

The impact of urbanization on painted turtle (*Chrysemys picta*) behaviour

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Abstract

Urbanization is a significant driver of the global biodiversity crisis. Turtles are particularly impacted by urbanization because of the vulnerability of riparian habitats to habitat loss and road mortality. Behaviour plays a crucial role in determining the success of urban animals. Behavioural responses to urbanization, however, are rarely studied in turtles even though many turtles are at-risk and sometimes live in urban areas. Therefore, we evaluated behavioural changes in painted turtles (*Chrysemys picta*) living in wetlands surrounded by a gradient of urbanization. We tested the consistency of painted turtle behaviour in the laboratory and examined the behaviour of painted turtles from 24 wetland sites across an urbanization gradient in Ottawa, Ontario, Canada. We assessed: (i) aggression by measuring the number of active defensive behaviours the turtles performed in response to handling, (ii) boldness by measuring the amount of time the turtles took to emerge from their shells and move from their initial locations in a circular arena and (iii) activity by measuring the amount of time the turtles spent moving in the same circular arena. We found that all behaviours were consistent in the laboratory. We also found that as the level of urbanization increased, turtles were more aggressive and bolder. Urbanization affects painted turtle behaviour, but further research is required to understand the mechanisms responsible and the conservation implications.

KEYWORDS

activity, aggression, anthropogenic disturbance, boldness, habitat loss, repeatability

1 | INTRODUCTION

We are currently facing a global decrease in biodiversity (Almond et al., 2022; Segan et al., 2016). Habitat loss is the primary cause of this reduction in biodiversity for terrestrial species (Sala et al., 2000). For instance, 16,919 mammal, bird and amphibian species lost an average of 18% of their natural habitat area since 1700 and this could rise to 23% by 2100 (Beyer & Manica, 2020). The impacts of habitat loss on wildlife populations include isolation, reduced genetic

diversity, decreased reproductive success and eventually extinction (Segan et al., 2016). As habitat loss continues, wildlife living near humans will be increasingly affected.

Urbanization is one of the primary drivers of habitat loss and is a major conservation concern (Lowry et al., 2013). Approximately 52% of the world's population is currently living in cities and urban area is expected to be multiplied by up to three times by 2050 (Liu et al., 2016). Urbanization not only affects wildlife through habitat loss, but also through novel perturbations, such as increased human

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contact, invasive species and pollution (Charmantier et al., 2017; Partecke et al., 2006). The ability to respond to these changes is a key factor in determining the success of urban animals.

Several behavioural traits appear to benefit animals living in more disturbed habitats, such as aggression, boldness and activity (Łopucki et al., 2021; Sol et al., 2013). Natural resources in urban environments tend to be more limited than in natural environments (Lowry et al., 2013). In addition, novel anthropogenic resources that urban animals may use to compensate for this are often clumped (Hurtado & Mabry, 2017). Due to this, urban animals may face heightened competition over resources, thus favoring more aggressive individuals (Hurtado & Mabry, 2017; Lowry et al., 2013). Urban environments also typically have high rates of disturbance because of increased interactions with humans and medium-sized predators (Bateman & Fleming, 2012; Hurtado & Mabry, 2017). Bolder animals may experience less stress from these disturbances, allowing for more time and energy to be devoted to beneficial activities such as foraging (Dammhahn et al., 2020; Lowry et al., 2013). Finally, active animals travel more frequently and have larger home ranges (Moule et al., 2016). Thus, these animals may be more likely to discover and take advantage of the novel resources present in urban environments (Dammhahn et al., 2020). It is important to better understand these behavioural changes occurring in response to urbanization, as this can help determine the extent to which animals can adapt to urban environments and identify which habitats are best suited to supporting certain species (Magle & Angeloni, 2011; Marzluff et al., 2008).

Reptiles are heavily impacted by human activities and approximately one-fifth of all reptile species are threatened with extinction (Böhm et al., 2013; Cox et al., 2022). Out of the most common human land-use changes, urbanization has the greatest negative effect on reptile species richness (Cordier et al., 2021). Approximately 61% of turtle species are threatened or extinct (Lovich et al., 2018), with freshwater turtles especially impacted by urbanization due to their high rates of road mortality and the vulnerability of riparian habitats to habitat loss (Ryan et al., 2014). Nevertheless, most research concerning urban animal behaviour is done on mammals and birds (Brum et al., 2022). Considering the vulnerability of turtles to

human activities and the limited research on the effects of urbanization on their behaviour, it is crucial to investigate how urbanization influences turtle behaviour.

Our objective was to examine the effect of a gradient of urbanization on painted turtle (*Chrysemys picta*) behaviour. Specifically, we examined the relationship between the level of urbanization and painted turtle aggression, boldness and activity. Our experimental design did not allow us to distinguish between the various mechanisms that could underlie behavioural differences.

Our first hypothesis was that as the level of urbanization increases, aggression should increase in painted turtles because of higher competition over resources due to reduced availability and higher resource clumping (Hurtado & Mabry, 2017; Lowry et al., 2013). More aggressive individuals should be able to outcompete their conspecifics and gain access to these limited resources. Our second hypothesis was that as the level of urbanization increases, boldness should increase in painted turtles because of the benefits of higher disturbance tolerance due to increased interactions with humans and predators (Bateman & Fleming, 2012; Lowry et al., 2013). Bolder individuals should be able to spend more time and energy on other activities such as basking or foraging. Our third hypothesis was that as the level of urbanization increases, activity should increase in painted turtles because of a higher likelihood of being able to find and take advantage of novel resources (Dammhahn et al., 2020). Therefore, overall, we predicted that as the level of urbanization increases, aggression, boldness and activity should increase in painted turtles.

2 | MATERIALS AND METHODS

2.1 | Species and study sites

Painted turtles are small to medium-sized and are widespread across North America (Ernst & Lovich, 2009). Painted turtles occupy a variety of freshwater habitats and are commonly observed in human-altered environments (DeCatanzaro & Chow-Fraser, 2010; Rizkalla & Swihart, 2006).

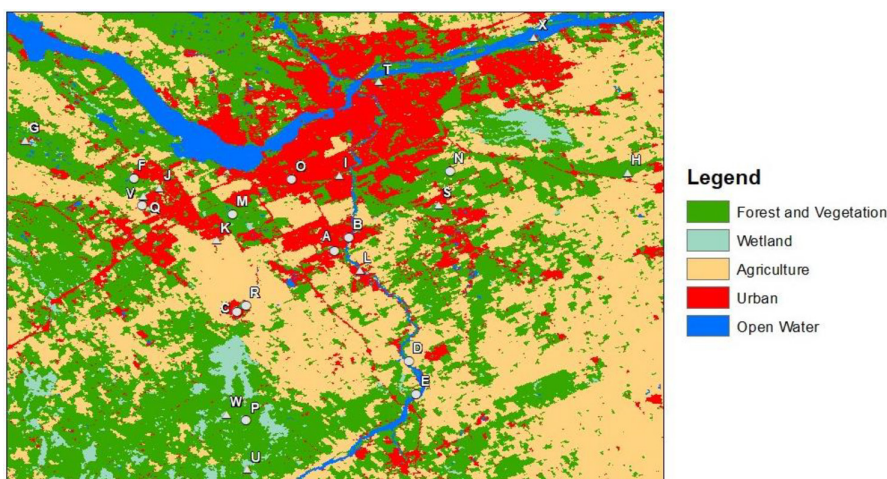


FIGURE 1 Wetlands (24; grey) along a gradient of urbanization where painted turtles were sampled in Ottawa, Ontario, Canada, in 2021 and 2022. Sites where turtles were used for field tests (circles) and sites where turtles were used for field and laboratory tests (triangles) are labeled alphabetically in order of sampling.

We collected data on 505 painted turtles from May to August in 2021 and 2022 in Ottawa, Ontario, Canada. As detailed below, we measured aggression, boldness and activity in turtles from 24 wetland sites spanning a gradient of urbanization (Figure 1). The percentage of urban area within a buffer with a 1000m radius around the wetlands ranged from 0% to 92% (Material S1, Figure S1).

2.2 | Captures and measurements

We sampled wetlands one at a time for 1 week. The timing of sampling was randomized with respect to urbanization to account for potential seasonal effects on turtle behaviour (Clavijo-Baquet & Magnone, 2017; Ruso et al., 2017). Turtles were captured with hoop nets (0.9m diameter, 3m length; Čapkun-Huot & Blouin-Demers, 2019; Larocque et al., 2012; Turcotte et al., 2023). Nets were deployed so they breached the surface and floats were placed inside (Larocque et al., 2012). We checked the nets every day and all adult painted turtles captured were tested. We took the turtles to shore and weighed them using a Pelosa 10kg spring scale and measured their plastron length with VWR digital calipers. We determined their sex based on secondary sexual characteristics (Morjan, 2003). To identify individual turtles, we used a file to make small notches in unique combinations in the marginal scutes according to the North American Code (Nagle et al., 2017).

2.3 | Field and laboratory behavioural tests

The behavioural tests in the field were performed adjacent to the wetlands we studied. The turtles were in a plastic circular arena for some of the tests (see below), which was placed in a shaded area to help standardize testing temperature and to avoid overheating. We recorded air and water temperatures to account for any temperature related behavioural differences. After the tests were completed, we released the turtles at their capture location.

We randomly selected 58 of the turtles that we tested in the field from 12 of our wetlands (Figure 1) and measured their behavioural responses in a controlled environment to estimate behavioural repeatability. We performed the same measurements and behavioural tests in the laboratory as those conducted in the field. Each turtle was tested once per day, with 40 of the turtles tested over 4 days and 18 of the turtles tested over 3 days (Material S1, Table S1).

For our analyses of turtle behaviour in the laboratory and the field, we controlled statistically for variation in testing conditions (e.g., water temperature and the proportion of different landcover types around the wetland of capture) and individual characteristics (e.g., mass and sex) to account for possible sampling bias according to the STRANGE framework (Webster & Rutz, 2020). The STRANGE framework was designed to help scientists identify and mitigate potential sampling biases in animal behaviour research

(Webster & Rutz, 2020). The acronym STRANGE stands for: Social background; Trappability and self-selection; Rearing history; Acclimation and habituation; Natural changes in responsiveness; Genetic make-up; and Experience. We attempted to limit the effects of handling and measurement techniques on behaviour by always performing the tests in the same way and order. No information was available on the past social experiences of turtles, because they were caught in the wild. We were not blinded to turtle and site identity.

We performed four behavioural tests for each turtle: (1) The number of active defensive behaviours performed while being handled, (2) the amount of time it took the turtles to emerge from their shells while in a plastic circular arena, (3) the amount of time it took the turtles to move from their initial location in the arena, (4) the total time the turtles spent moving in the arena (Material S1, Table S1).

2.3.1 | Active defensive behaviours

While taking the morphometric measurements of the turtles, we measured the number of active defensive behaviours they performed while being handled, which we used as an index of aggression. The active defensive behaviours we measured were: (1) kicking with the legs to free itself, (2) hissing, (3) gaping or biting, (4) defecation or urination. We then summed the active defensive behaviours that each turtle performed (e.g., if a turtle bit and kicked, it would have a score of 2; if it just kicked, it would have a score of 1) based on previous behavioural studies of turtles (Čapkun-Huot & Blouin-Demers, 2019; Pich et al., 2019; Polo-Cavia et al., 2011; Turcotte et al., 2023). We assumed that individuals that performed more active defensive behaviours were more aggressive.

2.3.2 | Time of shell emergence and initial movement

After taking the morphometric measurements, we put the turtles individually under a plastic bucket in the center of a circular arena (diameter=1.5m) for 2 min so that they could acclimate. The turtles were always placed in the same location in the arena and facing away from the experimenter performing the test. After 2 min, we removed the bucket and stood approximately 2–3m away while maintaining visibility. We then measured the amount of time it took the turtles to emerge from their shells as well as the amount of time it took for them to move from their initial location in the arena for a maximum of 10 min based on previous studies (Carlson & Tetzlaff, 2020; Kashon & Carlson, 2018; Pich et al., 2019; Turcotte et al., 2023). If a turtle did not emerge from its shell within 10 min, we stopped the tests and removed the turtle from the arena. We assumed that individuals that took less time to emerge from their shell and move from the initial location were bolder.

2.3.3 | Total time spent moving

If the turtle did move from its initial location within 10 min, we recorded it for 3 min starting from the moment of its initial movement and measured the amount of time it spent moving in the arena. Turtle activity in an arena is not commonly studied, so we based the measurement time on a study of turtle reaction to a simulated predator attack (Pich et al., 2019). We assumed that individuals that spent more time moving around the arena were more active.

2.4 | Ethics approval statement

All procedures were approved by the animal care committee at the University of Ottawa (protocol BL-3629-R1 A1). All fieldwork was conducted under a Wildlife Scientific Collector's Authorization from the Ontario Ministry of Natural Resources (numbers 1097807, 1099985). Fieldwork on City of Ottawa land was conducted under Consent to Enter permits from the City of Ottawa (CON2021-RSD-0022, CON2022-0009) and fieldwork on National Capital Commission land was conducted under Land Access Permits (numbers 23387, 24057) and with a Species at Risk Act permit (number SARA-OR-2022-0660) from Environment and Climate Change Canada. During the field experiments, turtles that were not being tested were kept under constant supervision in plastic tubs out of direct sunlight, with a small amount of water from their wetland of capture. During the laboratory experiments, turtles were tested in an adjacent room to where they were housed. Turtles were housed individually in tubs containing dechlorinated water and a basking platform and kept at 23°C on a natural photoperiod of 13 h of light and 11 h of dark. They were fed earthworms twice a week and provided with fresh, dark leafy greens (Juneau et al., 2015). The health status of the laboratory turtles was visually verified each day and prior to their release at their home wetland.

2.5 | Repeatability analyses

We performed statistical analyses with R, version 4.2.2 (R Core Team, 2022). We calculated the repeatability of turtle behaviour in response to our tests in the laboratory using the rpt function from the rptR package (Stoffel et al., 2017). Repeatability is the proportion of phenotypic variance that can be attributed to differences between individuals (Nakagawa & Schielzeth, 2010). A higher repeatability value indicates high among-individual variance relative to within-individual variance. Before we began our analyses, we examined the distributions of the data for each of the behaviours to select the best distribution for our models. The number of active defensive behaviours performed while being handled and the total time spent moving were best fitted by a normal distribution. The time of shell emergence was heavily skewed, with most turtles emerging from their shells at 0s (179 observations out of 213; Material S1, Figure S2). We thus decided to convert time of shell emergence into a binary variable, with turtles that emerged from their shells at 0s coded as '0' and turtles that did not

emerge from their shells at 0s coded as '1'. The data for the time of initial movement were also skewed because there were many turtles that started moving at 0 seconds (31 observations out of 170; Material S1, Figure S2). We used a $\log(x+1)$ transformation to try to render the distribution normal, but the log transformed data were still skewed (Material S1, Figure S2). As neither the raw or transformed data were normally distributed, we decided to examine both.

We first calculated the unadjusted repeatability for each behaviour with only turtle identity as a random effect. We then calculated the adjusted repeatability by adding the day of testing (day 1–4) and sex as fixed effects to adjust our models for among-individual differences and added site identity as a random effect. We included site identity as a random effect to control for the non-independence of observations from the same locations. We ran each test with 1000 bootstrap iterations. Finally, we calculated the Pearson and Spearman's correlations between the laboratory behaviours using the mean value of each behaviour for each individual.

2.6 | Landscape analyses

We extracted the landscape variables in ArcMap version 10.8.1 (ESRI, 2020) using the 2020 Land Cover of Canada layer (Latifovic, 2020). The original file contained 15 land cover classes and we condensed them into five (open water, wetland, forest/vegetation, urban and agriculture; Material S1, Table S2). We then created buffers in 100 m increments around each sampling wetland, centered on the locations of the hoop nets and extending up to 1000 m based on previous studies (Fyson & Blouin-Demers, 2021; Turcotte et al., 2023). The area of each land cover type was calculated as a percentage of the total area for each buffer.

We calculated the correlations between the land cover classes and behaviours at each buffer distance. The buffer distance with the maximum correlation between each land cover class and behaviour, the scale of maximum effect (Material S1, Table S3), was used in further analyses.

2.7 | Behavioural analyses

We used generalized linear mixed models to determine the relationship between urbanization and the behaviour of painted turtles that were tested in the field using the lme4 package (Bates et al., 2015). We examined the distributions for all the behaviours measured in the field. The total time spent moving was best fit by a normal distribution (Material S1, Figure S3). The number of active defensive behaviours performed while being handled and the time of initial movement were not normally distributed (Material S1, Figure S3). Because the lmer function that we used to create our models can generally handle non-normal functions (Schielzeth et al., 2020), however and since we could not perform a transformation on the number of active defensive behaviours as the data were discrete, we left them untransformed and fit them with normal distributions. The time

of shell emergence was heavily skewed, with many turtles emerging from their shells at 0s (288 observations out of 512; [Material S1, Figure S3](#)). Because of this, we converted the time of shell emergence into a binary variable, as done for the repeatability analyses. We then calculated the correlations between the land cover classes and the updated binary distribution for the time of shell emergence at each buffer distance following the methods previously described.

Next, we standardized all the continuous predictor variables (mean of zero, unit variance). We then created an initial model for each of the behaviours with only the fixed effects and removed effects that had a high general variance inflation factor ($GVI\frac{1}{2\text{ndf}} > 2$) or correlation value ($r > .7$) with other predictors ([Material S1, Tables S4 and S5](#)). The fixed effects that we used for each initial model were the calendar date of testing, air and water temperatures, time of testing, mass, plastron length, sex and the proportion of area for each land cover category at its scale of maximum effect. The descriptive statistics of the continuous fixed effects before they were standardized can be found in [Material S1, Table S6](#). Calendar date of testing, air and water temperatures and time of testing were included to account for any environmental effects on behaviour. The mass, plastron length and sex were included to account for any physiological effects on behaviour (Turcotte et al., 2023). The proportion of area for each land cover category was included to account for the effect of different land cover types on behaviour. We then added turtle and site identity as random effects to each model to account for individuals that were caught multiple times and to control for the non-independence of observations from the same wetlands. Next, we verified the model assumptions by checking their residual distributions and their relationships with fitted values. We then checked the significance of the random effects for each of the models using a likelihood ratio test (Crawley, 2007). The list of significant random effects for each model can be found in [Material S1, Table S7](#). Next, we tested the significance of the remaining fixed effects for each model by using a backward selection procedure and confirmed the deletion of each fixed effect with a likelihood ratio test (Crawley, 2007). Each final non-binary model was fitted with restricted maximum likelihood and then we calculated the 95% confidence intervals of the fixed effects (Zuur et al., 2009), the marginal and conditional R^2 values using the MuMIn package (Bartoń, 2023) and generated final model predictions with the ggeffects package (Wickham, 2016). We then calculated the Pearson and Spearman's correlations between all the field behaviours using the raw data for each individual.

3 | RESULTS

3.1 | Repeatability of behaviour

We estimated the repeatability of the behaviour of 58 turtles in the laboratory ([Material S1, Table S1](#)). We only made two observations of turtle urinating/defecating, so it was not included in our analyses.

We found significant adjusted repeatability estimates for the number of active defensive behaviours performed while being handled ($R = .582, p < .001, 95\% \text{ CI} = [0.394, 0.756]$), time of shell emergence ($R = .677, p < .001, 95\% \text{ CI} = [0.522, 0.774]$), time of initial movement ($R = .542, p < .001, 95\% \text{ CI} = [0.334, 0.679]$) as well as the $\log(x + 1)$ -transformed data ($R = .442, p < .001, 95\% \text{ CI} = [0.237, 0.634]$) and the total time spent moving ($R = .513, p < .001, 95\% \text{ CI} = [0.299, 0.629]$; [Table 1](#)). There were some differences between the adjusted and unadjusted repeatability estimates, but the unadjusted estimates were still all repeatable and significant ([Table 1](#)). When the models were adjusted with fixed effects, the repeatability estimates for shell emergence, time of initial movement and total time spent moving increased, while they decreased for the number of active defensive behaviours performed while being handled and the $\log(x + 1)$ transformed time of initial movement ([Table 1](#)). For all behaviours, the 95% CI of the unadjusted and adjusted repeatability estimates overlapped ([Table 1](#)).

3.2 | Behavioural correlations

The turtles' behaviours were similarly correlated in the laboratory and field, except for the total time spent moving ([Material S1, Table S8](#)). In the laboratory, there was a statistically significant

TABLE 1 Repeatability estimates for painted turtle behaviours measured in the laboratory (active defensive behaviours, time of shell emergence, time of initial movement and its the $\log(x + 1)$ transformed version and total time spent moving). The unadjusted repeatability estimates only include turtle identity as a random effect, while the adjusted repeatability estimates also include turtle sex and day of testing as fixed effects and site identity as a random effect. The repeatability estimate (R), standard error (SE), 95% confidence intervals (95% CI) and p -value (p) are included. The data were collected from 58 turtle living in wetlands along a gradient of urbanization in Ottawa, Ontario, Canada in 2021 and 2022.

Model	R	SE	95% CI	p
<i>Active defensive behaviours</i> (214 observations)				
Unadjusted	.743	0.048	[0.635, 0.817]	<.001
Adjusted	.582	0.096	[0.394, 0.756]	<.001
<i>Time of shell emergence</i> (213 observations)				
Unadjusted	.675	0.070	[0.52, 0.788]	<.001
Adjusted	.677	0.069	[0.522, 0.774]	<.001
<i>Time of initial movement</i> (170 observations)				
Unadjusted	.484	0.083	[0.305, 0.627]	<.001
Adjusted	.542	0.091	[0.334, 0.679]	<.001
<i>Time of initial movement (log(x + 1) transformed)</i> (170 observations)				
Unadjusted	.609	0.069	[0.466, 0.721]	<.001
Adjusted	.442	0.103	[0.237, 0.634]	<.001
<i>Total time spent moving</i> (170 observations)				
Unadjusted	.483	0.08	[0.308, 0.628]	<.001
Adjusted	.513	0.09	[0.299, 0.629]	<.001

relationship between the total time spent moving and the number of active defensive behaviours performed (Pearson's correlation = .23, $p = .002$), the time of shell emergence (Pearson's correlation = -.15, $p = .049$) and the non-transformed version of the time of initial movement (Pearson's correlation = -.22, $p = .004$; [Material S1, Table S8](#)). In the field, there was a statistically significant relationship between the total time spent moving and the time of initial movement (Pearson's correlation = -.26, $p < .001$), but no relationship with the number of active defensive behaviours performed or the time of shell emergence ([Material S1, Table S8](#)).

3.3 | Relationship between urbanization and behaviour

We obtained data from 505 painted turtles during the field behavioural tests ([Material S1, Table S1](#)). Overall, 25 of the turtles were tested twice as they were recaptured once and three turtles were tested three times as they were recaptured twice, for a total of 536 behavioural tests performed on the turtles ([Material S1, Table S1](#)). We only made five observations of turtle urinating/defecating, so it was not included in our analyses. As the level of urbanization increased, turtles performed more active defensive behaviours (Estimate = 0.09, $p = .048$, 95% CI = [0.001, 0.178], $N = 536$) and emerged from their shells sooner (Estimate = -0.236, $p = .022$, 95% CI = [-0.441 to -0.034], $N = 512$; [Table 2; Figure 2a,b](#)). As the level of urbanization increased, turtles did not move from their initial location in the arena sooner or spend more time moving in the arena ([Table 2](#)).

4 | DISCUSSION

We found that painted turtles behaved consistently over time in a laboratory environment. We also found that as the level of urbanization increases, turtles were more aggressive and bolder. Overall, painted turtle behaviour was related to the proportion of urban area around their home wetland. These findings contribute to the field of turtle behaviour by providing evidence that painted turtle behaviour is repeatable and affected by urbanization.

4.1 | Repeatability and behavioural correlations

The painted turtles' number of active defensive behaviours, time of shell emergence, time of initial movement and total time spent moving were all repeatable in the laboratory, similar to other studies (Bell et al., 2009; Holtmann et al., 2017). All these repeatability estimates were obtained over relatively short time frames and in controlled environments and these conditions often lead to higher repeatability (Bell et al., 2009; Holtmann et al., 2017). Turcotte et al. (2023) tested painted turtles in the field and in the lab over several years

and obtained repeatability estimates which may be more representative of reality.

The correlations between the turtles' behaviours were similar in the laboratory and field, with the exception of the total time spent moving. In the laboratory, turtles that spent more time moving performed more active defensive behaviours and emerged from their shells sooner and moved from their initial locations sooner. In the field however, there was only a relationship between the total time spent moving and the time of initial movement. These differences could be because the laboratory represented a novel environment, which can affect behavioural expression (Mouchet & Dingemans, 2021; Rudin et al., 2018). Testing over several days may have also affected behaviour because of potential habituation to the tests (Martin & Réale, 2008). Unfortunately, we did not have enough repeated behavioural measurements of individual turtles in the field to compare their behavioural differences in the field and in the laboratory.

4.2 | Aggression

As the level of urbanization increased, painted turtles performed more active defensive behaviours, indicating an increase in aggression. This increased aggression could be due to the heightened competition over resources in urban animal populations (Hurtado & Mabry, 2017; Łopucki et al., 2021). Resources are often scarce in urban environments due to habitat loss and fragmentation (Birnie-Gauvin et al., 2017; Lowry et al., 2013; Steffan-Dewenter & Schiele, 2008). Therefore, many urban animals change their behaviours to take advantage of the novel anthropogenic resources available, such as human food waste and crops (Birnie-Gauvin et al., 2017; Demeny et al., 2019). These anthropogenic resources are often clumped, which brings urban animals into closer contact with each other and can lead to higher levels of competition and aggression (Hurtado & Mabry, 2017).

A resource that may heighten competition in painted turtles in urban areas are basking sites. Painted turtles use basking sites to aid in thermoregulation (Edwards & Blouin-Demers, 2007; Zipko, 1982) and compete over them (Bury et al., 1979; Lovich, 1988). The management of urban bodies of water can result in basking structures being removed, or vegetation and trees near the shore that may eventually fall in the water and become basking sites being cut (Spinks et al., 2003). Shoreline modification, such as for beaches and docks, could also reduce the number of natural basking sites (Carrière & Blouin-Demers, 2010; Hill & Vodopich, 2013). In addition, human disturbances such as boating and the use of trails along the edge of the bodies of water could reduce access to basking sites for turtles, as they often flee from humans (Pittfield & Burger, 2017). Fewer available basking sites would increase the number of interactions between painted turtles and the likelihood of competition and therefore potentially increase aggressive behaviour.

TABLE 2 The significance of the fixed effects on painted turtle behaviours (active defensive behaviours, time of shell emergence, time of initial movement and the total time spent moving) living in wetlands along an urbanization gradient in Ottawa, Ontario, Canada in 2021 and 2022. Values from the final model for the behaviour (as shown by the bolded effects) are shown, or for when the fixed effect was removed during the backwards selection process (non-bolded effects). The final model for each non-binary behaviour was fitted with restricted maximum likelihood (REML), which changed the estimates of the fixed effects in the final model. The estimate of effect (Estimate), standard error (SE), *t*-value (z-value for the time of shell emergence model as it is binary), *p*-value (*p*) and 95% confidence intervals (95% CI) are included. The likelihood ratio test *p*-value (LRT *p*), when the fixed effect was removed, are also included. The number of observations and individuals for the final model are included for each behaviour, as well as the marginal and conditional R^2 values.

Fixed effect	Estimate	SE	t-Value	<i>p</i>	95% CI	LRT <i>p</i>
<i>Active defensive behaviours</i> 536 observations (505 Individuals); R^2 Marginal: .037; R^2 Conditional: .799						
Intercept	1.024	0.046	22.495	<.001	[0.934, 1.110]	–
Air temperature	0.098	0.045	2.173	.030	[0.009, 0.187]	–
Proportion of urban area within 1000 m	0.090	0.045	1.979	.048	[0.001, 0.178]	–
Proportion of open water area within 1000 m	0.163	0.045	3.590	<.001	[0.073, 0.251]	–
Plastron length	–0.064	0.045	–1.412	.159	–	.159
Proportion of wetland area within 200 m	–0.062	0.048	–1.290	.198	–	.197
Proportion of agricultural area within 100 m	–0.041	0.048	–0.857	.392	–	.391
Calendar date	–0.047	0.058	–0.813	.416	–	.416
Time	–0.018	0.043	–0.424	.672	–	.671
Sex	0.057	0.094	0.603	.547	–	.551
<i>Time of shell emergence</i> 512 Observations (483 Individuals); R^2 Marginal: .164; R^2 Conditional: .164						
Intercept	–0.290	0.099	–2.942	.003	[–0.484, –0.097]	–
Calendar date	–0.481	0.125	–3.837	<.001	[–0.729, –0.237]	–
Air temperature	–0.409	0.123	–3.320	.001	[–0.654, –0.170]	–
Time	–0.291	0.109	–2.662	.008	[–0.511, –0.081]	–
Plastron length	0.219	0.106	2.060	.039	[0.011, –0.428]	–
Proportion of wetland area within 300 m	0.231	0.103	2.245	.025	[0.030, 0.434]	–
Proportion of urban area within 1000 m	–0.236	0.104	–2.279	.023	[–0.441 to –0.034]	–
Sex	–0.071	0.227	–0.314	.754	–	.753
Proportion of open water area within 900 m	–0.012	0.101	–0.117	.907	–	.906
Proportion of agricultural area within 1000 m	–0.006	0.106	–0.055	.956	–	.955
<i>Time of initial movement</i> 460 Observations (433 Individuals); R^2 Marginal: .013; R^2 Conditional: .208						
Intercept	127.250	12.930	9.841	<.001	[101.907, 152.593]	–
Plastron length	15.306	5.911	2.589	.009	[3.720, 26.891]	–
Proportion of urban area within 1000 m	–11.912	11.862	–1.004	.325	–	.320
Proportion of forest and vegetation area within 200 m	–20.325	12.985	–1.565	.133	–	.132
Proportion of open water area within 500 m	–21.911	10.635	–2.060	.053	–	.051
Calendar date	–16.049	9.885	–1.624	.119	–	.108
Proportion of wetland area within 400 m	15.743	13.173	1.194	.245	–	.238
Time	–6.015	5.611	–1.072	.284	–	.289
Air temperature	–3.860	9.103	–0.424	.672	–	.671
Sex	3.413	12.722	0.268	.788	–	.788
Agricultural area within 600 m	1.413	10.337	0.137	.893	–	.891
<i>Total time spent moving</i> 459 Observations (432 Individuals); R^2 Marginal: .058; R^2 conditional: .559						
Intercept	92.424	3.523	26.238	<.001	[85.519, 99.328]	–

(Continues)

TABLE 2 (Continued)

Fixed effect	Estimate	S Er	t-Value	p	95% CI	LRT p
Proportion of agricultural area within 100m	7.581	3.148	2.408	.023	[1.410, 13.751]	–
Proportion of urban area within 1000m	6.689	3.496	1.913	.071	[-0.162, 13.541]	.049
Sex	5.346	3.981	1.343	.180	–	.179
Proportion of open water area within 1000m	-2.705	2.972	-0.910	.373	–	.367
Calendar date	1.146	3.211	0.357	.725	–	.721
Air temperature	-1.333	3.017	-0.442	.660	–	.658
Time	0.892	2.059	0.434	.665	–	.664
Plastron length	-0.791	2.493	-0.317	.751	–	.751
Proportion of wetland area within 600m	-0.983	3.425	-0.287	.777	–	.774
Proportion of forest and vegetation area within 300m	0.0390	5.419	0.007	.994	–	.994

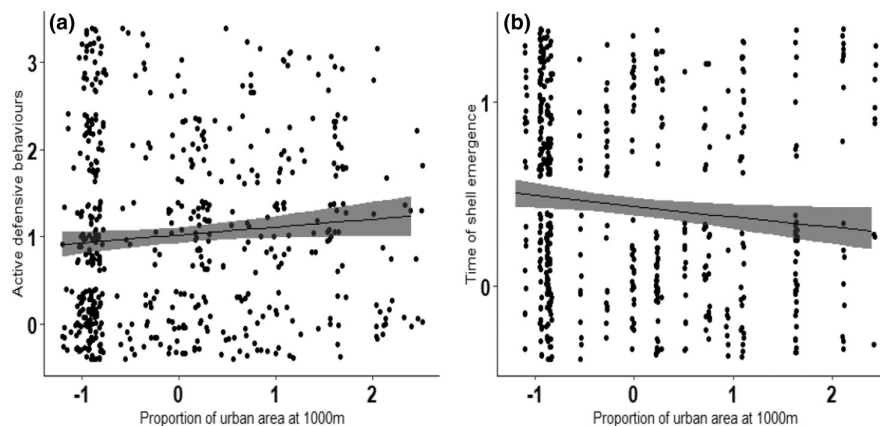


FIGURE 2 (a) Relationship between the number of active defense behaviours performed by painted turtles and the proportion of urban area within a 1000m radius of their home wetland in Ottawa, Ontario, Canada in 2021 and 2022. Each dot represents an observation ($N = 536$). (b) Relationship between the binary time of shell emergence of painted turtles and the proportion of urban area within a buffer with a 1000m radius of their home wetland ($N = 512$). The dots for the figures were jittered to avoid overlap. Predictor variables were standardized (mean zero, unit variance) and the grey areas represent 95% confidence intervals of the model-predicted effect (black line).

4.3 | Boldness

As the level of urbanization increased, painted turtles emerged from their shells sooner, indicating an increase in boldness. However, we did not find a relationship between the level of urbanization and the time of initial movement. This complicates the interpretation of our results, but we did show that some aspects of painted turtle boldness were affected by urbanization. Urban animals are often bolder than their non-urban counterparts, likely because they face a variety of disruptions (Lowry et al., 2013; Uchida et al., 2019). For example, many urban animals use anthropogenic food sources to supplement their diet, or use human-made structures for shelter, both of which can lead to increased interactions with humans and other anthropogenic disturbances (Sarkar & Bhadra, 2022; Torres et al., 2018). Over time, animals may become habituated to these disturbances and become bolder (Uchida et al., 2019; Vincze et al., 2016). Bolder individuals would be able to devote more time and energy to

important activities such as finding food (Dammhahn et al., 2020; Lowry et al., 2013).

There are numerous anthropogenic disturbances that could help explain increased boldness in urban populations of painted turtles. Human activities such as boating and the use of trails close to the shoreline of bodies of water disturb turtles while they are basking (Jain-Schlaepfer et al., 2017; Pittfield & Burger, 2017). Urban painted turtles likely experience this more than turtles from natural bodies of water and may become habituated to these disturbances. For instance, Polich and Barazowski (2016) found that painted turtles regularly exposed to the presence of humans had a shorter flight initiation distance than painted turtles that were not regularly exposed to humans. Selman et al. (2013) found that yellow-blotched sawback turtles (*Graptemys flavimaculata*) from areas with more boating were less disturbed by passing water boats than turtles from areas with less boating. Finally, Turcotte et al. (2023) found that painted turtles in areas with more boating activities are more risk-prone than turtles

from areas with less boat activities. Therefore, urban painted turtles may have developed bolder behaviours in response to disturbances like these to maximise their time spent performing critical activities such as basking.

4.4 | Activity

We did not find a relationship between the proportion of urban area and the amount of time painted turtles spent moving in an arena. One of the reasons that active behaviour is thought to be beneficial for urban animals is that active individuals have a higher likelihood of finding and being able to take advantage of novel anthropogenic resources (Dammhahn et al., 2020; Sol et al., 2013). Many of the resources needed by painted turtles, however, such as food and basking sites, are within their home wetland. Due to this, painted turtles do not need to access novel anthropogenic resources. Another potential explanation could be the high rates of road mortality suffered by turtles (Dupuis-Desormeaux et al., 2017; Gibbs & Shriver, 2002; Patrick & Gibbs, 2010). If active individuals are more likely to cross roads and therefore suffer from higher rates of mortality, then active behaviour may be selected against in urban populations.

4.5 | Future work

We could not determine what mechanisms were behind the behavioural changes in painted turtles as the level of urbanization increased and future research could examine this. Of particular interest would be to test whether responses were due to phenotypic plasticity or to genetic evolution. This could be done through a common garden experiment and hand-rearing juvenile turtles from urban and natural habitats in identical conditions, then comparing their behaviour in controlled environments. Miranda et al. (2013), Baxter-Gilbert et al. (2019) and Reichard et al. (2020) are examples of common garden experiments used to test the effect of urbanization on animal behaviour. In addition, future studies could investigate whether painted turtles select habitats differently in urban environments and if behavioural type plays a significant role in the process (Pereira et al., 2012; Thompson et al., 2018).

4.6 | Study limitations and STRANGEness of animals sampled

An important factor that we could not account for is the long generation times of turtles. Once wild painted turtles get past their juvenile stage, it is common for them to live for decades (COSEWIC, 2018). Therefore, if behavioural selection is taking place in urban painted turtle populations, it may not have been long enough since the Ottawa area became highly urbanized for this to have occurred. This potentially very long response should be considered when interpreting the effect of urbanization on turtle behaviour in general.

Only using one method of capture for our study may have affected the STRANGEness of the animals we sampled. Passive capture methods such as hoop nets may be more likely to trap active animals who are more inclined to interact with them and less likely to trap cautious animals who may avoid them. This could mean that by only using hoop nets, we may have introduced bias by making it more likely that we caught turtles that are not representative of the entire population, according to the STRANGE framework (Webster & Rutz, 2020). However, as we did find a relationship between urbanization and painted turtle behaviour, this potential bias may have been limited. This could have been because the potential bias was the same across all our wetlands and we sampled over a large spatial scale and from a range of urban and natural habitats.

5 | CONCLUSION

In conclusion, we found that painted turtle behaviour was repeatable in a controlled environment and that as the level of urbanization increased, so did aggression and boldness in painted turtles. These behavioural changes could be due to factors such as a decrease in the availability of basking sites in urban environments and an increase in the number of interactions with anthropogenic disturbances. Future studies should examine the mechanisms responsible for the observed behavioural changes in urban painted turtles, such as genetic evolution, phenotypic plasticity, or the non-random selection of their habitat according to their behaviour. Future work should also address the conservation implications of the behavioural changes.

AUTHOR CONTRIBUTIONS

Sebastian Blanchett: conceptualization (lead), data curation (lead), formal analysis (lead), investigation (lead), methodology (lead), project administration (lead), software (equal), supervision: (lead), validation (lead), visualization (lead), writing—original draft preparation (lead) and writing—review and editing (equal). Audrey Turcotte: data curation (supporting), formal analysis (supporting), methodology (supporting), software (equal), validation (supporting), visualization (supporting), writing—original draft preparation (support) and writing—review and editing (equal). Gabriel Blouin-Demers: conceptualization (supporting), funding acquisition (lead), project administration (supporting), resources (lead), supervision (supporting), writing—original draft preparation (supporting) and writing—review and editing (equal).

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data and R codes used for this study are available in the GitHub digital repository: <https://github.com/sblan099/Publication.git>.

CONSENT TO PARTICIPATE AND PUBLISH

All authors agree to participate and to publish the data produced from this research.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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