(2), 200–206.
- COSEWIC. (2019). *Midland and Eastern Painted Turtle (Chrysemys picta marginata): COSEWIC assessment and status report 2018*. <https://www.canada.ca/en/environment-climate-change/services/species-risk-public-registry/cosewic-assessments-status-reports/midland-eastern-painted-turtle-2018.html>
- Cowles, R. B., & Bogert, C. M. (1944). Preliminary study of the thermal requirements of desert reptiles. *Bulletin of the AMNH*, 83(5).
- Crawford, K. M., Spotila, J. R., & Standora, E. A. (1983). Operative environmental temperatures and basking behavior of the turtle *Pseudemys scripta*. *Ecology*, 64(5), 989–999. <https://doi.org/10.2307/1937806>
- Dall'Antonia, L., Lebboroni, M., Benvenuti, S., & Chelazzi, G. (2001). Data loggers to monitor activity in wild freshwater turtles. *Ethology Ecology & Evolution*, 13(1), 81–88. <https://doi.org/10.1080/08927014.2001.9522789>

- Daniels, K. (2018). *Inferences about the conservation utility of using unmanned aerial vehicles to conduct rapid assessments for basking freshwater turtles* [Master's thesis, The University of Tennessee at Chattanooga]. <https://scholar.utc.edu/theses/565>
- Dobie, L., Bird, D. M., & Elliott, K. H. (2025). Acoustic monitoring with miniature drones shows reduced *Myotis* bat occurrence with altitude and drone movement. *Scientific Reports*, 15(1), 12307. <https://doi.org/10.1038/s41598-025-96255-5>
- Edwards, A. L., & Blouin-Demers, G. (2007). Thermoregulation as a function of thermal quality in a northern population of painted turtles, *Chrysemys picta*. *Canadian Journal of Zoology*, 85(4), 526–535. <https://doi.org/10.1139/Z07-037>
- Ernst, C. H. (1972). Temperature-activity relationship in the painted turtle, *Chrysemys picta*. *Copeia*, 1972(2), 217–222. <https://doi.org/10.2307/1442479>
- Ernst, C. H. (1982). Environmental temperatures and activities in wild spotted turtles, *Clemmys guttata*. *Journal of Herpetology*, 16(2), 112–120. <https://doi.org/10.2307/1563803>
- Escobar, J. E. C., Rollins, M., & Unger, S. (2021). Preliminary data on an affordable UAV system to survey for freshwater turtles: Advantages and disadvantages of low-cost drones. *Journal of Unmanned Vehicle Systems*, 9(1), 67–75. <https://doi.org/10.1139/juvs-2018-0037>
- Fagundes, C. K., Amend, M., & Ferrara, C. R. (2022). The use of unmanned aerial vehicles (UAVs) to study a freshwater turtle population in the Brazilian amazon. *Herpetological Conservation and Biology*, 17(1), 43–50.
- Fenech, M. (2022). *Why do freshwater turtles aggregate at basking sites?* [Master's thesis, University of Ottawa]. <https://ruor.uottawa.ca/items/7b522482-33fd-4142-9413-51afa42f27fb>

- Floreano, D., & Wood, R. J. (2015). Science, technology and the future of small autonomous drones. *Nature*, *521*(7553), 460–466. <https://doi.org/10.1038/nature14542>
- Ganzhorn, D., & Licht, P. (1983). Regulation of seasonal gonadal cycles by temperature in the painted turtle, *Chrysemys picta*. *Copeia*, *1983*(2), 347–358.
<https://doi.org/10.2307/1444377>
- Grant, B. W. (1990). Trade-offs in activity time and physiological performance for thermoregulating desert lizards, *Sceloporus merriami*. *Ecology*, *71*(6), 2323–2333.
<https://doi.org/10.2307/1938643>
- Grigg, G. C., Drane, C. R., & Courtice, G. P. (1979). Time constants of heating and cooling in the eastern water dragon, *Physignathus lesueruii* and some generalizations about heating and cooling in reptiles. *Journal of Thermal Biology*, *4*(1), 95–103.
[https://doi.org/10.1016/0306-4565\(79\)90052-4](https://doi.org/10.1016/0306-4565(79)90052-4)
- Grigg, G. C., & Seebacher, F. (1999). Field test of a paradigm: Hysteresis of heart rate in thermoregulation by a free-ranging lizard (*Pogona barbata*). *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *266*(1425), 1291–1297.
<https://doi.org/10.1098/rspb.1999.0777>
- Hammond, K. A., Spotila, J. R., & Standora, E. A. (1988). Basking behavior of the turtle *Pseudemys scripta*: Effects of digestive state, acclimation temperature, sex, and season. *Physiological Zoology*, *61*(1), 69–77. <https://doi.org/10.1086/physzool.61.1.30163738>
- Harnnuengnit, C., Khambuo, S., & Tep, P. (2024). Basking behavior in cold-blooded and warm-blooded reptiles: A systematic review of interspecies treatment. *2024 5th International Conference on Big Data Analytics and Practices (IBDAP)*, 12–17.
<https://doi.org/10.1109/IBDAP62940.2024.10689681>

- Hartig, F. (2026). *DHARMA: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models* [Computer software]. <https://github.com/florianhartig/dharma>
- Hill, S. K., & Vodopich, D. S. (2013). Habitat use and basking behavior of a freshwater turtle community along an urban gradient. *Chelonian Conservation and Biology*, *12*(2), 275–282. <https://doi.org/10.2744/CCB-0961.1>
- Hochscheid, S., Bentivegna, F., & Speakman, J. R. (2002). Regional blood flow in sea turtles: Implications for heat exchange in an aquatic ectotherm. *Physiological and Biochemical Zoology: Ecological and Evolutionary Approaches*, *75*(1), 66–76. <https://doi.org/10.1086/339050>
- Hodgson, A. J., Kelly, N., & Peel, D. (2023). Drone images afford more detections of marine wildlife than real-time observers during simultaneous large-scale surveys. *PeerJ*, *11*, e16186. <https://doi.org/10.7717/peerj.16186>
- Hodgson, J. C., Mott, R., Baylis, S. M., Pham, T. T., Wotherspoon, S., Kilpatrick, A. D., Raja Segaran, R., Reid, I., Terauds, A., & Koh, L. P. (2018). Drones count wildlife more accurately and precisely than humans. *Methods in Ecology and Evolution*, *9*(5), 1160–1167. <https://doi.org/10.1111/2041-210X.12974>
- House, W. J., Nall, I. M., & Thomas, R. B. (2010). Interpond movements of western painted turtles (*Chrysemys picta*) in east-central Kansas. *The Southwestern Naturalist*, *55*(3), 403–410. <https://doi.org/10.1894/GC-201.1>
- Huey, R. B. (1982). Temperature, physiology, and the ecology of reptiles. *Physiological Ecology*, 25–95.
- Huey, R. B., & Slatkin, M. (1976). Cost and benefits of lizard thermoregulation. *The Quarterly Review of Biology*, *51*(3), 363–384. <https://doi.org/10.1086/409470>

- Ibáñez, A., Marzal, A., González-Blázquez, M., López, P., & Martín, J. (2015). Basking activity is modulated by health state but is constrained by conspicuousness to predators in male Spanish terrapins. *Ethology*, *121*(4), 335–344. <https://doi.org/10.1111/eth.12342>
- Jain-Schlaepfer, S. M. R., Blouin-Demers, G., Cooke, S. J., & Bulté, G. (2017). Do boating and basking mix? The effect of basking disturbances by motorboats on the body temperature and energy budget of the northern map turtle. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *27*(2), 547–558. <https://doi.org/10.1002/aqc.2693>
- James, G., Witten, D., Hastie, T., & Tibshirani, R. (2013). Linear regression. In G. James, D. Witten, T. Hastie, & R. Tibshirani (Eds.), *An introduction to statistical learning: With applications in R* (pp. 59–126). Springer. https://doi.org/10.1007/978-1-4614-7138-7_3
- Kelaher, B. P., Peddemors, V. M., Hoade, B., Colefax, A. P., & Butcher, P. A. (2020). Comparison of sampling precision for nearshore marine wildlife using unmanned and manned aerial surveys. *Journal of Unmanned Vehicle Systems*, *8*(1), 30–43. <https://doi.org/10.1139/juvs-2018-0023>
- Kingsolver, J. G. (1983). Thermoregulation and flight in *Colias* butterflies: Elevational patterns and mechanistic limitations. *Ecology*, *64*(3), 534–545. <https://doi.org/10.2307/1939973>
- Krawchuk, M. A., & Brooks, R. J. (1998). Basking behavior as a measure of reproductive cost and energy allocation in the painted turtle, *Chrysemys picta*. *Herpetologica*, *54*(1), 112–121.
- Larocque, S. M., Colotelo, A. H., Cooke, S. J., Blouin-Demers, G., Haxton, T., & Smokorowski, K. E. (2012). Seasonal patterns in bycatch composition and mortality associated with a freshwater hoop net fishery. *Animal Conservation*, *15*(1), 53–60. <https://doi.org/10.1111/j.1469-1795.2011.00487.x>

- Larocque, S. M., Cooke, S. J., & Blouin-Demers, G. (2012). A breath of fresh air: Avoiding anoxia and mortality of freshwater turtles in fyke nets by the use of floats. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 22(2), 198–205.
<https://doi.org/10.1002/aqc.1247>
- Lefevre, K., & Brooks, R. J. (1995). Effects of sex and body size on basking behavior in a northern population of the painted turtle, *Chrysemys picta*. *Herpetologica*, 51(2), 217–224.
- Linchant, J., Lisein, J., Semeki, J., Lejeune, P., & Vermeulen, C. (2015). Are unmanned aircraft systems (UASs) the future of wildlife monitoring? A review of accomplishments and challenges. *Mammal Review*, 45(4), 239–252. <https://doi.org/10.1111/mam.12046>
- Lindeman, P. V. (1999). Aggressive interactions during basking among four species of Emydid turtles. *Journal of Herpetology*, 33(2), 214–219. <https://doi.org/10.2307/1565717>
- Lovich, J. E., & Ennen, J. R. (2013). A quantitative analysis of the state of knowledge of turtles of the United States and Canada. *Amphibia-Reptilia*, 34(1), 11–23.
<https://doi.org/10.1163/15685381-00002860>
- McAuliffe, J. R. (1977). An hypothesis explaining variations of hemogregarine parasitemia in different aquatic turtle species. *The Journal of Parasitology*, 63(3), 580–581.
<https://doi.org/10.2307/3280024>
- McDougall, P. T., Réale, D., Sol, D., & Reader, S. M. (2006). Wildlife conservation and animal temperament: Causes and consequences of evolutionary change for captive, reintroduced, and wild populations. *Animal Conservation*, 9(1), 39–48. <https://doi.org/10.1111/j.1469-1795.2005.00004.x>

- McKnight, D. T., Wirth, W., Schwarzkopf, L., & Nordberg, E. J. (2021). Leech removal is not the primary driver of basking behavior in a freshwater turtle. *Ecology and Evolution*, *11*(16), 10936–10946. <https://doi.org/10.1002/ece3.7876>
- Mendonça, M. T. (1987). Photothermal effects on the ovarian cycle of the musk turtle, *Sternotherus odoratus*. *Herpetologica*, *43*(1), 82–90.
- Ministère des Forêts, de la Faune et des Parcs. (2021). *Procédure normalisée de fonctionnement: Tortues d'eau douce*. https://mffp.gouv.qc.ca/documents/faune/PD_PNF_tortue-eau-douce.pdf
- Monagas, W. R., & Gatten, R. E. (1983). Behavioural fever in the turtles *Terrapene carolina* and *Chrysemys picta*. *Journal of Thermal Biology*, *8*(3), 285–288. [https://doi.org/10.1016/0306-4565\(83\)90010-4](https://doi.org/10.1016/0306-4565(83)90010-4)
- Neil, W. T., & Allen, E. R. (1954). Algae on turtles: Some additional considerations. *Ecology*, *35*(4), 581–584. <https://doi.org/10.2307/1931051>
- Nordahl, O., Koch-Schmidt, P., Tibblin, P., Forsman, A., & Larsson, P. (2020). Vertical movements of coastal pike (*Esox lucius*)—On the role of sun basking. *Ecology of Freshwater Fish*, *29*(1), 18–30. <https://doi.org/10.1111/eff.12484>
- Obbard, M. E., & Brooks, R. J. (1979). Factors affecting basking in a northern population of the common snapping turtle, *Chelydra serpentina*. *Canadian Journal of Zoology*, *57*(2), 435–440. <https://doi.org/https://doi.org/10.1139/z79-051>
- Peterman, W. E., & Ryan, T. J. (2009). Basking behavior of Emydid turtles (*Chrysemys picta*, *Graptemys geographica*, and *Trachemys scripta*) in an urban landscape. *Northeastern Naturalist*, *16*(4), 629–636. <https://doi.org/10.1656/045.016.n412>

- R Core Team. (2023). *R: A language and environment for statistical computing* [Computer software]. R Foundation for Statistical Computing. <https://www.R-project.org/>
- Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews*, *82*(2), 291–318. <https://doi.org/10.1111/j.1469-185X.2007.00010.x>
- Rees, Al. F., Avens, L., Ballorain, K., Bevan, E., Broderick, A. C., Carthy, R. R., Christianen, M. J. A., Duclos, G., Heithaus, M. R., Johnston, D. W., Mangel, J. C., Paladino, F., Pendoley, K., Reina, R. D., Robinson, N. J., Ryan, R., Sykora-Bodie, S. T., Tilley, D., Varela, M. R., ... Godley, B. J. (2018). The potential of unmanned aerial systems for sea turtle research and conservation: A review and future directions. *Endangered Species Research*, *35*, 81–100. <https://doi.org/10.3354/esr00877>
- Rollinson, N., & Brooks, R. J. (2007). Proximate constraints on reproductive output in a northern population of painted turtles: An empirical test of the bet-hedging paradigm. *Canadian Journal of Zoology*, *85*(2), 177–184. <https://doi.org/10.1139/Z07-002>
- Rouleau, C. J. (2020). *Socioecology of the midland painted turtle (Chrysemys picta marginata)* [Master's thesis, Laurentian University]. <https://laurentian.scholaris.ca/items/ddde5468-c523-40f1-9347-00868801ca37>
- Sarkar, S., Sarkar, N. K., Das, P., & Maiti, B. R. (1996). Photothermal effects on ovarian growth and function in the soft-shelled turtle *Lissemys punctata punctata*. *Journal of Experimental Zoology*, *274*(1), 41–55. [https://doi.org/10.1002/\(SICI\)1097-010X\(19960101\)274:1%3C41::AID-JEZ5%3E3.0.CO;2-F](https://doi.org/10.1002/(SICI)1097-010X(19960101)274:1%3C41::AID-JEZ5%3E3.0.CO;2-F)
- Sawan, S., Mondal, T., Williams, A. C., Yadav, S. P., & Krishnamurthy, R. (2023). Hybrid drone-based survey of riverine habitat and crocodiles in complex landscapes. *International*

- Journal of Environmental Science and Technology*, 20(12), 13571–13582.
<https://doi.org/10.1007/s13762-022-04739-y>
- Schofield, G., Esteban, N., Katselidis, K. A., & Hays, G. C. (2019). Drones for research on sea turtles and other marine vertebrates – A review. *Biological Conservation*, 238, 108214.
<https://doi.org/10.1016/j.biocon.2019.108214>
- Schwarzkopf, L., & Brooks, R. J. (1985). Application of operative environmental temperatures to analysis of basking behavior in *Chrysemys picta*. *Herpetologica*, 41(2), 206–212.
- Sears, M. W., Angilletta, M. J., Schuler, M. S., Borchert, J., Dilliplane, K. F., Stegman, M., Rusch, T. W., & Mitchell, W. A. (2016). Configuration of the thermal landscape determines thermoregulatory performance of ectotherms. *Proceedings of the National Academy of Sciences*, 113(38), 10595–10600. <https://doi.org/10.1073/pnas.1604824113>
- Selman, W., & Qualls, C. P. (2011). Basking ecology of the yellow-blotched sawback (*Graptemys flavimaculata*), an imperiled turtle species of the Pascagoula River system, Mississippi, United States. *Chelonian Conservation and Biology*, 10(2), 188–197.
<https://doi.org/10.2744/CCB-0886.1>
- Signer, C., Ruf, T., & Arnold, W. (2011). Hypometabolism and basking: The strategies of alpine ibex to endure harsh over-wintering conditions. *Functional Ecology*, 25(3), 537–547.
<https://doi.org/10.1111/j.1365-2435.2010.01806.x>
- Turcotte, A., Garant, D., & Blouin-Demers, G. (2023). Effects of human disturbance on risk-taking behavior in painted turtles. *Ethology*, 129(8), 406–420.
<https://doi.org/10.1111/eth.13377>
- Van Dijk, P. P. (2010). IUCN Red List of Threatened Species: *Chrysemys picta*. *IUCN Red List of Threatened Species*. <https://www.iucnredlist.org/fr>

- Wagner, B., Garnick, S. W., Ryan, M. F., Isaac, J. L., Begg, A., & Nitschke, C. R. (2025). Thermal drone surveys to detect arboreal fauna: Improving population estimates and threatened species monitoring. *Ecological Applications*, 35(6), e70091. <https://doi.org/10.1002/eap.70091>
- Weston, M. A., O'Brien, C., Kostoglou, K. N., & Symonds, M. R. E. (2020). Escape responses of terrestrial and aquatic birds to drones: Towards a code of practice to minimize disturbance. *Journal of Applied Ecology*, 57(4), 777–785. <https://doi.org/10.1111/1365-2664.13575>
- Wirth, W., & Ariel, E. (2020). Temperature-dependent infection of freshwater turtle hatchlings, *Emydura macquarii krefftii*, inoculated with a ranavirus isolate (*Bohle iridovirus*, *Iridoviridae*). *Facets*, 5(1), 821–830. <https://doi.org/10.1139/facets-2020-0012>
- Witt, R. R., Beranek, C. T., Howell, L. G., Ryan, S. A., Clulow, J., Jordan, N. R., Denholm, B., & Roff, A. (2020). Real-time drone derived thermal imagery outperforms traditional survey methods for an arboreal forest mammal. *PLOS ONE*, 15(11), e0242204. <https://doi.org/10.1371/journal.pone.0242204>
- Ydenberg, R. C., & Dill, L. M. (1986). The economics of fleeing from predators. In *Advances in the Study of Behavior* (Vol. 16, pp. 229–249). Elsevier. [https://doi.org/10.1016/S0065-3454\(08\)60192-8](https://doi.org/10.1016/S0065-3454(08)60192-8)