Why do freshwater turtles aggregate at basking sites?

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ABSTRACT

Many animals, including reptiles, aggregate for asocial reasons, social reasons, or both. Freshwater turtles aggregate at basking sites, but it remains unclear why they do so. Previous studies have suggested basking aggregations may occur at basking sites that have preferred habitat characteristics, or because aggregation increases the detection of predators. I tested these two hypotheses with painted turtles (*Chrysemys picta*) and northern map turtles (*Graptemys geographica*), two locally abundant species that aggregate at basking sites at Petrie Island, Ottawa, Ontario, Canada. I predicted that basking sites with larger aggregations of basking turtles should have more available basking area, more open canopy, and be further from the shoreline. I also predicted that turtles in larger basking aggregations should escape into the water from further away than turtles in smaller basking aggregations when approached by a potential predator. I conducted basking surveys in 2021, where I photographed basking turtles and measured basking site characteristics at each available basking site. I conducted disturbance trials in 2022, where I measured the flight initiation distance of basking turtles. I found that painted turtles aggregated at basking sites with more available basking area and a south-facing orientation while northern map turtles aggregated at basking sites with more available basking area and further away from the shoreline. I also found that painted turtles and northern map turtles fled basking sites from further away when basking in larger groups. The biological effects of basking site characteristics on the number of basking turtles were small, and so were those of the number of basking turtles on flight initiation distance, suggesting there may be additional reasons why freshwater turtles aggregate at basking sites.

RÉSUMÉ

Plusieurs animaux, incluant les reptiles, se regroupent pour des raisons asociales, sociales ou les deux. Les tortues d'eau douce se regroupent aux sites de lézardage, mais peu d'information est disponible sur les raisons de ces rassemblements. Certaines études ont suggéré que les tortues se regroupent lors du lézardage puisque les sites de qualité sont limités ou parce que l'agrégation leur permet de détecter plus facilement les prédateurs. J'ai testé ces deux hypothèses chez la tortue peinte (*Chrysemys picta*) et la tortue géographique (*Graptemys geographica*), deux espèces se regroupant aux sites de lézardage et qui sont localement abondantes à l'île Pétrie, Ottawa, Ontario, Canada. J'ai prédit que les sites de lézardage avec de plus grands regroupements devraient avoir une plus grande surface de lézardage disponible, une canopée plus ouverte et être plus loin de la rive. J'ai aussi prédit que les tortues se trouvant dans de grands regroupements de lézardage devraient avoir une plus grande distance de fuite à l'approche d'un prédateur potentiel que les tortues faisant partie de plus petits regroupements. À l'été 2021, j'ai photographié des tortues en lézardage et j'ai mesuré les caractéristiques de tous les sites de lézardage potentiels. En 2022, j'ai mis en place des essais de perturbation où je mesurais la distance de fuite des tortues en lézardage. J'ai identifié que les tortues peintes se regroupaient aux sites de lézardage qui avaient une plus grande surface de lézardage disponible et orientés vers le sud. Chez les tortues géographiques, les regroupements étaient plus fréquents sur les sites de lézardage avec une plus grande surface de lézardage disponible et plus loin de la rive. J'ai aussi identifié que les tortues peintes et géographiques lézardant en grands groupes avaient une plus grande distance de fuite. Les effets des caractéristiques du site de lézardage sur le nombre de tortues en lézardage étaient faibles, ainsi que ceux du nombre de tortues en lézardage sur la distance de fuite, suggérant qu'il y a possiblement d'autres facteurs pouvant expliquer l'agrégation des tortues aux sites de lézardage.

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1 INTRODUCTION

Aggregation occurs in many animals from simple multicellular organisms to large mammals (Parish & Edelstein-Keshet, 1999). Aggregation is the tendency for individuals to be spatially closer to one another than what would be expected by chance (Fryxell, 1990). Two striking examples of animal aggregations are the annual migration of 1.3 million wildebeest in the Serengeti-Mara ecosystem (Thirgood et al., 2004) and swarms of hundreds of millions of desert locusts in Saudi Arabia (Rainy, 1951). Depending on the species, aggregations can be labelled different names such as herds, schools, or swarms (Allee, 1927).

Animals can aggregate for two, non-mutually exclusive reasons: asocial and social (Allee, 1927; Ebensperger, 2001; Dolan & Bulter 2006). Asocial aggregations occur when individuals are attracted to the same resources that are either limited or clumped (Carr & MacDonald, 1986; Johnson et al., 2002). For example, white sharks aggregate at Neptune Island, Australia to forage at large seal colonies (Schilds et al., 2019). Similarly, large herbivores aggregate around rare watering holes during the dry season in Kruger National Park, South Africa (Thrash et al., 1995). Likewise, some amphibians aggregate at scarce wetlands to breed (Wells, 1977; Knutson et al., 2004)..

Animals can also aggregate for social reasons where individuals are attracted to one another (Wilson, 1975) and several hypotheses have been proposed to explain social aggregations. The selfish herd hypothesis (Hamilton, 1971) and the many eyes hypothesis (Pulliam, 1973) both propose that social aggregations reduce the risk of predation. The selfish herd hypothesis states that an individual reduces its probability of predation through risk dilution by aggregating with conspecifics. Support for the selfish herd hypothesis has been found in many animals including Adelie penguins (McDowall & Lynch, 2019), sheep (King et al., 2012), guppies (Kimbell & Morrell, 2015), sticklebacks (Krause & Tegeder, 1994), fiddler crabs (Viscido & Wethey, 2002), digger wasps (Wcislo, 1984), and ocean skaters (Foster & Treherne, 1981). The many eyes hypothesis, on the other hand, states that, as group size increases, more time can collectively be spent surveilling for predators, while individuals can devote more time towards other activities, such as foraging (Pulliam, 1973; Lima, 1995; Roberts, 1996; Ebensperger et al., 2006). Support for the many eyes hypothesis has also been found in many animals, including big horn sheep (Rieucau & Martin, 2008), capybaras (Yàber & Herrera, 1994), foraging starlings (Powell, 1974), and southern mountain cavy (Taraborelli, 2008).

Other hypotheses unrelated to predation have also been proposed to explain social aggregations. Firstly, cooperative foraging among aggregated individuals may permit access to more or different food resources than would be available to solitary foragers (Majer et al., 2018). Cooperative foraging has been observed in crab spiders (Dumke et al., 2018), killer whales (Guinet et al., 2000), vampire bats (Wilkinson, 1990), and some velvet spiders (Majer et al., 2018). Secondly, aggregated individuals may receive thermoregulatory benefits by minimizing heat loss and thereby lowering energy expenditure, allowing energy reallocation to other functions such as growth or reproduction (Wilson, 2009; Gilbert et al., 2010). For example, barbary macaques aggregate for thermoregulation, thus reducing energy expenditures and increasing their probability of overwinter survival (Campbell et al., 2018). Likewise, abandoned penguin chicks aggregate to conserve heat (Wilson, 2009) and aggregations of common green bottle fly larvae experience faster development through warmer temperatures (Aubernon et al., 2019). Thirdly, aggregating may offer individuals more mating opportunities, thus facilitating mate acquisition (Molley et al., 2012). Shoals of giant Australian cuttlefish (Hall & Hanlon, 2002), white-streaked grouper (Nanami et al., 2013), cod (Bekkevold et al., 2002), and swarms of mosquitos (Butail et al., 2013) all aggregate to mate.

Reptiles aggregate for both asocial and social reasons (Gardner et al., 2016; Bauwens & Claus, 2021). Several snakes, including ratsnakes, rattlesnakes and garter snakes, form large overwintering aggregations at hibernacula with preferred thermal characteristics (Carpenter, 1953; Prior et al., 2001; Gregory, 2004; Gienger & Beck, 2011). Furthermore, some freshwater turtles aggregate at overwintering sites (Litzgus et al., 1999; Ultsch et al., 2000; Bulté et al., 2018; Feng et al., 2019). Moreover, some reptiles nest in aggregations when suitable nesting sites are scarce (Christian & Tracy, 1985; Graves & Duvall 1995, Doody et al., 2009). Many reptiles use basking for thermoregulation (Boyer, 1965; Bradshaw & Main, 1968; Lillywhite, 1980), however, suitable basking sites can be scarce leading to aggregations at basking sites (Bauwens & Claus, 2021). Basking site aggregations occur in lizards (Wikelski, 1999; Lanham & Bull, 2004), snakes (Myres & Eells, 1968; Graves & Duvall, 1987; Clark et al., 2012; Bauwens & Claus, 2021), and freshwater turtles (Boyer, 1965; Gordon & MacCulloch, 1980; Flaherty & Bider, 1984; Pluto & Bellis, 1986; Lindeman, 1999; Moore & Seigel, 2006; Selman & Qualls, 2011; Nordberg & McKnight, 2020). Aggregations for asocial reasons may lead to social interactions between individuals.

Reptiles also aggregate for social reasons despite being perceived as largely asocial animals (Doody et al., 2013). For example, some lizards aggregate to reduce the risk of predation by increasing vigilance (Lanham & Bull, 2004; Santoyo-Brito et al., 2020). Additionally, some sea turtles and lizards nest in aggregations to decrease the risk of predation of individual nests (Rand, 1968; Richard & Hughes, 1972; Bock & Rand, 1989; Eckrich & Owens, 1995; Doody et al., 2009; Tanner et al., 2019). Aggregations of reptiles may also occur for both asocial and social reasons because these reasons for aggregation are not mutually exclusive.

Freshwater turtles commonly aggregate at basking sites (Boyer, 1965; Gordon & MacCulloch, 1980; Flaherty & Bider, 1984; Pluto & Bellis, 1986; Capula et al., 1994; Lindeman, 1999; Moore & Seigel, 2006; Selman & Qualls, 2011; Nordberg & McKnight, 2020). Basking aggregations are especially common in map turtles (genus *Graptemys*) (Lindeman, 2013) and closely related emydid turtles (Boyer, 1965). The primary function of basking appears to be thermoregulation (Boyer, 1965; Schwarzkopf & Brooks, 1985; Bulté & Blouin-Demers, 2010), but basking may also help turtles rid themselves of ectoparasites (Boyer, 1965; Vogt, 1979). It is still unclear, however, why many species of freshwater turtles aggregate at basking sites.

Previous studies have suggested freshwater turtles aggregate at basking sites simply because basking sites with preferred habitat characteristics are limited (Boyer, 1965; Gordon & MacCulloch, 1980). Freshwater turtles tend to aggregate at basking sites with more available basking area (Flaherty & Bider 1984; Pluto & Bellis, 1986), more open canopy (Boyer, 1965; Cook & Martini-Lamb, 2004; Pittfield & Burger, 2017), with deeper water (Pluto & Bellis, 1986; Cadi & Joly, 2003), and further away from the shoreline (Flaherty & Bider, 1984; Pluto & Bellis 1986; Cadi & Joly, 2003). Basking aggregations may also have a social component (Boyer, 1965; Gordon & MacCulloch, 1980; Flaherty & Bider, 1984). For instance, aggregation could occur if group basking increases the detection of predators (Boyer, 1965; Jacobi & Kahl, 2021), as suggested by the many eyes hypothesis.

The objective of my research is to determine whether freshwater turtles aggregate at basking sites for asocial reasons, social reasons, or both. First, I tested the hypothesis that freshwater turtles aggregate at basking sites that have preferred physical and thermal characteristics. I predicted that basking sites with larger aggregations of basking turtles should have more available basking area, more open canopy that allows more solar radiation for basking, and be further from the shoreline thus making turtles safer from terrestrial predators. Second, I tested the hypothesis that freshwater turtles aggregate at basking sites to detect predators from further away. Thus, I predicted that turtles in larger basking aggregations should escape into the water from further away than turtles in smaller basking aggregations when approached by a potential predator.

2 METHODS

2.1 Study site and study species

I studied northern map turtles (*Graptemys geographica*) and painted turtles (*Chrysemys picta*), two locally abundant freshwater turtle species that aggregate at basking sites. I conducted my field work from 2 May to 11 September in 2021 and from 30 April to 19 August in 2022 at Petrie Island, Ottawa, Ontario, Canada (45.5059° N, 75.4911° W). My methods were approved by the Animal Care Committee at the University of Ottawa (protocol number BLe-3634-R1) in accordance with the guidelines of the Canadian Council on Animal Care and conducted with permits from the Ontario Ministry of Natural Resources (Wildlife Scientific Collector's Authorization; permit number 1097846).

2.2 Basking surveys

In 2021, I conducted basking surveys by patrolling the shoreline of Petrie Island by canoe. Basking surveys were concentrated on Turtle Pond, Muskrat Bay, Middle Channel, South Passage, and Crappie Bay (Figure 1) because these bays and channels are where the majority of basking sites are located. All basking turtles were photographed from at least 10 m away using a Nikon Coolpix P950 (24-2000mm-83x zoom NIKKOR ED lens). This camera was used for its ability to capture detailed photos from a long distance which reduced the disturbance of basking turtles during basking surveys. The photos were later examined to identify the total number of basking turtles on each basking site. The species and sex of each basking turtle was determined based on morphological traits. Both adult male northern map turtles and painted turtles have proportionally longer and thicker tails than adult females (Figure 2). Particularly in adult northern map turtles, females are significantly larger than males (Figure 2). Particularly in adult painted turtles, males have proportionally longer front claws (Figure 2).

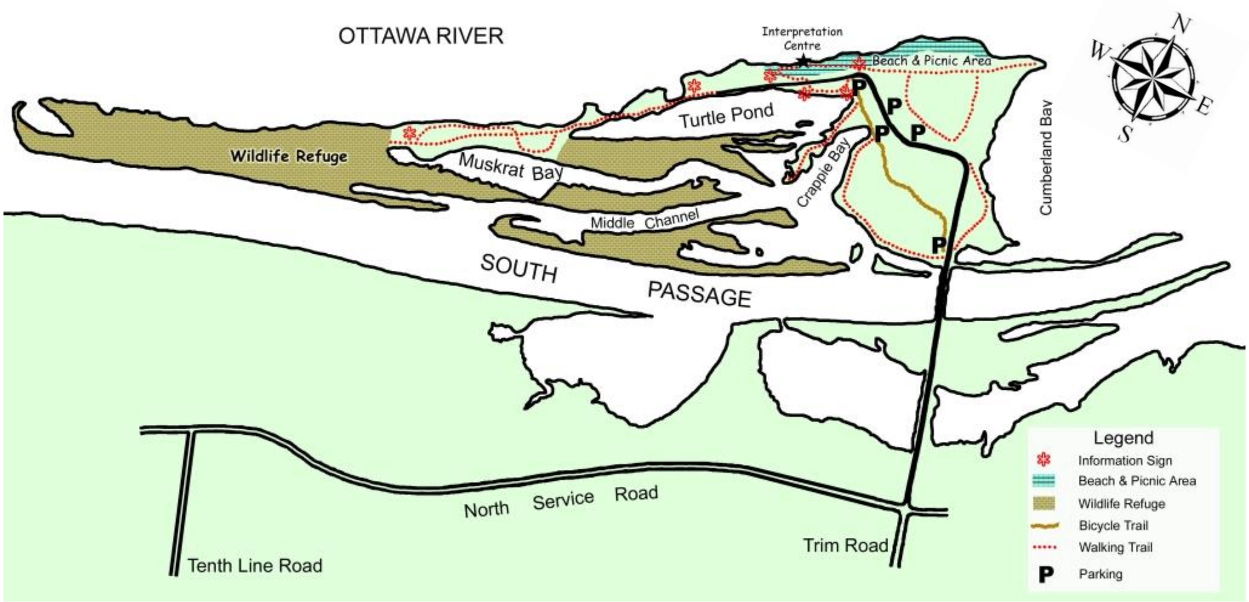

Figure 1. Map of Petrie Island, Ottawa, Ontario, Canada (Friends of Petrie Island, n.d.).

Figure 2. Morphological features of male and female painted turtles and northern map turtles. Adult female northern map turtles are significantly larger than males (top). Adult male painted turtles have proportionally longer front claws than females (bottom). Both adult male northern map turtles and painted turtles have proportionally longer and thicker tails than adult females (top). Photos by Malcolm Fenech.

2.3 Basking site characteristics

I defined an available basking site to be any fallen tree or branch that had an accessible area for basking turtles with direct access from the water. No emergent rocks were available for basking in my study area. All available basking sites were mapped with a handheld GPS unit (Garmin GPSmap 78s). At each available basking site, I measured available basking area (m^2), distance to the closest shoreline (m), canopy coverage (%), and the basking site orientation (north or south). Previous studies suggested that these characteristics are important features of basking sites (Boyer, 1965; Flaherty & Bider, 1984; Pluto & Bellis, 1986; Peterman & Ryan, 2009; Lambert et al., 2013; Vignoli et al., 2015; Kleewein, 2015; Pittfield & Burger, 2017).

To measure available basking area, each basking site was divided into simple geometric shapes (e.g., rectangle, circle, triangle) and the area of each shape was measured using a measuring tape, then the area of each shape was calculated, and all areas were summed to obtain the total area. To measure the distance to the nearest shoreline, a measuring tape was used to measure the closest portion of a basking site to the nearest shoreline. Canopy coverage was measured by placing a wide-angle camera (GoPro Hero 3) at each basking site to take a picture of the overhead canopy. The camera was set to a wide field of view (FOV) to capture a picture with a FOV of 130^o. Image distortion from the wide FOV was later removed using Adobe Premiere Pro. I imported the image into ImageJ 1.53k (Schneider et al., 2012) and converted the image to 8-bit which changed the image to black and white. The threshold of the image was then adjusted to ensure all canopy pixels were detected. Once all canopy pixels were detected by ImageJ, a canopy coverage percentage was obtained from the number of pixels of canopy as a function of the total number of pixels. Basking site orientation was determined by the side of the channel or bay the basking site was located on (Figure 1).

2.4 Disturbance trials

In 2022, I conducted disturbance trials of freshwater turtle aggregations at basking sites by canoe. Disturbance trials started from at least 10 m from each basking site and the canoe was paddled towards the turtles at a constant rate of approximately 1 m/s. Once the first turtle escaped into the water, the flight initiation distance (FID) was measured between the bow of the canoe and the basking site using a Bosch GLM400C Blaze outdoor laser measure. Previous studies have measured FID in basking freshwater turtles using human disturbances to simulate a potential predator (López et al., 2005; Polich & Barazowski, 2016; Pittfield & Burger, 2017; Jacobi & Kahl, 2021). Prior to each disturbance trial, all basking turtles were photographed using a Nikon Coolpix P950 (24-2000mm-83x zoom NIKKOR ED lens). The photos were later examined to identify the total number of basking turtles on each basking site. The species and sex of each basking turtle was determined using morphological traits (see section *2.2*). After each disturbance trial, the basking site temperature and surface water temperature at the basking site were measured using a Fluke 566 IR thermometer. The air temperature was measured using a thermometer (Fisherbrand Traceable thermometer). Basking sites were only subjected to one daily disturbance trial to minimize the chance of sampling an individual turtle more than once in a single day.

2.5 Statistical analyses

I used two generalized linear mixed effects models (package: lme4, function: glmer) in R 4.2.2 (R Development Core Team, 2022), one for map turtles and one for painted turtles, to determine whether freshwater turtles aggregate at basking sites with preferred physical and thermal characteristics. I used the number of basking turtles as the response variable. I excluded 149 observations where aggregations were a mix of the two species. Also, I excluded 237 observations of juvenile turtles. Candidate models were built with up to six predictors variables: available basking area (m^2), distance to the nearest shoreline (m), canopy coverage (%), Julian date, time of day, and basking site orientation. Julian date was included in the models to control for seasonal effects on basking site aggregations. Time of day was included in the models to control for time effects on basking site aggregations. Basking site orientation was included in the models as a binomial variable (North or South). The basking site ID number was used as a random effect in both models. I compared the fit of candidate models using AIC (package: AICcmodavg, function: aictab). If candidate models had a delta AICc less than 2, I averaged the models (package: MuMIn, function: model.avg).

I used two generalized linear mixed effects models (package: lme4, function: glmer) in R 4.2.2 (R Development Core Team, 2022), one for map turtles and one for painted turtles, to determine whether freshwater turtles aggregate at basking sites to better detect predators. I used FID as the response variable. I excluded 66 trials where aggregations were a mix of the two species. Also, I excluded 49 trials of juvenile turtles. Candidate models were built with up to six predictor variables: the number of basking turtles, air to surface water temperature difference (^oC), basking site temperature (^oC), time of day, sex ratio of basking turtles, and Julian date. I compared the fit of candidate models using AIC (package: AICcmodavg, function: aictab). If candidate models had a delta AICc less than 2, I averaged the models (package: MuMIn, function: model.avg).

3 RESULTS

3.1 Basking site characteristics that influenced turtle basking site aggregations

I conducted basking surveys on 75 days during which I collected 934 observations of basking painted turtles and 480 observations of basking northern map turtles. The model that best explained the number of basking painted turtles included available basking area, distance to shoreline, canopy coverage, Julian date, basking site orientation, and time of day (see Table A1). Two models were averaged to best explain the number of basking northern map turtles and included available basking area, distance to shoreline, canopy coverage, Julian date, and site orientation (see Table A2).

Both painted turtles and northern map turtles basked in larger groups at sites with more available basking area (Table 1, Figure 3A, & Figure 4A). For painted turtles, a basking site with an available basking area of 0.25 m^2 had an average of 1 basking turtle while a basking site with an available basking area of 1.75 m^2 had an average of 1.4 turtles. For northern map turtles, a basking site with an available basking area of 0.25 m^2 had an average of 1.1 turtles while a basking site with an available basking area of 1.75 m^2 had an average of 2.3 turtles. Both painted turtles and northern map turtles also basked in larger groups earlier in the active season (Table 1, Figure 3D, & Figure 4C).

Larger groups of painted turtles used south-facing basking sites (Table 1 & Figure 3E). On average, 1.5 painted turtles used south-facing basking sites compared to an average of 1.2 painted turtles for north-facing basking sites. Canopy coverage did not influence the number of painted turtles at basking sites (Table 1 & Figure 3C) or the distance to the nearest shoreline from the basking site (Table 1 & Figure 3B).

Larger groups of northern map turtles used basking sites further from the shoreline (Table 1 & Figure 4B). A basking site 3 m from the shoreline had an average of 1.2 northern map turtles while a basking site 8 m from the shoreline had an average of 1.5 northern map turtles. Basking site orientation and canopy coverage did not affect how many northern map turtles used a particular basking site (Table 1 & Figure 4D).

Table 1. Summary statistics for the generalized linear mixed models of basking site characteristics that influenced turtle basking site aggregations at Petrie Island, Ottawa in 2021. Response variables tested were number of basking painted turtles and number of basking northern map turtles. Significant (< 0.05) p-values are in bold.

Model: Basking site characteristics that influenced painted turtle basking site aggregation

Variable	Estimate	p-value
Intercept	0.53	0.067
Available basking area (m^2)	0.19	**0.0027**
Distance to shoreline (m)	0.0079	0.19
Canopy coverage (%)	-0.0026	**0.046**
Julian date	-0.0051	**< 0.001**
Basking site orientation	0.26	**0.014**
Time of day	0.00040	**0.032**

Model: Basking site characteristics that influenced northern map turtle basking site aggregation

Variable	Estimate	p-value
Intercept	0.70	**0.015**
Available basking area (m^2)	0.40	**< 0.001**
Distance to shoreline (m)	0.050	**0.0083**
Canopy coverage (%)	-0.0017	0.49
Julian date	-0.0053	**< 0.001**
Basking site orientation	0.31	0.085

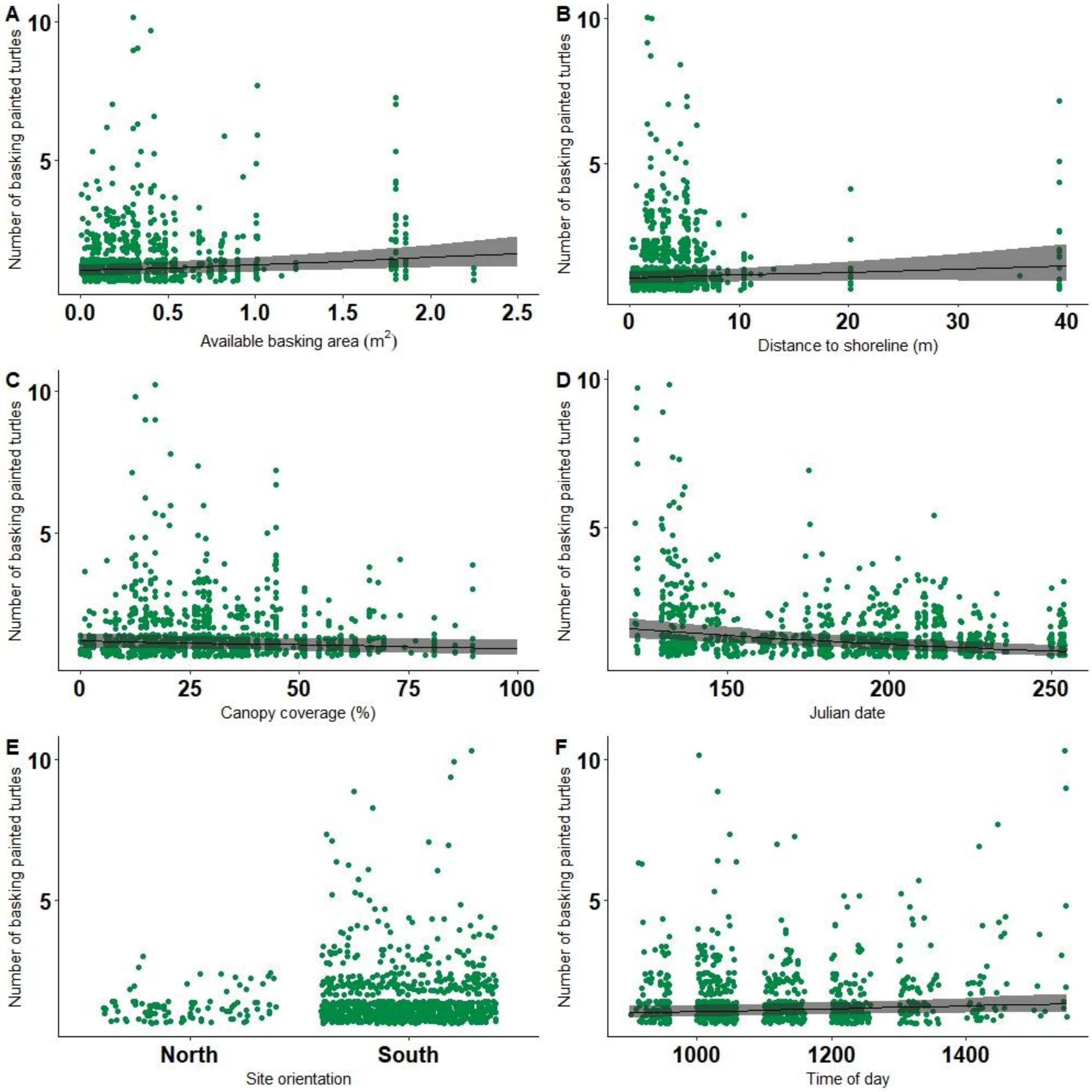

Figure 3. Graphs from the generalized linear mixed model of basking site characteristics that influenced painted turtle basking site aggregation at Petrie Island, Ottawa in 2021. Graphs of predictor variables include: A) available basking area, B) distance to shoreline, C) canopy coverage, D) Julian date, E) basking site orientation, and F) time of day. Line is a linear regression, and the shaded area indicates a 95 % confidence interval.

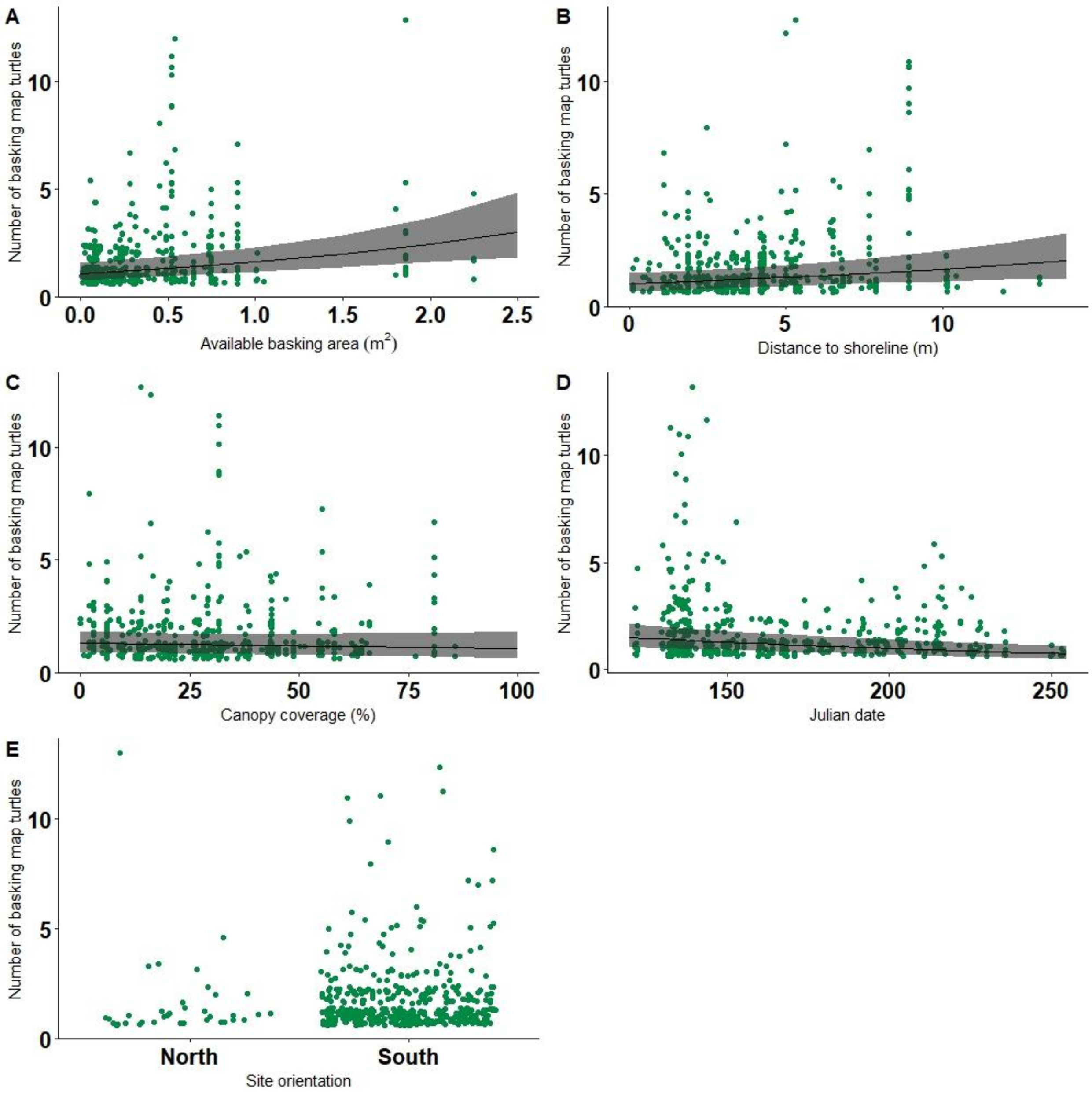

Figure 4. Graphs from the generalized linear mixed model of basking site characteristics that influenced northern map turtle basking site aggregation at Petrie Island, Ottawa in 2021. Graphs of predictor variables include: A) available basking area, B) distance to shoreline, C) canopy coverage, D) Julian date, and E) basking site orientation. Line is a linear regression, and the shaded area indicates a 95 % confidence interval.

3.2 Flight initiation distance of basking turtles

I conducted 319 disturbance trials on basking painted turtles and 176 disturbance trials on basking northern map turtles. Two models were averaged to best explain FID of basking painted turtles and included the number of turtles, Julian date, and the air temperature to surface water temperature difference (Supplementary Table 3). The model that best explained FID of basking northern map turtles included the number of turtles, Julian date, and the sex ratio of basking turtles (Supplementary Table 4).

Painted turtles and northern map turtles both fled basking sites from further away when turtles were more numerous (Table 2, Figure 5A, & Figure 6A). For painted turtles, the mean FID was 5.3 m with one turtle using a basking site while the mean FID was 8.2 m with five turtles using a basking site. For northern map turtles, the mean FID was 12 m with one turtle using a basking site while the mean FID was 16 m with five turtles using a basking site. Additionally, painted turtles fled from further away earlier in the active season (Table 2 & Figure 5B) while Northern map turtles fled from further away when the basking group comprised more females (Table 2 & Figure 6C). Finally, air temperature to surface water temperature difference did not affect the FID of basking painted turtles and Julian date did not affect the FID of basking northern map turtles.

Table 2. Summary statistics for generalized linear mixed models of the flight initiation distance of aggregated basking turtles at Petrie Island, Ottawa in 2022. Response variables tested were flight initiation distance of basking painted turtles and northern map turtles. Significant (< 0.05) p-values are in bold.

Model: Flight initiation distance of aggregated basking painted turtles

Variable	Estimate	p-value
Intercept	0.09	**0.0029**
Number of basking painted turtles	-0.0099	**0.0026**
Julian date	0.00047	**0.0074**
Air temperature to surface water temperate difference	0.00055	**0.76**

Model: Flight initiation distance of aggregated basking northern map turtles

Variable	Estimate	p-value
Intercept	0.13	**< 0.001**
Number of basking northern map turtles	-0.0031	**0.0073**
Julian date	-0.00021	0.079
Sex ratio of basking turtles	-0.025	**0.014**

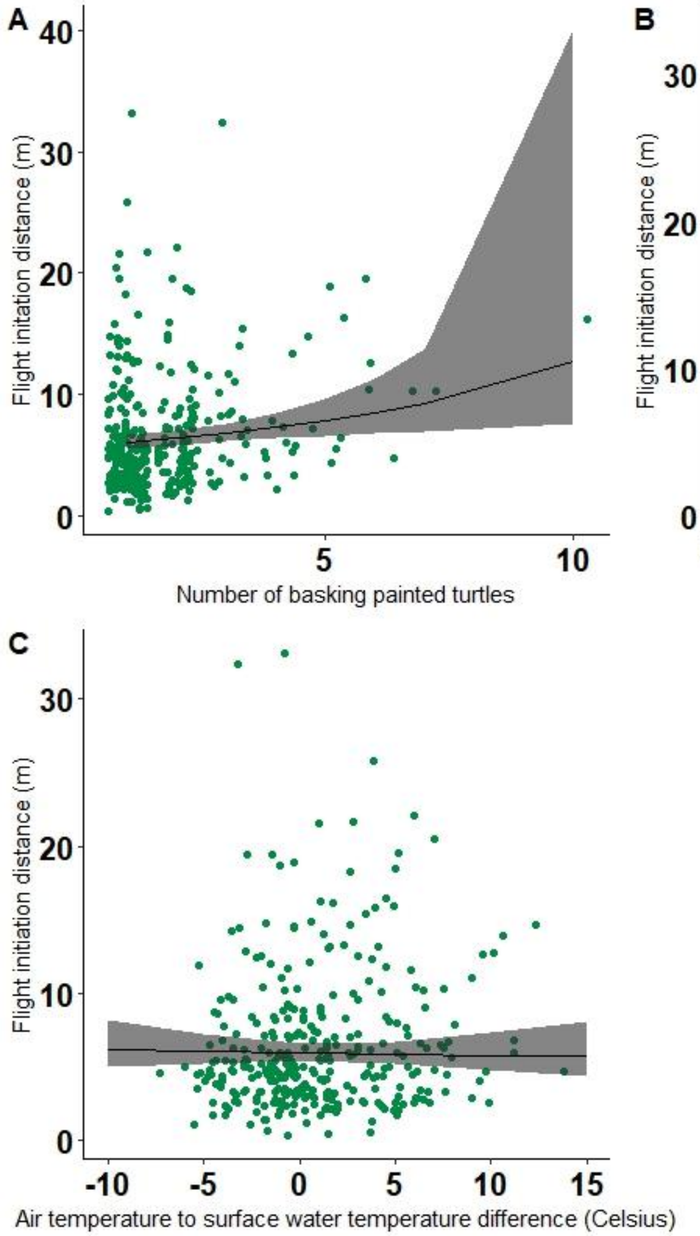

Figure 5. Graphs from generalized linear mixed model for the flight initiation distance of aggregated basking painted turtles at Petrie Island, Ottawa in 2022. Graphs of predictor variables include: A) Number of basking painted turtles, B) Julian date, and C) air temperature to surface water temperature difference. Line is a linear regression, and the shaded area indicates a 95 % confidence interval.

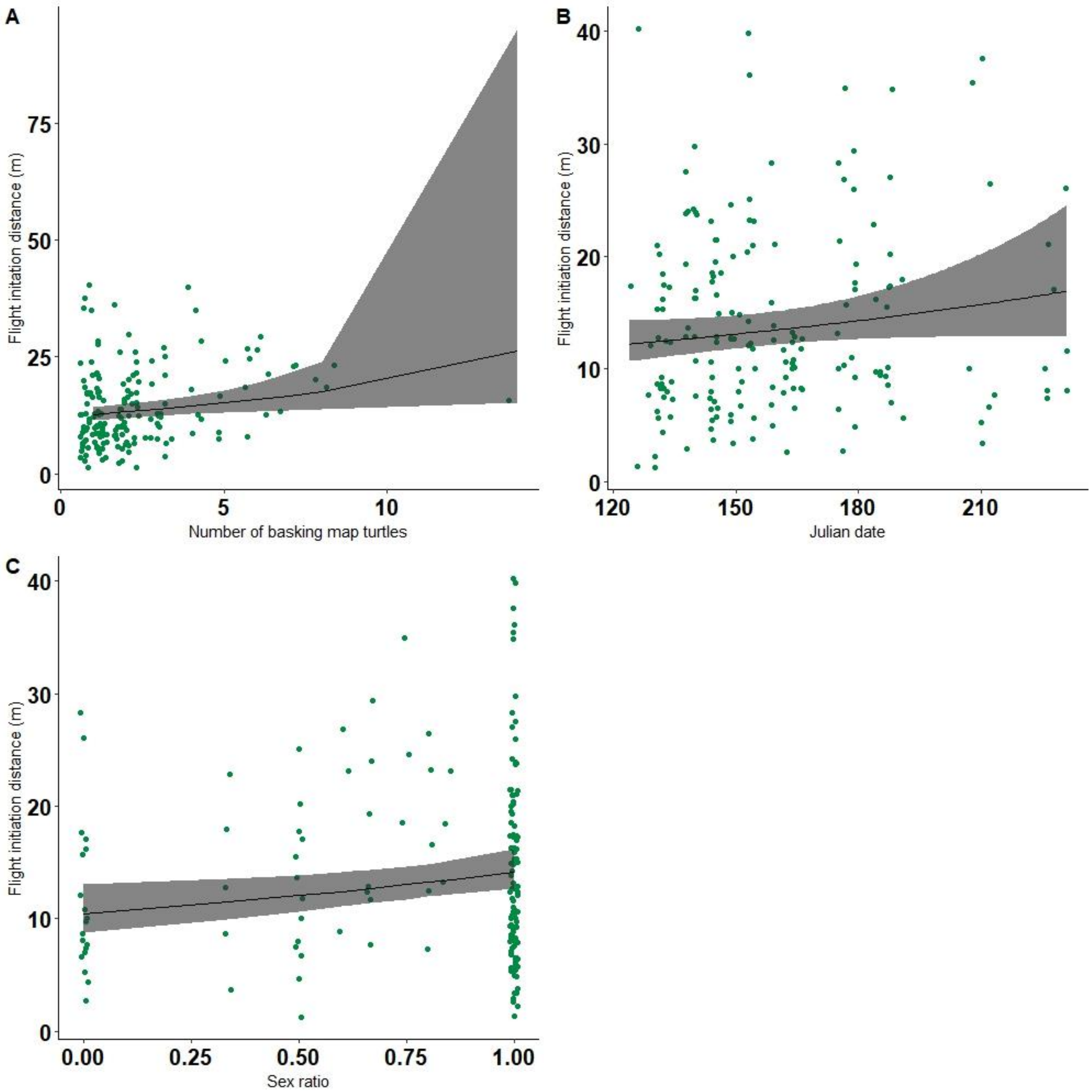

Figure 6. Graphs from generalized linear mixed model for the flight initiation distance of aggregated basking northern map turtles at Petrie Island, Ottawa in 2022. Graphs of predictor variables include: A) Number of basking northern map turtles B) Julian date, and C) sex ratio of basking turtles (0 = all male and 1 = all female). Line is a linear regression, and the shaded area indicates a 95 % confidence interval.

4 DISCUSSION

The objective of my research was to determine whether freshwater turtles aggregate at basking sites for asocial reasons, social reasons, or both. Previous studies have suggested that aggregations may occur because basking sites with preferred habitat characteristics are limited (Boyer, 1965; Gordon & MacCulloch, 1980) or to better detect predators (Boyer, 1965; Jacobi & Kahl, 2021). I tested both of these hypotheses because the reasons for aggregation are non-mutually exclusive.

4.1 Do freshwater turtles aggregate at basking sites for asocial reasons?

The first hypothesis I tested was that freshwater turtles aggregate at basking sites that have preferred physical and thermal characteristics. If freshwater turtles aggregate at basking sites with preferred physical and thermal characteristics, I expected more turtles to use basking sites with more available basking area, more open canopy that would allow for more solar radiation, and further from the shoreline to be safer from terrestrial predators. I found that painted turtles do indeed aggregate at basking sites with more available basking area and with a south-facing orientation. In addition, I found that northern map turtles aggregate at basking sites with more available basking area and further from the shoreline. However, I only detected small biological effects for every basking site characteristic I measured because the estimated effect size for each basking site characteristic was less than 0.5 (Table 1). I may have detected statistically significant, yet small biological effects for the basking site characteristics I measured because of the large number of observations I collected. Furthermore, excluding the mixed species observations of aggregation at basking sites may have minimized the biological effect that I detected.

Available basking area was the strongest predictor of basking site use. Simply, more available basking area may allow for more turtles to use a basking site simultaneously. Previous studies of northern map turtles have also indicated that aggregations typically occur on larger basking sites (Flaherty & Bider 1984; Pluto & Bellis, 1986). Freshwater turtles sometimes stack on top of one another at basking sites (Hennemann, 1979; Selman & Qualls, 2011), but I rarely observed this behaviour at my study site as this likely only occurs when available basking sites are extremely scarce.

Larger groups of northern map turtles used basking sites further away from the shoreline, while painted turtles did not. Previous studies have also indicated that northern map turtles prefer to use basking sites further away from the shoreline (Flaherty & Bider, 1984; Pluto & Bellis, 1986), especially larger female map turtles (Pluto & Bellis, 1986). Using basking sites further from the shoreline may afford turtles better visibility of predators and, thus, a more rapid escape (López et al., 2005; Lambert et al., 2013). When artificial basking sites are provided in areas where turtles bask on the shoreline because of a lack of alternatives, turtles switch to using the artificial basking sites presumably because it reduces their risk of predation by terrestrial predators (Capula et al., 1994). Turtles can also bask further away from the shoreline to benefit from a more open canopy (Boyer, 1965).

A more open canopy may allow more solar radiation to reach basking turtles which, in turn, facilitates thermoregulation. However, canopy cover did not influence the size of basking site aggregations of painted turtles and northern map turtles despite freshwater turtles generally preferring to use basking sites with a more open canopy (Boyer, 1965). Painted turtles typically use basking sites with less than 50% canopy cover (Pittfield & Burger, 2017) and Pacific pond turtles are more likely to use basking sites with 0-20% canopy coverage (Cook & Martini-Lamb, 2004). Additionally, semi-aquatic wood turtles select habitats with more open canopy to assist with thermoregulation (Compton et al., 2002; Arvisais et al., 2004; Dubois et al., 2009). Basking site orientation may also affect how much solar radiation basking turtles receive. Painted turtles used south-facing basking sites more, but not northern map turtles. The importance of basking site orientation was first documented by Boyer (1965) and Petermann & Ryan (2009) observed that turtles shift from using basking sites on the western bank of a river to the eastern bank with the time of day, following the direction of the sun. Basking site orientation may not be a preferred basking site characteristic selected by northern map turtles as they could be selecting basking sites for other preferred habitat characteristics or aggregating at basking sites for social reasons.

Basking is critical for thermoregulation in freshwater turtles, especially when water temperatures are cold (Edwards & Blouin-Demers, 2007; Bulté & Blouin-Demers, 2010). I found larger aggregations of painted turtles and northern map turtles at basking sites early in the active season. More intensive use of basking sites earlier in the active season is likely due to a more urgent need to thermoregulate when the water is cold. As the water warms, turtles can forgo using basking sites and instead bask at the surface of the water.

Freshwater turtles may indeed aggregate at basking sites for asocial reasons, however, multiple basking site characteristics likely contribute to why freshwater turtles aggregate at basking sites. For example, turtles may not aggregate on a basking site solely based on available basking area if the basking site does not have other preferred characteristics such as a south-facing orientation or located further from the shoreline. In addition, the small biological effect sizes for basking site characteristics and lack of aggregation at some basking sites suggest that basking sites with preferred habitat characteristics are abundant at my study site. Lastly, the small biological effect sizes of the basking site characteristics I measured may also be a result of aggregations at basking sites occurring for social reasons.

4.2 Do freshwater turtles aggregate at basking sites for social reasons?

The second hypothesis I tested was that freshwater turtles aggregate at basking sites to detect predators from further away. If that is the case, I expected turtles in larger aggregations to escape into the water from further away than turtles in smaller aggregations when approached by a potential predator. Painted turtles and northern map turtles fled from further away when more turtles were present at basking sites. However, I only detected a small biological effect for the number of basking turtles on FID as the estimated effect size was less than 0.01 (Table 2). Excluding disturbance trials of mixed species aggregation may have affected the detected biological effect of the number of basking turtles on FID, along with the lack of disturbance trials conducted on larger basking site aggregations. Painted turtles also fled from further away earlier in the active season and northern map turtles fled from further away when there were more females basking, however, both with small biological effect sizes.

Both painted turtles and northern map turtles detected a potential predator from further away when more turtles used a basking site. A previous study of the flight initiation distance of basking turtles also indicated that aggregated turtles fled basking sites sooner when aggregations were larger (Jacobi & Kahl, 2021). With earlier detection of predators, turtles aggregated at basking sites may thermoregulate less effectively as turtles that abandon basking sites may not return (Moore & Segal, 2006; Bulté et al., 2020). However, basking turtles in urban areas may acclimate to disturbances (Polich & Barazowski, 2016), thus aggregating at basking sites would not be a detrimental behaviour at my study site.

Painted turtles fled basking sites from further away earlier in the active season. The thermoregulatory cost of abandoning a basking site is higher when the water is cold (Jain-Schlaepfer et al., 2017). I measured the difference between air temperature and water surface temperature which should be a good index of the cost of abandoning a basking site, but this variable did not explain flight initiation distance. Using the body temperature of basking turtles to predict flight initiation distance may be a better way to measure the cost of abandoning a basking site when water temperatures are cold.

Basking northern map turtles fled from further away when more females were present at basking sites. Female turtles may be more wary of potential predators whereas males may be bolder thus having a lower FID. A previous study did not find differences in boldness between male and female box turtles (Carlson & Tetzlaff, 2019), however, variation in boldness between individual turtles (Cassola et al., 2020) can affect their flight initiation distance.

Freshwater turtles may indeed aggregate at basking sites to better detect predators; however, aggregations at basking sites may also be a result of other social reasons. Aggregation may occur at basking sites as turtles may simply copy others, in a similar way nesting female turtles use cues from conspecifics to find suitable nesting habitat (Kell et al., 2022). Aggregations at basking sites may also allow freshwater turtles to assess potential mates and increase mating opportunities, as speculated in smooth softshell turtles (Plummer, 1977). Males may also aggregate to assess rivals as some basking aggregations consist entirely of male turtles and aggressive interactions are frequently documented between turtles (Lindeman, 1999), especially males (Rovero et al., 1999).

5 CONCLUSION

I found painted turtles and northern map turtles may aggregate at basking sites for both asocial reasons and social reasons. Specifically, turtles aggregate at basking sites with preferred basking site characteristics and to detect predators from further away, however, with small biological effect sizes. The size of aggregations may be dependent on several asocial reasons and social reasons which make basking site aggregations highly variable and difficult to predict accurately. Future studies should further investigate why turtles aggregate at basking sites by using artificial basking sites with varying habitat characteristics and to further investigate additional social reasons for aggregation.

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7 APPENDIX

Table A1. Summary statistics for the top five models produced by AIC model selection for the generalized linear mixed models of basking site characteristics that influence painted turtle basking site aggregations at Petrie Island, Ottawa in 2021.

Model	AICc	Delta_AICc	AICcWt
Number.of.painted.turtles ~ Julian.Date + Time + Basking.site.area + Distance.to.shoreline + Canopy.coverage + Site.orientation + (1 | Basking.site.number)	2494.00	0.00	0.59
Number.of.painted.turtles ~ Julian.Date + Basking.site.area + Canopy.coverage + Site.orientation + (1 | Basking.site.number)	2497.86	2.96	0.14
Number.of.painted.turtles ~ Julian.Date + Basking.site.area + Distance.to.shoreline + Canopy.coverage + Site.orientation +	2497.91	3.01	0.13

(1 | Basking.site.number)			
Number.of.painted.turtles ~ Julian.Date + Time + Basking.site.area + Distance.to.shoreline + (1 | Basking.site.number)	2499.06	4.16	0.07
Number.of.painted.turtles ~ Julian.Date + Time + Basking.site.area + Distance.to.shoreline + Canopy.coverage + (1 | Basking.site.number)	2499.32	4.42	0.07

Table A2. Summary statistics for the top five models produced by AIC model selection for the generalized linear mixed models of basking site characteristics that influence northern map turtle basking site aggregation at Petrie Island, Ottawa in 2021.

Model	AICc	Delta_AICc	AICcWt
Number.of.map.turtles ~ Julian.Date + Basking.site.area + Distance.to.shoreline + Site.orientation + (1 | Basking.site.number)	1450.94	0.00	0.57
Number.of.map.turtles ~ Julian.Date + Basking.site.area + Distance.to.shoreline + Canopy.coverage + Site.orientation + (1 | Basking.site.number)	1452.51	1.57	0.26
Number.of.map.turtles ~ Julian.Date + Time + Basking.site.area + Distance.to.shoreline + Canopy.coverage + Site.orientation + (1 | Basking.site.number)	1454.32	3.38	0.11

Number.of.map.turtles ~ Julian.Date + Basking.site.area + (1 | Basking.site.number)	1455.31	4.37	0.06
Number.of.map.turtles ~ Basking.site.area + Distance.to.shoreline + Canopy.coverage + Site.orientation + (1 | Basking.site.number)	1470.28	19.34	0.00

Table A3. Summary statistics for the top five models produced by AIC model selection for the generalized linear mixed models of the flight initiation distance of aggregated basking painted turtles at Petrie Island, Ottawa in 2022.

Model	AICc	Delta_AICc	AICcWt
Flight.initiation.distance ~ Julian.Date + Painted.turtles + (1 | Site.number)	1715.14	0.00	0.46
Flight.initiation.distance ~ Julian.Date + Air.SW.temp.difference + Painted.turtles + (1 | Site.number)	1717.10	1.96	0.17
Flight.initiation.distance ~ Julian.Date + Air.SW.temp.difference + Painted.turtles + Sex.ratio + (1 | Site.number)	1717.41	2.27	0.15
Flight.initiation.distance ~ Julian.Date + Time + Painted.turtles + Sex.ratio + (1 | Site.number)	1717.42	2.28	0.15

Flight.initiation.distance ~ Julian.Date + Basking.site.temp + Air.SW.temp.difference + Painted.turtles + (1 | Site.number)	1718.69	3.54	0.08

Table A4. Summary statistics for the top five models produced by AIC model selection for the generalized linear mixed models of the flight initiation distance of aggregated basking northern map turtles at Petrie Island, Ottawa in 2022.

Model	AICc	Delta_AICc	AICcWt
Flight.initiation.distance ~ Julian.Date + Map.turtles + Sex.ratio + (1 | Site.number)	1184.86	0.00	0.48
Flight.initiation.distance ~ Julian.Date + Air.SW.temp.difference + Map.turtles + Sex.ratio + (1 | Site.number)	1187.01	2.14	0.16
Flight.initiation.distance ~ Julian.Date + Time + Basking.site.temp + Map.turtles + Sex.ratio + (1 | Site.number)	1187.31	2.45	0.14
Flight.initiation.distance ~ Julian.Date + Time + Air.SW.temp.difference + Map.turtles + Sex.ratio + (1 | Site.number)	1187.41	2.54	0.13

Flight.initiation.distance ~ Julian.Date + Map.turtles + (1 | Site.number)	1188.38	3.51	0.08

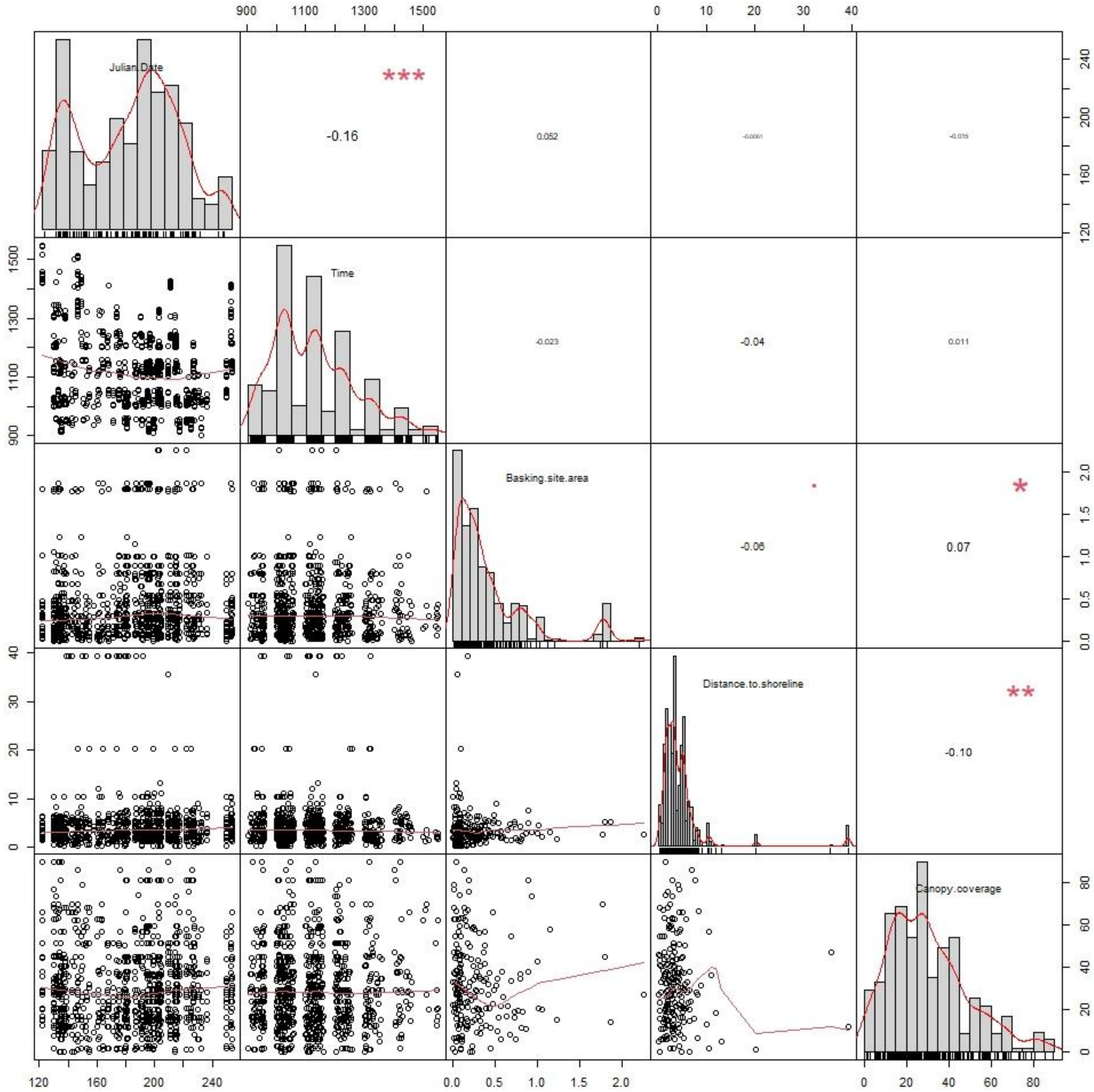

Figure A1. Correlation matrix for predictor variables used to model the basking site characteristics that influence painted turtle basking site aggregation at Petrie Island, Ottawa in 2021. Basking site orientation is excluded as it is a categorical variable and impossible to include in a correlation matrix. Correlation ≥ 0.7 is considered high. Asterisks represent p-values (*** = 0.001, ** = 0.01, * = 0.05).

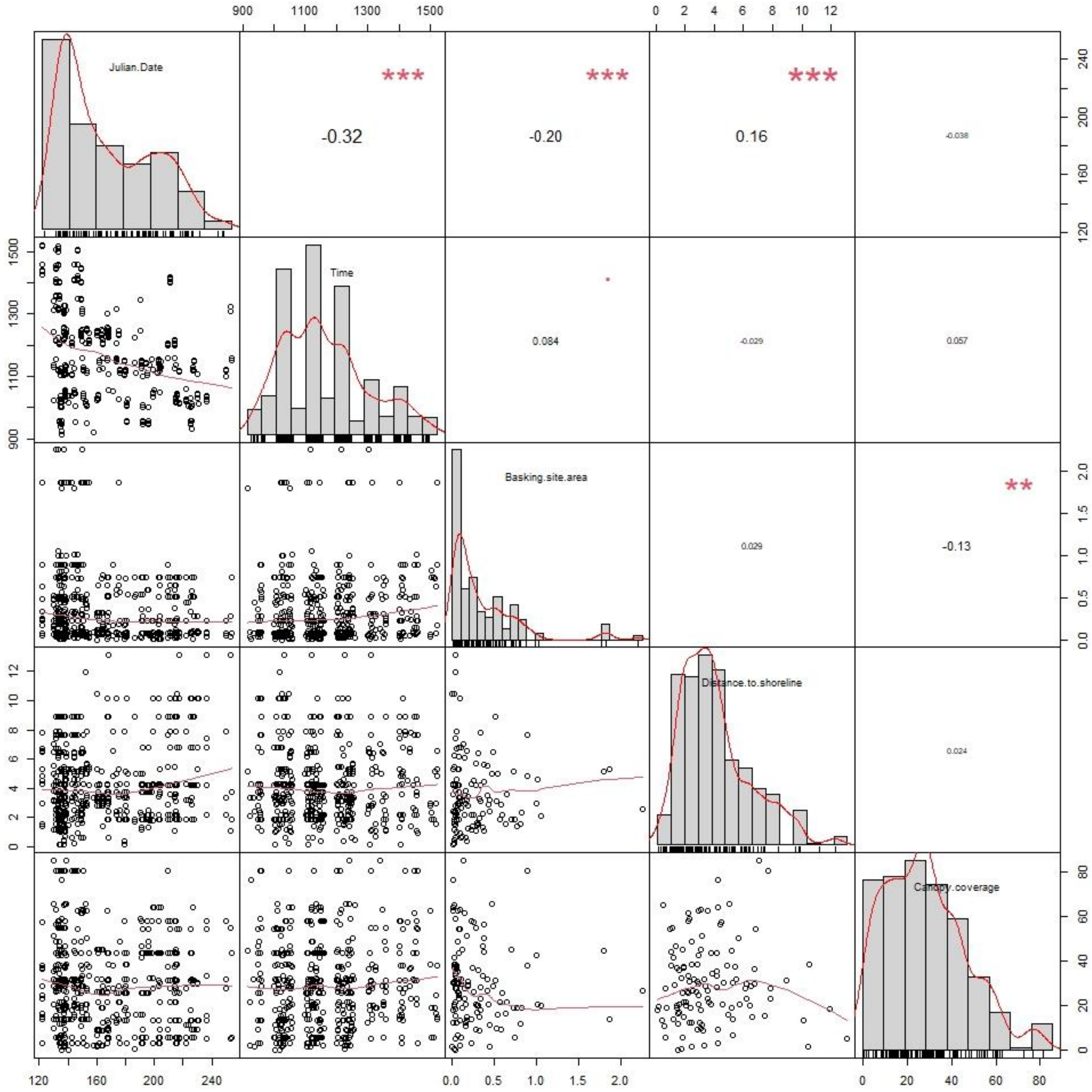

Figure A2. Correlation matrix for predictor variables used to model the basking site characteristics that influence northern map turtle basking site aggregate at Petrie Island, Ottawa in 2021. Basking site orientation is excluded as it is a categorical variable and impossible to include in a correlation matrix. Correlation ≥ 0.7 is considered high. Asterisks represent p-values (*** = 0.001, ** = 0.01, * = 0.05).

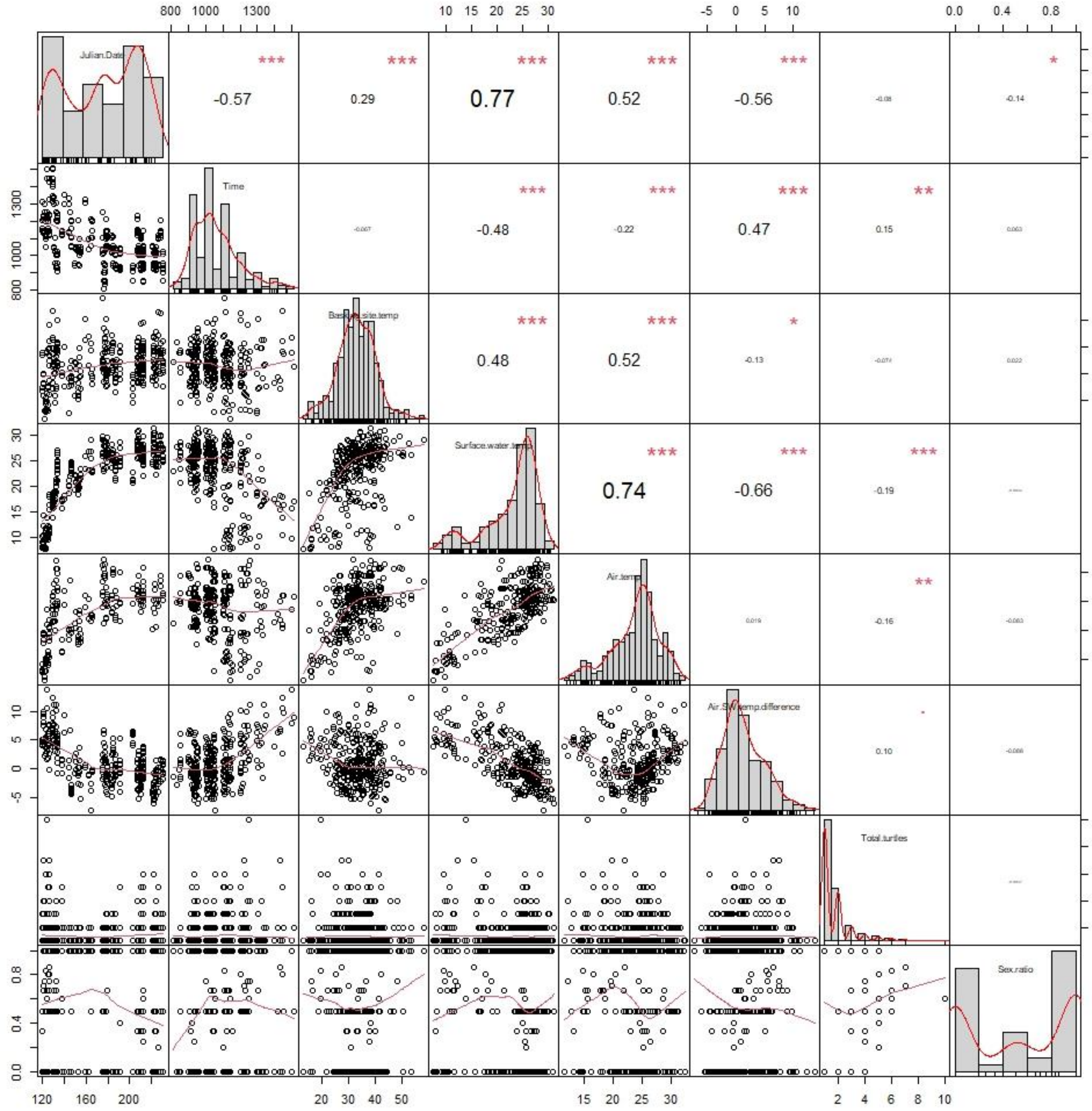

Figure A3. Correlation matrix for predictor variables used to model the flight initiation distance of aggregate basking painted turtles at Petrie Island, Ottawa in 2022. Correlation ≥ 0.7 is considered high. Asterisks represent p-values (*** = 0.001, ** = 0.01, * = 0.05).

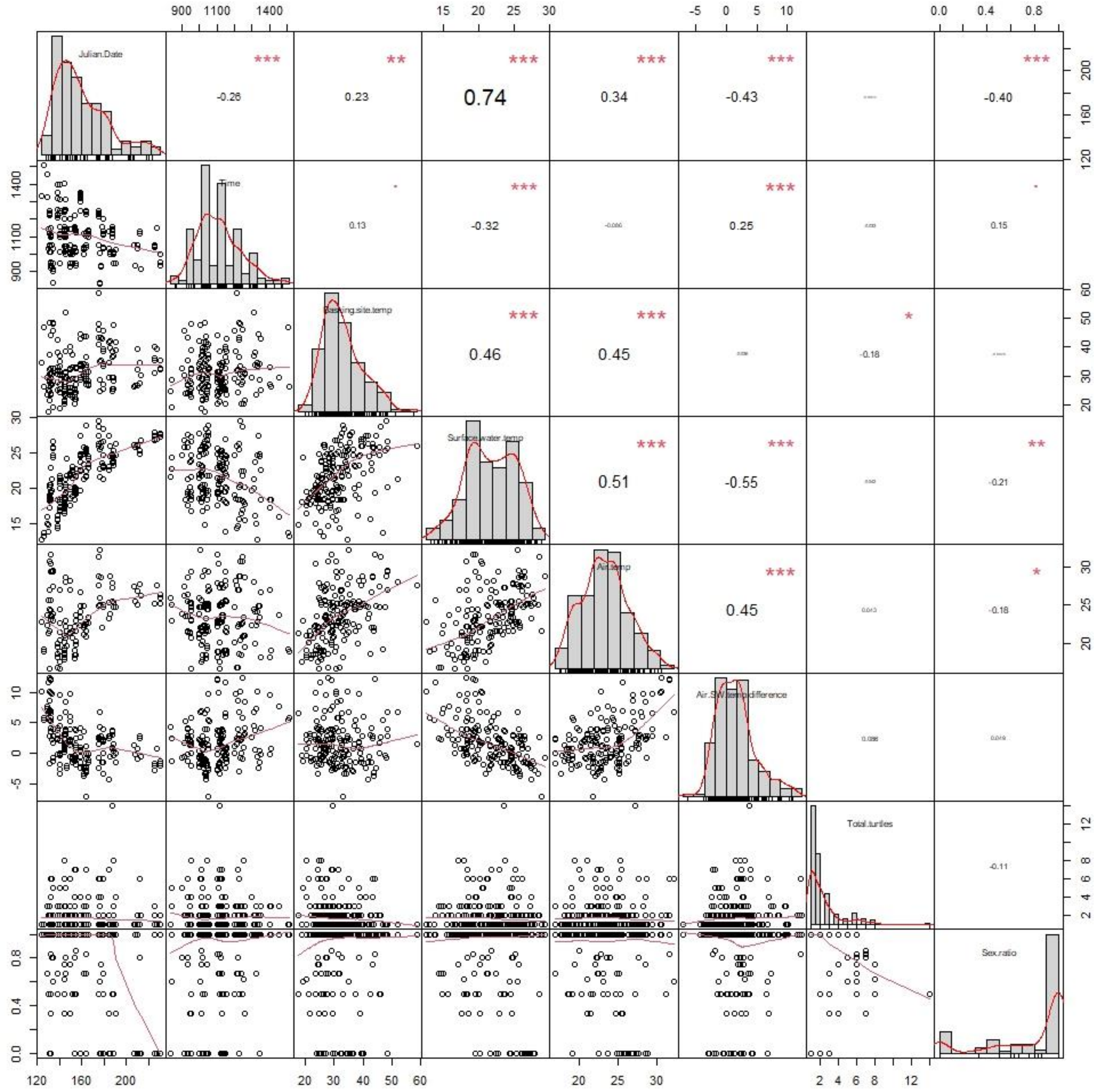

Figure A4. Correlation matrix for predictor variables used to model the flight initiation distance of aggregate basking northern map turtles at Petrie Island, Ottawa in 2022. Correlation ≥ 0.7 is considered high. Asterisks represent p-values (*** = 0.001, ** = 0.01, * = 0.05).

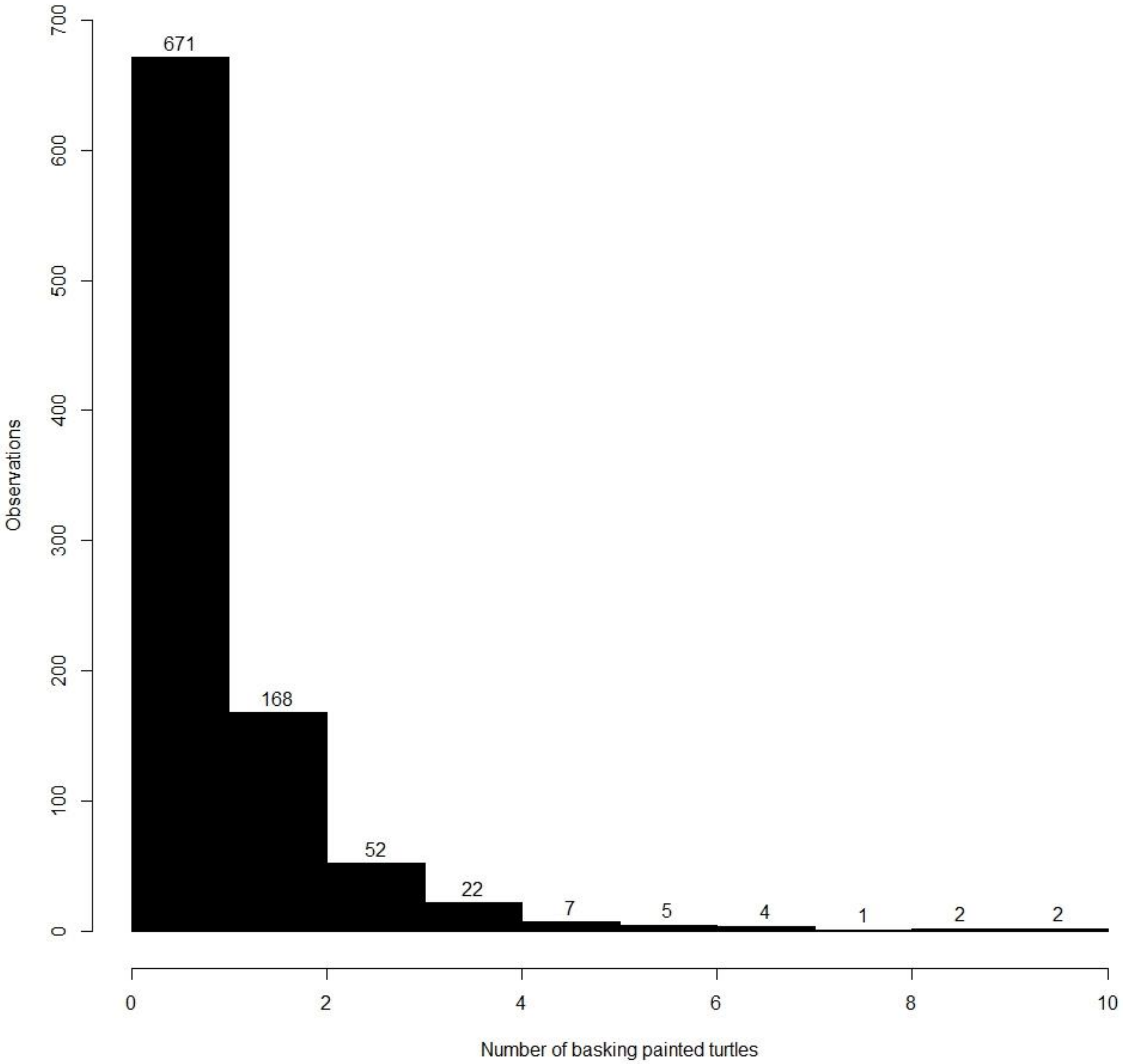

Figure A5. Histogram of the observations of the number of basking painted turtles during basking surveys in 2021 at Petrie Island, Ottawa.

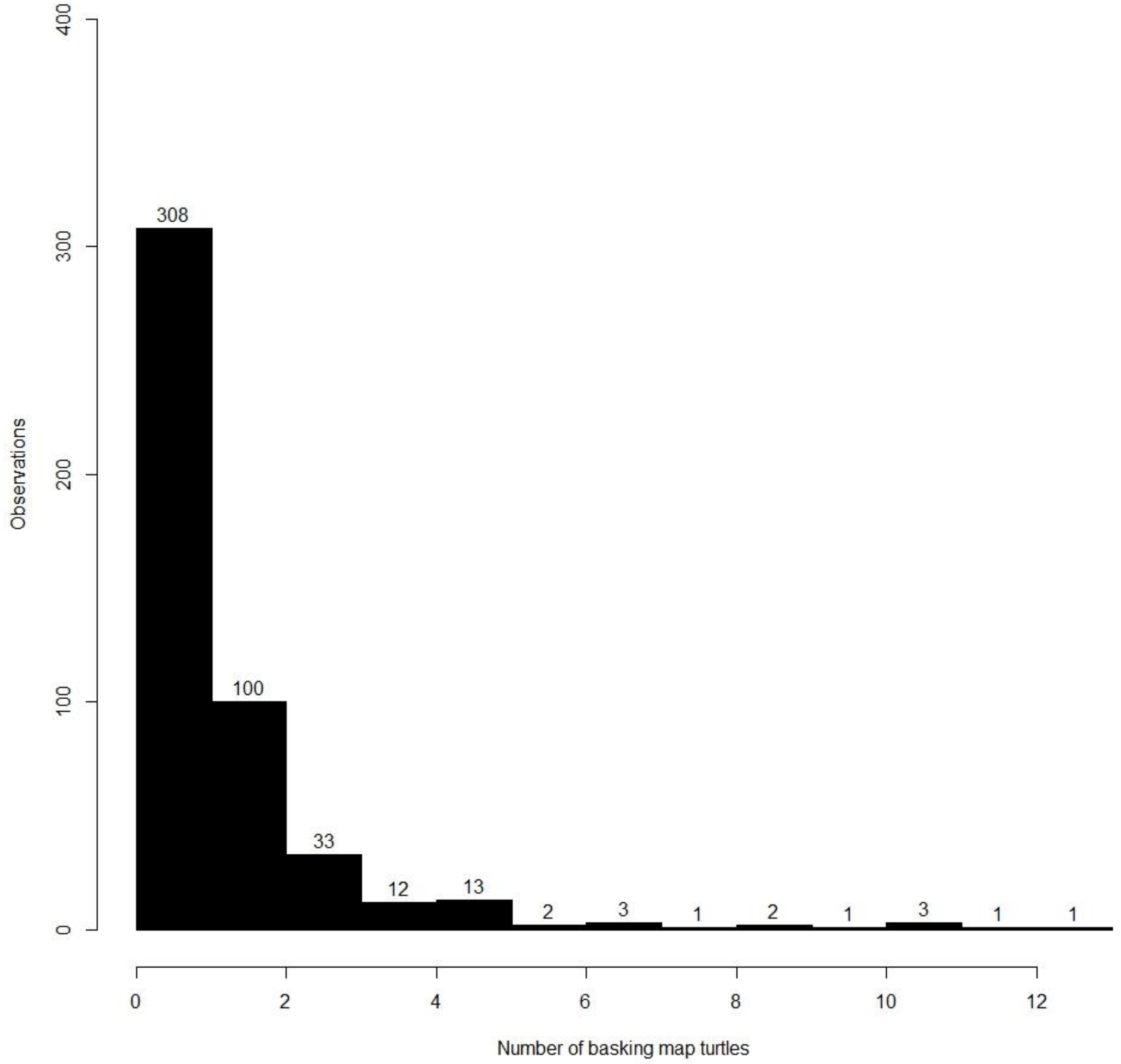

Figure A6. Histogram of the observations of the number of basking northern map turtles during basking surveys in 2021 at Petrie Island, Ottawa.

Table A5. Descriptive statistics for basking site characteristics that influences painted turtle basking aggregations at Petrie Island, Ottawa in 2021.

Statistic	Value
Mean number of basking painted turtles	1.5
Number of basking painted turtles standard deviation	1.1
Number of basking painted turtles range	1-10
Mean canopy coverage (%)	30.23
Canopy coverage standard deviation (%)	18.81
Canopy coverage range (%)	0.02-89.58
Mean available basking area (m^2)	0.42
Available basking area standard deviation (m^2)	0.45
Available basking area range (m^2)	0.0077-2.25
Mean distance to shoreline (m)	4.47
Distance to shoreline standard deviation (m)	5.42
Distance to shoreline range (m)	0.15-39.30

Table A6. Descriptive statistics for basking site characteristics that influenced northern map turtle basking site aggregations at Petrie Island, Ottawa in 2021.

Statistic	Value
Mean number of basking northern map turtles	1.8
Number of basking northern map turtles standard deviation	1.6
Number of basking northern map turtles range	1-13
Mean canopy coverage (%)	29.60
Canopy coverage standard deviation (%)	19.01
Canopy coverage range (%)	0.01-85.5
Mean available basking area (m^2)	0.36
Available basking area standard deviation (m^2)	0.42
Available basking area range (m^2)	0.0077-2.25
Mean distance to shoreline (m)	4.25
Distance to shoreline standard deviation (m)	2.52
Distance to shoreline range (m)	0.11-13.12

Table A7. Descriptive statistics for the flight initiation distance of aggregated basking painted turtles at Petrie Island, Ottawa in 2022.

Statistic	Value
Mean flight initiation distance (m)	6.62
Flight initiation distance standard deviation (m)	4.92
Flight initiation distance range (m)	0.349-33.102
Mean number of basking painted turtles	1.7
Number of basking painted turtles standard deviation	1.2
Number of basking painted turtles range	1-10
Mean air temperature (°C)	24.1
Air temperature standard deviation (°C)	4.2
Air temperature range (°C)	11.5-32.3
Mean basking site temperature (°C)	33.1
Basking site temperature standard deviation (°C)	7.3
Basking site temperature range (°C)	12.9-58.1
Mean surface water temperature (°C)	23.1
Surface water temperature standard deviation (°C)	5.6
Surface water temperature range (°C)	7.6-31.2
Mean air temperature to surface water temperature difference (°C)	1.0
Air temperature to surface water temperature difference standard deviation (°C)	3.73
Air temperature to surface water temperature difference range (°C)	-7.3-13.8

Table A8. Descriptive statistics for the flight initiation distance of aggregated basking northern map turtles at Petrie Island, Ottawa in 2022.

Statistic	Value
Mean flight initiation distance (m)	14.04
Flight initiation distance standard deviation	8.14
Flight initiation distance range	1.21-40.26
Mean number of basking painted turtles	2.3
Number of basking painted turtles standard deviation	1.9
Number of basking painted turtles range	1-14
Mean air temperature (^{o}C)	23.5
Air temperature standard deviation (^{o}C)	3.5
Air temperature range (^{o}C)	16.8-32.2
Mean basking site temperature (^{o}C)	31.6
Basking site temperature standard deviation (^{o}C)	7.5
Basking site temperature range (^{o}C)	17.6-58.8
Mean surface water temperature (^{o}C)	21.7
Surface water temperature standard deviation (^{o}C)	3.7
Surface water temperature range (^{o}C)	12.7-29.4
Mean air temperature to surface water temperature difference (^{o}C)	1.8
Air temperature to surface water temperature difference standard deviation (^{o}C)	3.6
Air temperature to surface water temperature difference range (^{o}C)	-7.1-12.4