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

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ABSTRACT

Urbanization is one of the major causes of the global biodiversity crisis with reptiles being particularly vulnerable, due to factors such as habitat loss and road mortality. Behaviour plays a crucial role in determining the success of urban animals, but behavioural responses to urbanization are rarely studied in reptiles. I studied the differences in aggression, boldness, and exploration in painted turtles (*Chrysemys picta*) living in urban and undisturbed areas. I hypothesized that aggression, boldness, and exploration would increase in urban painted turtles. I studied painted turtles from 24 sites across an urban to undisturbed gradient in Ottawa, Ontario, Canada over the summers of 2021 and 2022. I captured turtles with hoop nets and tested their behaviour in the field, and the repeatability of their behaviour in the laboratory. I found that urbanization had a statistically significant, positive effect on painted turtle aggression and boldness, and no effect on exploration. Overall, I determined that urbanization is affecting painted turtle behaviour, but further research is required to better understand the factors behind this.

RESUMÉ

L'urbanisation est l'une des principales causes de la crise mondiale de la biodiversité, les reptiles étant particulièrement vulnérables en raison de facteurs tels que la perte d'habitat et la mortalité routière. Le comportement joue un rôle crucial dans la détermination du succès des animaux urbains, mais les réactions comportementales à l'urbanisation sont rarement étudiées chez les reptiles. J'ai étudié les différences d'agressivité, d'audace et d'exploration chez les tortues peintes (*Chrysemys picta*) vivant dans les zones urbaines et intactes. J'ai émis l'hypothèse que l'agressivité, l'audace et l'exploration seraient favorisées chez les tortues peintes urbaines. J'ai étudié des tortues peintes de 24 sites à travers un gradient urbain à non perturbé à Ottawa, Ontario, Canada au cours des étés 2021 et 2022. J'ai capturé des tortues avec des verveux et analysé leur comportement sur le terrain, et ainsi que la répétabilité de leur comportement en laboratoire. J'ai constaté que l'urbanisation avait un effet statistiquement significatif et positif sur l'agressivité et l'audace des tortues peintes, et aucun effet sur l'exploration. Dans l'ensemble, j'ai déterminé que l'urbanisation affecte le comportement des tortues peintes, mais d'autres recherches sont nécessaires pour mieux comprendre les facteurs à l'origine de cet effet.

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INTRODUCTION

One of the greatest ecological threats the world is currently facing is the global decrease in biodiversity (Segan et al., 2016). According to The Living Planet Report, there was a decline of 68% in global biodiversity from 1970 to 2016 (Almond et al., 2020). Habitat loss is among the primary causes of this biodiversity loss; it is the main driver of losses for terrestrial species (Sala et al., 2000). Since 1700, there has been an 18% decrease in species natural habitat area on average, and this could rise to 23% by 2100 (Beyer and Manica, 2020). The impacts of habitat loss on wildlife populations includes isolation, reduced genetic diversity, decreased reproductive success, and eventually extinction (Segan et al., 2016). One of the major causes of habitat loss is urbanization, with approximately 52% of the world's population currently living in cities, and urban area expected to be multiplied by up to 3 times by 2050 (Liu et al., 2017). As urban centers grow to accommodate larger human populations, wildlife living in nearby habitats will be increasingly affected.

Urbanization, the continued expansion of cities and infrastructure into natural habitats, is a major conservation concern (Lowry et al., 2013). Urbanization not only impacts wildlife through habitat loss, but also through introducing novel perturbations into the environment, such as increased human contact, invasive species, and pollution (Partecke et al., 2006; Charmantier et al., 2017). These perturbations can result in drastic consequences for urban wildlife, with decreases in abundance and diversity being common (Cordier et al., 2021). Therefore, as urbanization continues, increasing numbers of wildlife populations will be negatively affected.

The impacts of the expansion of urban areas on wildlife has been examined, including how urbanization impacts diversity, health, and human-animal conflict (Partecke et al., 2006; Soulsbury and White, 2015; Murray et al., 2019). It is also important, however, to better understand behavioural changes occurring in response to urbanization, as this can aid in determining the extent to which animals

can adapt to urban environments and identify which urban habitats are best suited to supporting certain species (Marzluff et al., 2008; Magle and Angeloni, 2011). Behaviour also helps shape how animals interact with humans, which is a critical aspect of urban life for any species (Soulsbury and White, 2015).

There are two primary ways in which urbanization can alter an animal's behaviour: phenotypic plasticity and genetic evolution. Phenotypic plasticity is the capacity of organisms to alter their phenotype in response to their environment. These changes tend to occur over shorter periods of time compared to genetic evolutionary changes and are not heritable (Snell-Rood, 2013). Two major forms of behavioural plasticity are developmental behavioural plasticity and activational behavioural plasticity (Snell-Rood, 2013). Developmental behavioural plasticity is when individuals develop learned personalities in response to their environment, such as shyness or boldness. For example, Brünnich's guillemot's (*Uria lomvia*) specialize in different foraging behaviours depending on the resource availabilities of their environments (Woo et al., 2008). Activational behavioural plasticity is when individuals activate different behaviours in response to different environments, such as changes in foraging behaviour in response to predator abundance. For example, Toth, (2015) found that female smooth newts (*Lissotriton vulgaris*) differed in egg laying behaviours (such as size and number of eggs) depending on temporal and environmental factors.

Genetic evolution takes place over longer periods of time compared to changes due to phenotypic plasticity and involves the random and non-random selection of heritable traits in a population (Gompel and Prud'homme, 2009). There are two primary steps to genetic evolution. The first is random mutations and recombination introducing genetic variation among individuals of a population, which results in different phenotypes. Second, these variations are sorted out over generations either by random sampling or natural selection. For example, Miranda et al., (2013) found behavioural differences in urban European blackbirds (*Turdus merula*) hand raised in identical conditions to rural European

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blackbirds. As both populations were raised in identical conditions, this suggests that the differences in behaviours were due to genetic differences and not to plastic ones.

Animals often change their behaviour in response to urbanization, and it plays a major role in determining their success in urban environments. For example, urban Indian rock agamas (*Psammophilus dorsalis*) are reactive in social situations (expressed as low aggression and high hypothalamo-pituitary adrenal (HPA) axis reactivity and activity), compared to their rural counterparts who respond proactively (high aggression and low reactivity and activity of the HPA axis) (Batabyal and Thaker, 2019). Urban juvenile house finches (*Haemorhous mexicanus*) are less disturbed by humans while completing tasks compared to rural juvenile finches (Cook et al., 2017). Urban grey kangaroos (*Macropus giganteus*) are more vigilant than non-urban grey kangaroos (Hume et al., 2019). Though these behavioural changes can aid in urban animals' survival, they can also result in increased costs for them, such as a loss in resources, foraging time, mating opportunities, and the reproduction or survival of offspring (Hurtado and Mabry, 2017). Thus, studying behaviour allows us to better understand how animals are responding to the changes related to urbanization. The majority of behavioural studies focus on mammals and birds, with much less research on other animal groups. This is particularly true for reptiles, with few studies on the impact of urbanization on their behaviour, despite reptiles being one of the groups most negatively impacted by it (French et al., 2018).

Reptiles are among the groups most affected by changes imposed by human activities (Cordier et al., 2021). Some of the greatest threats that reptiles currently face are habitat loss and degradation resulting from urbanization (Gibbons et al., 2000). In fact, Cordier et al., (2021) found that out of the six most common human land-use changes (agriculture, cattle raising, urbanization, deforestation, silviculture, and selective logging), urbanization had the greatest negative effect on reptile species richness. Freshwater turtles are especially impacted by urbanization due to their high rates of road mortality and the vulnerability of riparian habitats to urbanization (Ryan et al., 2014). For instance, seven

of the eight native turtle species in Ontario are listed as at-risk by The Committee on the Status of

Endangered Wildlife in Canada (COSEWIC), suggesting an urgent need to better understand the factors

driving the decline in turtle populations in urban areas (Species at Risk Registry, 2021). Painted turtles

(*Chrysemys picta*) are the most common turtles in Ontario and are often found in disturbed habitats. As

such, painted turtles are ideal to document the impact of urbanization on the behaviour of turtles and

thus understand the potential ways in which they are adapting to living in urban environments.

The objective of my project is to measure differences in behaviour in painted turtles living in

urban and in undisturbed areas. My experimental design did not allow me to distinguish between the

mechanisms behind any potential behavioural changes in the turtles, so I simply tested whether the

behaviour of urban turtles differed from those of more natural sites. Based on the literature and studies

that have tested the effects of urbanization on animal behaviour, some common traits that appear to

benefit animals living in more disturbed habitats are aggression, boldness, and exploration (Sol et al.,

2013; Łopucki et al., 2021). Therefore, I tested the effects of urbanization on painted turtle aggression,

boldness, and exploration.

One hypothesis is that aggression could be increased in urban environments because of higher

competition over resources due to reduced availability and higher resource clumping. Resources in

urban environments tend to be more limited than in undisturbed environments. This means that animals

may face high levels of competition over these resources, thus favoring more aggressive individuals

(Lowry et al., 2013; Hurtado and Mabry, 2017). If the resources that painted turtles use in urban

environments are reduced in availability, then urban painted turtles may face increased competition over

them. Aggressive individuals may be able to outcompete their conspecifics and gain access to these

resources. Therefore, I expected that as urbanization increases, aggression should increase in painted

turtles.

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Another hypothesis is that boldness could be increased in urban environments because of the benefits of higher disturbance tolerance due to increased interactions with humans and predators. Urban areas typically have high rates of disturbance due to factors including increased interactions with humans and medium-sized predators (mesopredators) (Bateman and Fleming, 2012; Hurtado and Mabry, 2017). Bolder animals may experience less stress from these disturbances, allowing for more time and energy devoted to other beneficial activities (Lowry et al., 2013; Dammhahn et al., 2020). If urban painted turtles more frequently interact with common urban elements such as humans and mesopredators, then urban turtles may face higher rates of disturbances. Bolder individuals may experience less stress from these disturbances and be able to spend more time and energy on other activities such as basking or finding food. Therefore, I expected that as urbanization increases, boldness should increase in painted turtles.

A third hypothesis is that exploratory behaviour could be increased in urban environments because of a higher likelihood of being able to find and take advantage of novel resources. Explorative animals travel more frequently and have larger home ranges. Thus, these animals are more likely to discover and take advantage of the novel resources present in urban areas (Dammhahn et al., 2020). If there are resources available in urban environments that painted turtles can take advantage of, such as basking and nesting sites, then exploratory individuals may be more likely to come across these resources and use them. Therefore, I expected that as urbanization increases, exploratory behaviour should increase in painted turtles.

MATERIALS AND METHODS

Study Area and Sites

I collected data on painted turtles from May to August of 2021 and 2022 in Ottawa, Ontario, Canada. I measured aggression, boldness, and exploration in painted turtles from 24 sites that covered a range of urban to undisturbed environments (Figure 1). The sites were at least 1.5 km apart to limit potential dispersion between sites and spatial autocorrelation (Čapkun-Huot et al., 2021).

Captures and Measurements

I sampled sites one at a time for one week. The timing of sampling was randomized with respect to urbanization to account for potential seasonal effects on turtle behaviour (Clavijo-Baquet and Magnone, 2017; Ruso et al., 2017). The turtles were captured by placing hoop nets in wetlands. To ensure that the turtles were able to breathe in the nets, I placed them so that at least half of the net breached the surface of the water and placed floats in the nets (Larocque et al., 2012). The nets were checked every day and all adult painted turtles captured were tested. I took the turtles to shore and weighed them using a spring scale, measured their plastron length with vernier calipers, and determined their sex based on secondary sexual characteristics. Males have flatter carapaces, longer foreclaws, longer tails, and the cloaca is located further out in relation to the shell margin (Morjan, 2003). To identify individual turtles, I used a file to make small notches in unique combinations in each turtle's marginal scutes (Cagle, 1939).

Field Behavioural Tests

I measured the turtles' behaviours using several tests, with two assumptions First, that the tests were valid techniques to measure the behaviours. Second, that the turtles would react similarly to humans as they would to conspecifics and predators. While taking the morphometric measurements of the turtles, I tested their aggression by recording behavioural reactions to handling similar to other

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behavioural studies on turtles (Polo-Cavia et al., 2011; Čapkun-Huot and Blouin-Demers; 2019; Pich et al., 2019; Turcotte et al., 2023). I recorded whether the turtle kicked with its legs in an attempt to free itself, hissed, gaped or bit, and defecated or urinated. I then summed the reactions that each turtle used (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). After taking the morphometric measurements, I put the turtles individually under a plastic bucket in a circular arena (diameter = 1.5 m) for two minutes so that they could acclimate. After acclimation, I removed the bucket and recorded the turtle in the arena with a camera on a tripod, while standing approximately 2-3 m away so as not to disturb it. The arena was placed in a shaded area to help standardize testing temperature and to avoid overheating. I recorded air and water temperature to account for any temperature related behavioural differences. I then tested boldness by measuring 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 minutes. Using a maximum time of 10 minutes while testing shell emergence and initial time of movement for turtles in the field is a standard practice (Kashon and Carlson, 2018; Pich et al., 2019; Carlson and Tetzlaff, 2020). If the turtle did move from its initial location, I then tested its exploratory behaviour by recording it for another 3 minutes, and measured the amount of time it spent moving in the arena during those 3 minutes. Turtle exploratory behaviour is not commonly studied in the field, so I based the 3-minute time limit on a study of turtle reaction to a simulated predator attack (Pich et al., 2019). After the tests were completed, I released the turtles at their capture location.

Laboratory Behavioural Tests

I estimated the repeatability of the behavioural tests in the laboratory for turtles from 12 sites spanning the urban to undisturbed gradient. Turtles were housed individually in tubs containing dechlorinated water and a basking platform and kept at 23° C on a natural photoperiod (13 L: 11 D). Turtles were fed earthworms twice a week and provided with fresh, dark leafy greens (Juneau et al.,

2015). I performed the same measurements and behavioural tests in the laboratory as those conducted in the field. Each turtle was tested once per day for four consecutive days and then released at its site of capture.

Repeatability Analyses

All my statistical analyses were performed with RStudio, version 4.2.2 (R Core Team, 2022). I calculated the among-individual repeatability of turtle behaviour in the laboratory using the rpt function from the rptR package (Stoffel et al., 2017), to determine if the behaviours the turtles displayed in response to the tests were consistent. Among-individual repeatability is the proportion of phenotypic variance that can be attributed to differences between individuals (Nakagawa and Schielzeth, 2010). A higher repeatability value indicates increased among-individual behavioural repeatability. Before I began my repeatability analyses, I examined the distributions for each of the behaviours, in order to select the best distribution for my models. The handling reactions and 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 0 seconds (179 observations out of 213) (Supplementary Material, Figure 1). I thus decided to convert time of shell emergence into a binary variable, with turtles that emerged from their shells at 0 seconds coded as "0" and turtles that did not emerge from their shells at 0 seconds coded as "1". For the time of initial movement, the data were also skewed because there were many turtles that started moving at 0 seconds (31 observations out of 170) (Supplementary Material, Figure 1), so I performed a log(x+1) transformation and ran my analyses on the original version of the time of initial movement, and the log transformed version.

I first calculated the unadjusted repeatability for each behaviour with only turtle ID as a random effect. I then calculated the adjusted repeatability by adding site identity as a random effect, and the day of testing (day 1-4) and sex as fixed effects. I used turtle ID and site identity as random effects to

measure among-individual behavioural repeatability and to account for potential spatial autocorrelation, respectively. I ran each test with 1,000 bootstrap iterations. Finally, I calculated the Pearson and Spearman's correlation values between all of the laboratory behaviours using the raw data for each individual.

Landscape Analyses

I conducted the landscape analyses 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 I condensed them into 5 (open water, wetland, forest/vegetation, urban, and agriculture). I then created buffers in 100 m increments around each sampling site, centered on the locations of the hoop nets and extending up to 1000 m. These distances were based on other landscape analysis studies involving freshwater turtles (Fyson and 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. I then determined the distance at which each land cover class had the maximum effect on each of the behaviours. I first determined the distributions for all the behaviours, in order to select the best distributions for my models. In addition, if I needed to perform any transformations, I would recalculate the distance at which each land cover class had a maximum impact on the transformed behaviour. The data for the total time spent moving were normally distributed, but the time of shell emergence data were heavily skewed with over half of the turtles emerging from their shells at 0 seconds (288 observations out of 472) (Supplementary Material, Figure 2), so I converted it into a binary variable as discussed above. The time of initial movement data were also skewed as many turtles started moving at 0 seconds (41 observations out of 460) (Supplementary Material, Figure 2), so I used a log(x+1) transformation, and I ran my analysis on both versions of the data for comparison, as discussed above. The handling reaction data were not normally distributed, but as the lmer function that I used to create my model for handling reaction can generally handle non-

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normal functions, and I could not perform a transformation as the data were discrete, I left them untransformed.

I then compared the correlation values of all buffer distances for each land cover class with the behaviours. I only kept the maximally correlated buffer distances for each behaviour (the scale of maximum effect) and used them for further analyses (Supplementary Material, Table 1). Finally, I calculated the Pearson and Spearman's correlation values between all of the behaviours using the raw data for each individual.

Behavioural Analyses

I used generalized linear mixed models to determine the relationship between urbanization and painted turtle behaviour using the lme4 package (Bates et al., 2015). I used the same distributions for the behaviours that I determined during the landscape analyses and standardized all the continuous predictor variables (mean of zero, unit variance). Next, I created an initial model for each of the behaviours with only the fixed effects, and removed fixed effects that had a high GVIF ($GVIF^{1/2 \times df} > 2$) or correlation value (r > 0.7) with other predictors. The fixed effects that I used for each initial model were the Julian date of testing, air and water temperature, time of testing, weight, plastron length, sex, and the proportion of area for each land cover category at its scale of maximum effect. Julian date of testing, air and water temperature, and time of testing were included to account for any environmental effects on the turtles' behaviour. Weight, plastron length, and sex were included to account for any physiological effects on the turtles' behaviour, such as those found in 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 (Turcotte et al., 2023). I then added turtle ID and site identity as random effects to each model to account for individuals I caught multiple times and potential spatial autocorrelation between the sites. Next, I verified the model assumptions by checking their residual

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distributions and their relationships with fitted values. I then checked the significance of the random effects for each of the models using a likelihood ratio test (LRT) (Crawley, 2007). Turtle ID was significant for handling reactions and the total time spent moving, and site identity was significant for time of initial movement, the log(x+1) transformed version of the time of initial movement, and the total time spent moving (Table 1). I then 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 an LRT (Crawley, 2007). Each final model was fitted with restricted maximum likelihood, and I 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).

For the time of initial movement and total time spent moving, I used model averaging to create the final models. Two of the models during the backwards selection process for the time of initial movement had an LRT p-value that was close to being significant (p = 0.051) after the proportion of open water area at 500 m fixed effect was removed (p = 0.054). This resulted in urbanization changing from having a significant effect on behaviour (p = 0.026) to having a non-significant effect (p = 0.11). I decided to compare the parsimony of these models by calculating their AICc values (Table 2) using the aictab function from the AICcmodavg package (Mazerolle, 2023). The aictab function generates AICc value for a set of models, which measures their parsimony by balancing the goodness-of-fit of the model with the number of parameters used. The close to significant p-value of the LRT of the models suggested that they had an equivalent fit of the data (Crawley, 2007) and the delta AICc of less than 2 for the models suggested that were equally parsimonious (Symonds and Moussalli, 2011). Due to this, and to the fact that I was primarily interested in the effect of urbanization on behaviour, I decided to average these two models using the model.avg function from the MuMIn package (Bartoń, 2023). The model.avg function calculates estimates, standard errors, and confidence intervals for the fixed effects in a set of models

that are derived from weighted averages of these values across the models in the set. I then created an updated model using the extracted conditional average estimate for the fixed effects, which are averaged only over the models where the fixed effects appear (Bartoń, 2023). I also used model averaging for the total time spent moving, for similar reasons. Two of the models during the backwards selection process had an LRT that was barely significant (p = 0.049) after the proportion of urban area at 1000 m fixed effect was removed (p = 0.052). The AICc values of the models were also within 2 of each other (Table 2). The p-values of the LRTs for all the turtle behaviours can be found in Table 4.

RESULTS

Description of Turtle Behaviour

In total, 504 painted turtles were tested for the field behavioural tests, with 23 of the turtles being captured twice, and 3 of the of the turtles being captured 3 times. In total, 533 observations were made of the turtles' handling reactions, 512 observations were made of their time of shell emergence, 460 observations were made of their time of initial movement, and 459 observations were made of their total time spent moving. Turtle urinating/defecating was removed as one of the handling reactions for my analysis, as only 5 observations were made. It is also worth mentioning that I used different methods at my first site when testing the turtles time of shell emergence, time of initial movement, and total time spent moving, so I did not use this site's data for the analyses of these behaviours.

Repeatability of Behaviour

I estimated the repeatability of the behavioural tests for 58 turtles (21 females and 37 males). In total, 214 observations were made for the repeatability of the turtles' handling reactions, 213 observations were made for the repeatability of the turtles' time of shell emergence, 170 observations were made for the repeatability of their initial time of movement, and 170 observations were made for the repeatability of the total time they spent moving. Turtle urinating/defecating was removed as one of the handling reactions for my analysis, because only 2 observations were made. I found significant adjusted repeatability estimates for the turtles' handling reactions (R = 0.582, p = 3.46E-25, 95% CI = [0.394, 0.756]), time of shell emergence (R = 0.677, p < 0.0001, 95% CI = [0.522, 0.774]), their initial time of movement (R = 0.542, p < 0.0001, 95% CI = [0.334, 0.679]) as well as the log-transformed version (R = 0.442, p < 0.0001, 95% CI = [0.237, 0.634]) and the total time spent moving (R = 0.513, p < 0.0001, 95% CI = [0.299, 0.629]) (Table 3). There were some differences between the adjusted and unadjusted repeatability estimates, but the unadjusted estimates were still all repeatable and significant (Table 3).

When the models were adjusted with fixed effects, the repeatability estimates for shell emergence, initial time of movement, and total time spent moving increased, while they decreased for handling reactions and the log(x+1) transformed time of initial movement (Table 3). For all of the behaviours the 95 % CI of the unadjusted and adjusted repeatability estimates overlapped (Table 3).

For the correlations of the turtles' laboratory behaviours, turtles that displayed more reactions while being handled emerged from their shells sooner (Pearson's correlation = -0.45, p < 0.0001), moved from their initial spot sooner (non-transformed: Pearson's correlation = -0.33, p < 0.0001; log-transformed: Pearson's correlation = -0.20, p = 0.01) and spent more time moving (Pearson's correlation = 0.23, p = 0.002) (Supplementary Material, Table 2).

Relationship Between Urbanization and Behaviour

The proportion of urban area at 1000 m for the sites ranged from 0 to 0.918 (mean = 0.341, 95% CI = [0.2313 to 0.4523]) (Supplementary Material, Figure 3). Urbanization had a statistically significant and positive effect on the turtles' number of handling reactions (Estimate = 0.09, p = 0.048, 95% CI = [0.001 to 0.178]) (Table 4; Figure 2a), and a statistically significant and negative effect on their time of shell emergence (Estimate = -0.236, p = 0.022, 95% CI = [-0.441 to -0.034]) (Table 4; Figure 2b) and time of initial movement (Estimate = -28, p = 0.04896, 95% CI = [-53.89 to -2.109]) (Table 4; Figure 2c). For reference, the Estimate is the estimated amount by which the log odds of the response variable (turtle behaviour) would increase if the predictor variable (urbanization at 1000 m) was one unit higher (one standard deviation, as urbanization at 1000 m is scaled). Urbanization did not have a statistically significant effect on the log(x+1) transformed version of the turtles' time of initial movement (Table 4), or the total time spent moving (Table 4). Out of the fixed effects, air temperature most commonly affected behaviour, with a significant effect on three of the behaviours (handling reaction, shell emergence, and log(x+1) transformed time of initial movement) (Table 4).

Interpreting the effect of urbanization on boldness is complicated by the fact that urbanization had a significant effect on the turtles' time of initial movement but did not have a significant effect on the log(x+1) transformed version of it. However, as the time of shell emergence was significantly affected, it does seem that overall, urbanization impacted some aspects of the turtles' boldness.

Similar to the turtles' laboratory behaviours, turtles that displayed more handling reactions in the field emerged from their shells sooner (Pearson's correlation = -0.42, $p < 0.0001$) and started moving sooner (non-transformed: Pearson's correlation = -0.28, $p < 0.0001$; log-transformed: Pearson's correlation = -0.27, $p < 0.0001$) (Supplementary Material, Table 2). However, there was not a strong or significant correlation with the total time spent moving (Pearson's correlation = 0.03, $p = 0.43$) (Supplementary Material, Table 2).

DISCUSSION

My expectations that as the level of urbanization increases, aggression, exploration, and boldness should increase in painted turtles were partly supported. I found that my measure for aggression (the number of handling reactions) increased with urbanization, and my measures for boldness (the initial time of movement and time of shell emergence) decreased with urbanization, indicating an increase in boldness. My measure for exploration (the total amount of time spent moving) also increased with urbanization, though the relationship was not statistically significant. Overall, urbanization did have an effect on some aspects of painted turtle behaviour.

Aggression

Competition over resources is one of the primary reasons given for the increased aggression of urban animals (Hurtado and Mabry, 2017; Łopucki et al., 2021). Basking sites are likely an important resource for painted turtles, as basking is a critical activity for them, since it is used to aid in thermoregulation (Zipko, 1982). Painted turtles also compete for basking sites (Bury et al., 1979; Lovich, 1988), further reinforcing the idea that they are an important resource. However, urban bodies of water are more managed than undisturbed ones, so structures that turtles could use for basking may be removed from the water, or vegetation and trees near the shore that may eventually fall in the water and become basking sites could be cut down (Spinks et al., 2003). Shoreline modification, such as for beaches and docks, could also reduce the number of natural basking sites (Hill and 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 flee from human presence while basking (Pittfield and Burger, 2017). All these factors combined mean that urban painted turtles would likely have fewer basking sites to choose from, which would increase the likelihood of competition over them, and therefore increase aggressive behaviour.

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One important resource that likely did not affect painted turtles' aggression is food, as their aquatic lifestyles and generalist diets likely helped to alleviate the pressure of finding food in urban environments that many other animals face. Natural food sources are often reduced in urban environments, with the remaining natural sources being clumped in food hotspots, due to factors such as habitat loss and fragmentation (Steffan-Dewenter and Schiele, 2008; Lowry et al., 2013; Birnie-Gauvin et al., 2017). Because of this, many urban animals change their feeding habits to take advantage of the novel anthropogenic food sources presented to them, such as human food waste and crops (Birnie-Gauvin et al., 2017; Demeny et al., 2019). These food sources are also often clumped, which brings urban animals into closer contact with each other and can lead to higher levels of competition and aggression (Hurtado and Mabry, 2017). Painted turtles are likely less impacted by these factors than most other urban animals. They do not use many of the most common anthropogenic food sources since most of them are found on land and painted turtles feed in the water. Painted turtles also have generalist diets, consuming a variety of aquatic plants and animals (Lindeman, 1996). These factors combined would help to reduce the likelihood of competition between painted turtles over food, due to the lack of competition over high-density urban food sources and having a variety of natural food sources available to them in their own habitats.

Boldness

Boldness is often expected to increase in urban animals, due to having to interact with a variety of anthropogenic disturbances, with one of the most common being humans (Lowry et al., 2013; Dammhahn et al., 2020). For example, many urban animals will 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 (Torres et al., 2018; Sarkar and Bhadra, 2022). Since painted turtles are aquatic, they do not use many resources provided by humans, which will reduce their contact with them. However, one way that humans do interact with turtles is while using trails close to the shorelines of

bodies of water, which has been found to disturb painted turtles while they are basking (Pittfield and Burger, 2017). Urban painted turtles likely experience this more than turtles from natural bodies of water, which could explain the increase in boldness. These results are further supported by Polich and Barazowski, (2016), who 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. Boating is another common anthropogenic disturbance of turtles, as it can disturb them while they are basking (Jain-Schlaepfer et al., 2017). Therefore, it would be expected that turtles in urban areas with higher rates of boating would be bolder, to maximise their time spent basking. Reinforcing this idea, 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. It is worth noting however that only five of the sites used for this study were on a river where boating could occur, which could have reduced its effect.

Another factor of urbanization that could cause increased boldness in painted turtles is the rise in abundance of mesopredators in urban environments. Increased risk of predation has been associated with higher levels of boldness in animals (Riesch et al., 2009; Harris et al., 2010; Money et al., 2017). This is due to predators introducing increased risk into an animals' environment, so bolder behaviour may be developed as individuals must take increased risks to access resources (Riesch et al., 2009). Higher rates of predation have been suggested as a potential reason for the increase of aggression in urban animals (Lowry et al., 2013). Many of the common predators of painted turtles (such as raccoons and coyotes) are mesopredators (Bateman and Fleming, 2012; COSEWIC, 2018). Therefore, it could be expected that painted turtles in urban areas would experience higher levels of predation or attempted predation and demonstrate bolder behaviours in response to this.

Exploration

The limited movement of painted turtles may reduce the benefits of exploratory behaviour in urban environments. One of the primary reasons that exploratory behaviour is thought to be beneficial for urban animals is that it would increase the likelihood of them finding and being able to take advantage of novel anthropogenic resources (Dammhahn et al., 2020). However, painted turtles may not be under the same pressure to use these novel resources as many other urban animals. All of the turtles' food and basking sites are found within their body of water, so they would not need to find more of these resources outside of their immediate environment. One exception to this could be nesting sites. Turtles lose many of their natural nesting sites in urban areas due to habitat loss and fragmentation (Gibbons et al., 2000; Cordier et al., 2021), and therefore would potentially need to find new anthropogenic ones to compensate for this. There would likely be some benefit for exploratory behaviour due to this, as exploratory turtles would have a higher chance of coming across these new nesting sites. However, painted turtles exhibit nesting site fidelity and return to the same sites over the years (Christens and Bider, 1987; Rowe et al., 2005). This would likely reduce the overall benefits of exploratory behaviour, as it would limit how often they would need to find new nesting sites.

For the turtles' exploration test, it is worth noting that it may be difficult to directly link this test with exploratory behaviour in the wild, since the test was done on land and turtles spend the majority of their time in water. It could instead be interpreted as a representation of risk-taking behaviour, or boldness, as it is risky for turtles to be out of their shells and moving. In terms of risk-taking, basking is a very important activity for painted turtles, but it is also one of the times that they are most vulnerable to predation (Costa, 2014; Nordberg and McKnight, 2020). This is compounded in urban environments where there is usually a higher number of mesopredators who may predate or attempt to predate painted turtles, as previously discussed (Bateman and Fleming, 2012; COSEWIC, 2018). However, mesopredators often change their times of activity so that they are more active at night to avoid conflict

with humans (Gaynor et al., 2018). This would reduce their activity during the day when painted turtles are basking, which would therefore decrease the risk of turtles being attacked while basking and decrease the need for risk-taking behaviour. This potentially explains why urbanization did not affect the amount of time turtles spent moving.

Generation Time

One factor that could be influencing painted turtle behaviour in urban environments is their long generation times. Generation time has been found to affect the speed of evolution in animals, with organisms with longer generation times tending to evolve at slower rates (Weller and Wu, 2015). Once wild painted turtles get past their juvenile stage, it is common for them to live for decades (COSEWIC, 2018), with a long-term study by Congdon et al., 2003 recording individuals reaching 61 years of age. They can also take over a decade to reach sexual maturity (COSEWIC, 2018). Therefore, it may not have been long enough since the Ottawa area became highly urbanized for behavioural selection to have occurred. This could be a potential explanation for why urbanization did not have a significant effect on the painted turtles' exploratory behaviour and should be considered when interpreting the effect of urbanization on turtle behaviour in general.

Study Limitations

There were some limitations with my study that could have affected my results. One of these is my relatively small sample size of 24 sites, which could have reduced the statistical power of my analyses. This is further compounded by the omission of 1 site from my analysis of the boldness and exploration behaviours, as previously discussed.

In addition, the effect of roads on turtle risk-taking and boldness may have been diluted. Roads are a common part of urban environments that introduce a high risk for painted turtles, due to mortality resulting from vehicular collisions (Gibbs and Shriver, 2002; Patrick and Gibbs, 2010; Dupuis-Désormeaux

et al., 2017). Since there is a higher density of roads in urban areas, it would be expected that urban turtles would have to cross them more often, and thus be more inclined to take risks and be bolder. However, all the sites for my study were relatively close to roads since I had to access them by foot, as opposed to another transportation method, such as by boat. This may have reduced the effect of roads on risk taking and boldness in the painted turtles and make it difficult to fully assess their impact.

Future Work

Though I could not determine if the behavioural differences in urban painted turtles were due to phenotypic plasticity or genetic evolution, future research could test this by using a common garden experiment. This would involve hand-rearing juvenile turtles from urban and undisturbed habitats in identical conditions, then comparing their behaviour in controlled environments. This would test whether heritable traits or phenotypic plasticity determine the turtles' behaviours (Schwinning et al., 2022). Studies by Miranda et al., (2013), Baxter-Gilbert et al., (2019), and Reichard et al., (2020) provide examples of common garden experiments used to test the effect of urbanization on animal behaviour.

CONCLUSION

In conclusion, I found that urbanization had a statistically significant, positive effect on painted turtle aggression and boldness, but it did not have a significant effect on exploration. Due to the limitations of my study design, however, I could not test the mechanisms behind these behavioural changes in urban painted turtles. The results for aggression and boldness could be due to a decrease in the availability of basking sites in urban areas, and an increase in the number of interactions with anthropogenic disturbances. The lack of effect on exploration could be due to the limited movement of painted turtles and their long generation times. The field of reptile behaviour is still limited compared to many other animal groups, such as birds and mammals. Hopefully, my study will help provide additional information to this expanding field of research, as well as give a better idea about the impacts of urbanization on painted turtles, and turtles in general. Future studies could use methods such as common garden experiments to determine if the behavioural changes in urban painted turtles were due to genetic evolution or to phenotypic plasticity.

TABLES

Table 1. The significance of the random effects (site identity and turtle ID) of the initial models for the painted turtles' behaviours (handling reaction, time of shell emergence, time of initial movement and the log(x+1) transformed version of it, and the total time spent moving). The results were achieved by using likelihood ratio tests. Statistically significant random effects for each behaviour were bolded. Both random effects were kept in a model only if they were significant by themselves and together (see total time spent moving). The Akaike information criterion (AIC), Bayesian information criterion (BIC), logarithm of the likelihood function (loglik), deviance (deviance), chi-squared value (Chisq), and p-value (p) were included. The number of observations and individuals were included for each behaviour.

Random Effect(s)	AIC	BIC	logLik	deviance	Chisq	p
Handling reaction				533 Observations (504 Individuals)		
Site Identity	1521.2	1576.5	-747.59	1495.2	0.0522	0.8192
Turtle ID	1486.8	1542.2	-730.41	1460.8	34.397	4.49E-09
Site + ID	1486.8	1542.2	-730.41	1460.8	0.0008	0.9772
Time of shell emergence				512 Observations (484 Individuals)		
Site Identity	638.52	689.24	-307.26	614.52	0.0737	0.786
Turtle ID	637.56	688.28	-306.78	613.56	1.0357	0.3088
Site + ID	637.56	688.28	-306.78	613.56	9.00E-04	0.9758
Time of initial movement				460 Observations (433 Individuals)		
Site Identity	5622.5	5680.2	-2797.2	5594.5	12.539	0.0003
Turtle ID	5633.2	5690.9	-2802.6	5605.2	1.8135	0.1781
Site + ID	5621.6	5679.2	-2796.8	5593.6	11.641	0.0006
Time of initial movement (log(x+1) transformed)				460 Observations (433 Individuals)		
Site Identity	1686.3	1739.8	-830.15	1660.3	8.0127	0.0046
Turtle ID	1693.4	1746.9	-833.69	1667.4	0.936	0.3333
Site + ID	1685.5	1739	-829.73	1659.5	7.9245	0.0048
Total time spent moving				459 Observations (432 Individuals)		
Site Identity	4683.4	4741	-2327.7	4655.4	11.665	0.0006
Turtle ID	4690.6	4748.2	-2331.3	4662.6	4.4534	0.0348
Site + ID	4679.5	4737.1	-2325.7	4651.5	11.125	0.0008

Table 2. The AICc values for the models created during the backwards selection process for the turtles'
time of initial movement and total time spent moving. As the models that had close to significant
likelihood-ratio test p-values (bolded) for each behaviour had AICc values within two of each other, this
suggests that the models were equally parsimonious. The number of parameters (K), small-sample size
corrected Akaike information criterion (AICc), the difference between the AICc value of the model and
the AICc value of the best-fitting model (Delta AICc), AICc weight (AICcWt), cumulative AICc weight
(Cum.Wt), and log-likelihood value (LL) were included. The number of observations and individuals were
included for each behaviour.

Model	K	AICc	Delta AICc	AICcWt	Cum.Wt	LL
Time of initial movement			460 Observations (433 Individuals)			
Model 1	12	5619.2	0	0.74	0.74	-2797.3
Initial model	13	5621.3	2.1	0.26	1	-2797.3
Model 5	8	5670.8	51.57	0	1	-2827.2
Model 6	7	5671.3	52.08	0	1	-2828.5
Model 4	9	5671.5	52.26	0	1	-2826.6
Model 3	10	5672.5	53.23	0	1	-2826.0
Model 7	6	5673.1	53.82	0	1	-2830.4
Model 2	11	5674.4	55.15	0	1	-2825.9
Total time spent moving			459 Observations (432 Individuals)			
Model 2	12	4676.3	0	0.41	0.41	-2325.8
Model 7	7	4677.5	1.26	0.22	0.62	-2331.6
Model 1	13	4678.3	2.04	0.15	0.77	-2325.7
Model 6	8	4678.8	2.52	0.12	0.88	-2331.2
Initial model	14	4680.4	4.17	0.05	0.93	-2325.7
Model 5	9	4680.7	4.47	0.04	0.98	-2331.2
Model 4	10	4682.6	6.37	0.02	0.99	-2331.1
Model 3	11	4684.5	8.28	0.01	1	-2331.0
Model 8	6	4729.1	52.79	0	1	-2358.4
Model 9	5	4730.8	54.58	0	1	-2360.4

Table 3. Repeatability estimates for the painted turtles' behaviours (handling reactions, time of shell emergence, time of initial movement and the log(x+1) transformed version of it, and total time spent moving). The unadjusted repeatability estimates only included turtle ID as a random effect, while the adjusted repeatability estimates also included 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 (CI), and p-value (p) were included. The data was collected from 58 turtles, and the number of observations were included for each behaviour.

Model	R	SE	95% CI	p
Handling reaction				214 observations
Unadjusted	0.743	0.048	[0.635, 0.817]	1.42E-33
Adjusted	0.582	0.096	[0.394, 0.756]	3.46E-25
Time of shell emergence				213 observations
Unadjusted	0.675	0.07	[0.52, 0.788]	1.04e-18
Adjusted	0.677	0.069	[0.522, 0.774]	1.89e-16
Time of initial movement				170 observations
Unadjusted	0.484	0.083	[0.305, 0.627]	2.5E-08
Adjusted	0.542	0.091	[0.334, 0.679]	1.73E-09
Time of initial movement (log(x+1) transformed)				170 observations
Unadjusted	0.609	0.069	[0.466, 0.721]	1.65E-16
Adjusted	0.442	0.103	[0.237, 0.634]	6.68E-12
Total time spent moving				170 observations
Unadjusted	0.483	0.08	[0.308, 0.628]	2.24E-09
Adjusted	0.513	0.09	[0.299, 0.629]	9.25E-10

Table 4. The significance of the fixed effects for the painted turtles' behaviours (handling reaction, time of shell emergence, time of initial movement (averaged), the log(x+1) transformed version time of initial movement, and the total time spent moving (averaged)). These results were achieved through backwards selection, where the least significant fixed effect was removed from a model, then the estimates of the model were recalculated. This process was repeated until all the fixed effects were significant. The values shown are from the final model for the behaviour (as shown by the bolded effects), or for when the fixed effect was removed during the backwards selection process (non-bolded effects). The final model for each behaviour was fitted with restricted maximum likelihood (REML), which changed the estimates of the fixed effects in the final model, which is why some of the final model fixed effects are not significant. 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) were included. The LRT p-value (LRT p) when the fixed effect was removed (or in the case of averaged models, when the fixed effect was initially removed) was also included. The number of observations and individuals were included for each behaviour, as well as the marginal and conditional R^2 values.

Fixed Effect	Estimate	Std. Error	t value	p	95% CI	LRT p
Handling reaction	533 Observations (504 Individuals); R^2 Marginal: 0.037; R^2 Conditional: 0.799					
Intercept	1.024	0.046	22.495	< 2e-16	[0.934 to 1.11]	
Air temperature	0.098	0.045	2.173	0.030	[0.009 to 0.187]	
Proportion of urban area within 1000m	0.090	0.045	1.979	0.048	[0.0008 to 0.178]	
Proportion of open water area within 1000m	0.163	0.045	3.590	0.0004	[0.073 to 0.251]	
Plastron length	-0.064	0.045	-1.412	0.159		0.1591
Proportion of wetland area within 200m	-0.062	0.048	-1.290	0.198		0.1975
Proportion of agricultural area within 100m	-0.041	0.048	-0.857	0.392		0.3916
Julian date	-0.047	0.058	-0.813	0.416		0.4162
Time	-0.018	0.043	-0.424	0.672		0.6715
Sex	0.057	0.094	0.603	0.547		0.551

Time of shell emergence					512 Observations (484 Individuals); R^2 Marginal: 0.164; R^2 Conditional: 0.164	
Intercept	-0.290	0.099	-2.942	0.003	[-0.484 to -0.097]	
Julian date	-0.481	0.125	-3.837	0.0001	[-0.729 to -0.237]	
Air temperature	-0.409	0.123	-3.320	0.001	[-0.654 to -0.17]	
Time	-0.291	0.109	-2.662	0.008	[-0.511 to -0.081]	
Plastron length	0.219	0.106	2.060	0.039	[0.011 to 0.428]	
Proportion of wetland area within 300m	0.231	0.103	2.245	0.025	[0.03 to 0.434]	
Proportion of urban area within 1000m	-0.236	0.104	-2.279	0.023	[-0.441 to -0.034]	
Sex	-0.071	0.227	-0.314	0.754		0.7538
Proportion of open water area within 900m	-0.012	0.101	-0.117	0.907		0.9065
Proportion of agricultural area within 1000m	-0.006	0.106	-0.055	0.956		0.9559
Time of initial movement (averaged)					460 Observations (433 Individuals); R^2 Marginal: 0.065; R^2 Conditional: 0.215	
Intercept	124.8	11.96	10.44	1.55E-08	[101.3 to 148.2]	
Plastron length	16.4	5.91	2.77	0.006	[4.807 to 27.97]	
Proportion of forest and vegetation area within 200m	-26.1	13.53	-1.93	0.071	[-52.6 to 0.4437]	
Proportion of urban area within 1000m	-28.0	13.21	-2.12	0.049	[-53.89 to -2.1]	
Proportion of open water area within 500m	-21.8	11.95	-1.83	0.086	[-45.25 to 1.568]	0.051
Julian date	-16.0	9.89	-1.62	0.119		0.1085
Proportion of wetland area within 400m	15.7	13.17	1.19	0.245		0.238
Time	-6.0	5.61	-1.07	0.284		0.2896
Air temperature	-3.9	9.10	-0.42	0.672		0.6716
Sex	3.4	12.72	0.27	0.789		0.7885
Agricultural area within 600m	1.4	10.34	0.14	0.893		0.8914
Time of initial movement (log(x+1) transformed)					460 Observations (433 Individuals); R^2 Marginal:0.059; R^2 Conditional: 0.185	
Intercept	4.067	0.144	28.17	< 2e-16	[3.784 to 4.35]	
Air temperature	-0.260	0.112	-2.31	0.023	[-0.479 to -0.039]	
Plastron length	0.254	0.078	3.25	0.001	[0.1 to 0.406]	
Proportion of open water area within 100m	-0.310	0.155	-2.00	0.060	[-0.613 to -0.006]	
Proportion of wetland area within 400m	0.182	0.127	1.43	0.167		0.1665
Julian date	-0.214	0.142	-1.51	0.142		0.1349
Sex	-0.242	0.167	-1.45	0.148		0.1488

Proportion of agricultural area within 400m	0.147	0.103	1.42	0.166		0.1686
Time	0.065	0.077	0.85	0.397		0.3991
Proportion of urban area within 1000m	-3.624	9.976	-0.36	0.720		0.3061

Total time spent moving (averaged) 459 Observations (432 Individuals); R^2 Marginal:0.058; R^2 Conditional: 0.559

Intercept	92.42	3.523	26.23	9.51E-16	[85.51 to 99.32]	
Proportion of agricultural area within 100m	7.58	3.148	2.41	0.023	[1.41 to 13.75]	
Proportion of urban area within 1000m	6.69	3.496	1.91	0.071	[-0.162 to 13.54]	0.0499
Sex	5.35	3.981	1.34	0.180		0.1799
Proportion of open water area within 1000m	-2.71	2.972	-0.91	0.373		0.367
Julian date	1.15	3.211	0.36	0.725		0.7214
Air temperature	-1.33	3.017	-0.44	0.660		0.6588
Time	0.89	2.059	0.43	0.665		0.6648
Plastron length	-0.79	2.493	-0.32	0.751		0.7514
Proportion of wetland area within 600m	-0.98	3.425	-0.29	0.777		0.7745
Proportion of forest and vegetation area within 300m	0.04	5.419	0.01	0.994		0.9941

FIGURES

Figure 1. A map of the 24 field sites (black circles) where painted turtles were sampled in Ottawa, Ontario, Canada from 2021 and 2022. The map was created using the 2020 Land Cover of Canada layer (Latifovic, 2020).
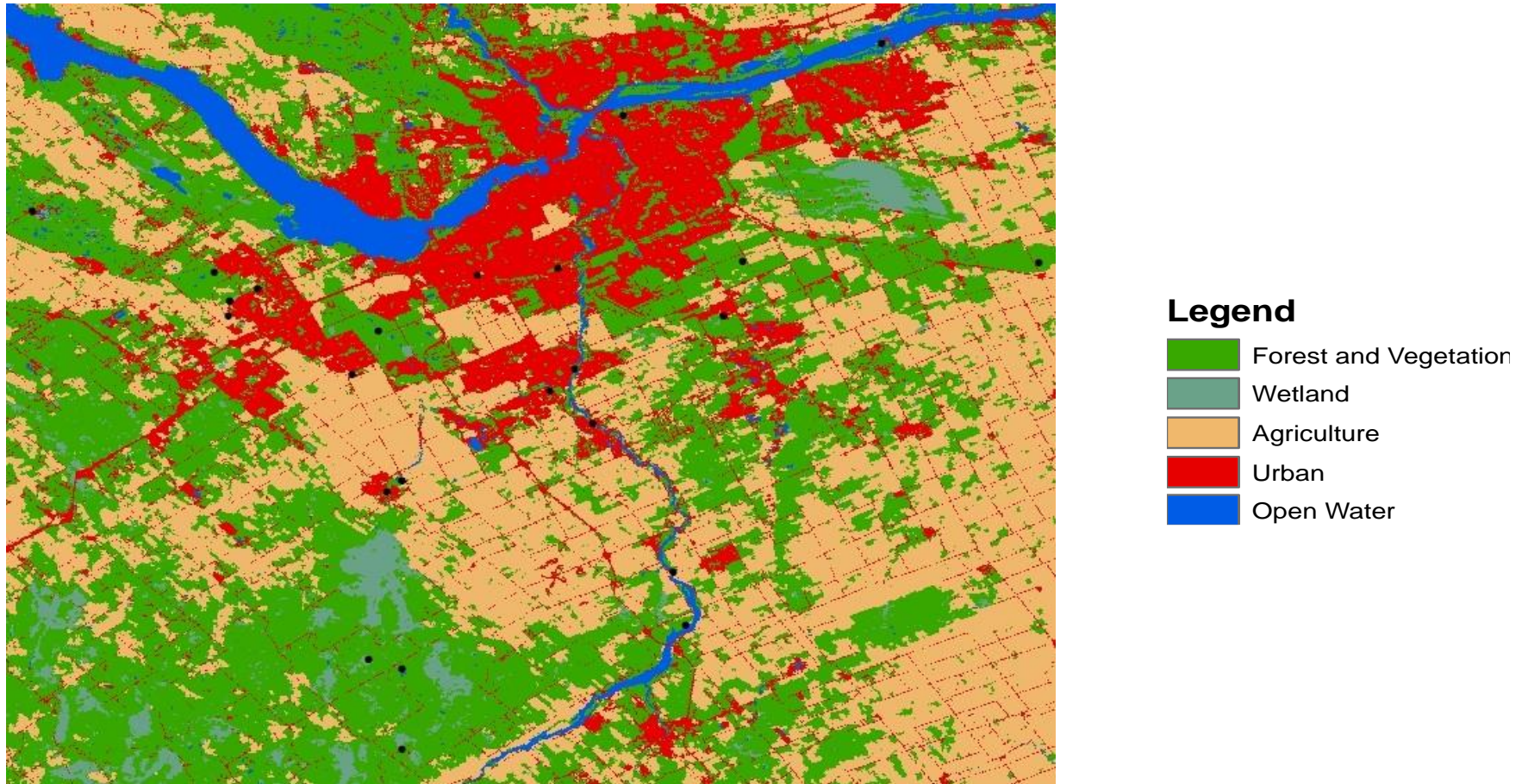
Figure 2. a) Relationship between the number of handling reactions displayed by painted turtles and the proportion of urban area within 1000 m of their sample site. Each dot represents an observation (N = 533), and the values were jittered for easier visualization. b) Relationship between the binary time of shell emergence of painted turtles and the proportion of urban area within 1000 m of their sample site. Each dot represents an observation (N = 512), and the values were jittered for easier visualization. c) Relationship between the time of initial movement of painted turtles and the proportion of urban area within 1000 m of their sample site. Each dot represents an observation (N = 460). Predictor variables were standardized for all figures (mean zero, unit variance), and the grey areas represent 95% confidence intervals of the model-predicted effect (black line).
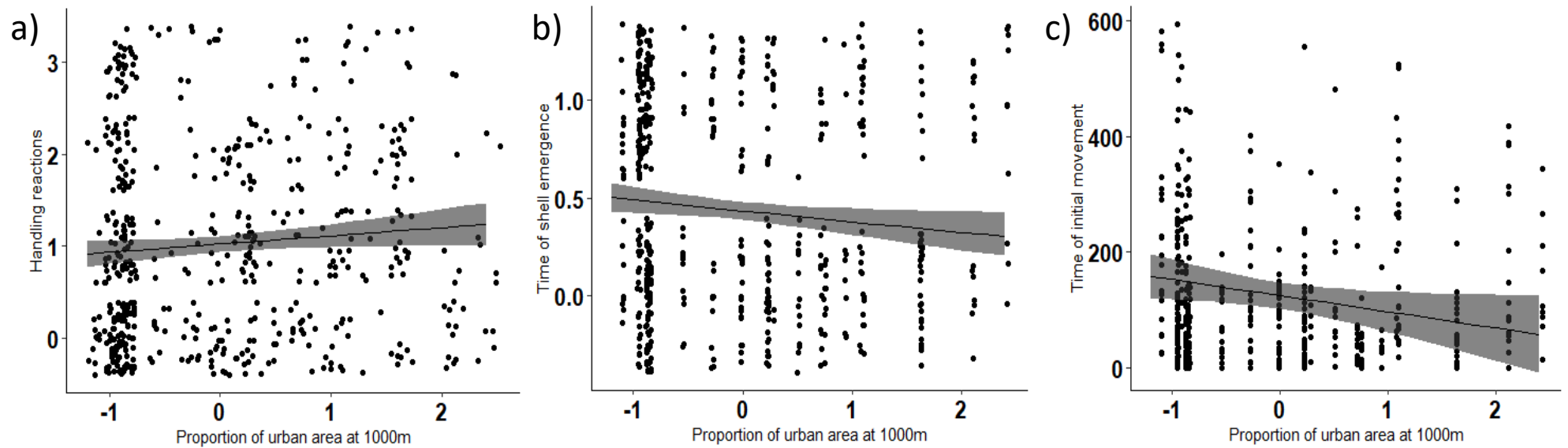
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SUPPLEMENTARY MATERIAL

Supplemental Table 1. The maximally correlated buffer distance in meters for the painted turtle behaviours (handling reactions, time of shell emergence (binary), total time spent moving, time of initial movement, log(x+1) transformed time of initial movement) for each landcover type.

Behaviour	Forest and Vegetation	Wetland	Agriculture	Urban	Open Water
Handling reactions	1000	200	100	1000	400
Time of shell emergence (binary)	1000	300	1000	1000	900
Total time spent moving	300	600	100	1000	1000
Time of initial movement	200	400	600	1000	500
Log(x+1) transformed time of initial movement	1000	400	400	1000	100

Supplemental Table 2. Pearson and Spearman correlation coefficients and p-values between the painted turtles' number of handling reactions

and other behaviours (time of shell emergence (binary), time of initial movement, log(x+1) transformed time of initial movement, and total time

spent moving) in the laboratory and field.

Behaviour	Pearson correlation coefficients	Pearson correlation p-values	Spearman correlation coefficients	Spearman correlation p-values
Laboratory Behaviours				
Time of shell emergence (binary)	-0.4545	2.94E-12	-0.4235	1.11E-10
Time of initial movement	-0.3324	9.43E-06	-0.2442	0.0013
Log(x+1) transformed time of initial movement	-0.1969	0.01	-0.2442	0.0013
Total time spent moving	0.228	0.0027	0.2096	0.006
Field Behaviours				
Time of shell emergence (binary)	-0.4236	0.00E+00	-0.4416	0.000000e+00
Time of initial movement	-0.2759	1.75E-09	-0.3028	3.27E-11
Log(x+1) transformed time of initial movement	-0.2663	6.58E-09	-0.3028	3.27E-11
Total time spent moving	0.0361	4.40E-01	0.0507	2.78E-01

Supplemental Figure 1. Count plots of the distributions of observations across different behaviours measured in painted turtles in the laboratory.

a) Time of initial movement (Start), b) time of shell emergence (Shell), c) handling reactions (Aggression), d) log(x+1) transformed version of time of initial movement (log.Start) e) binary version of time of shell emergence (BIN.Shell), f) total time spent moving (Move).
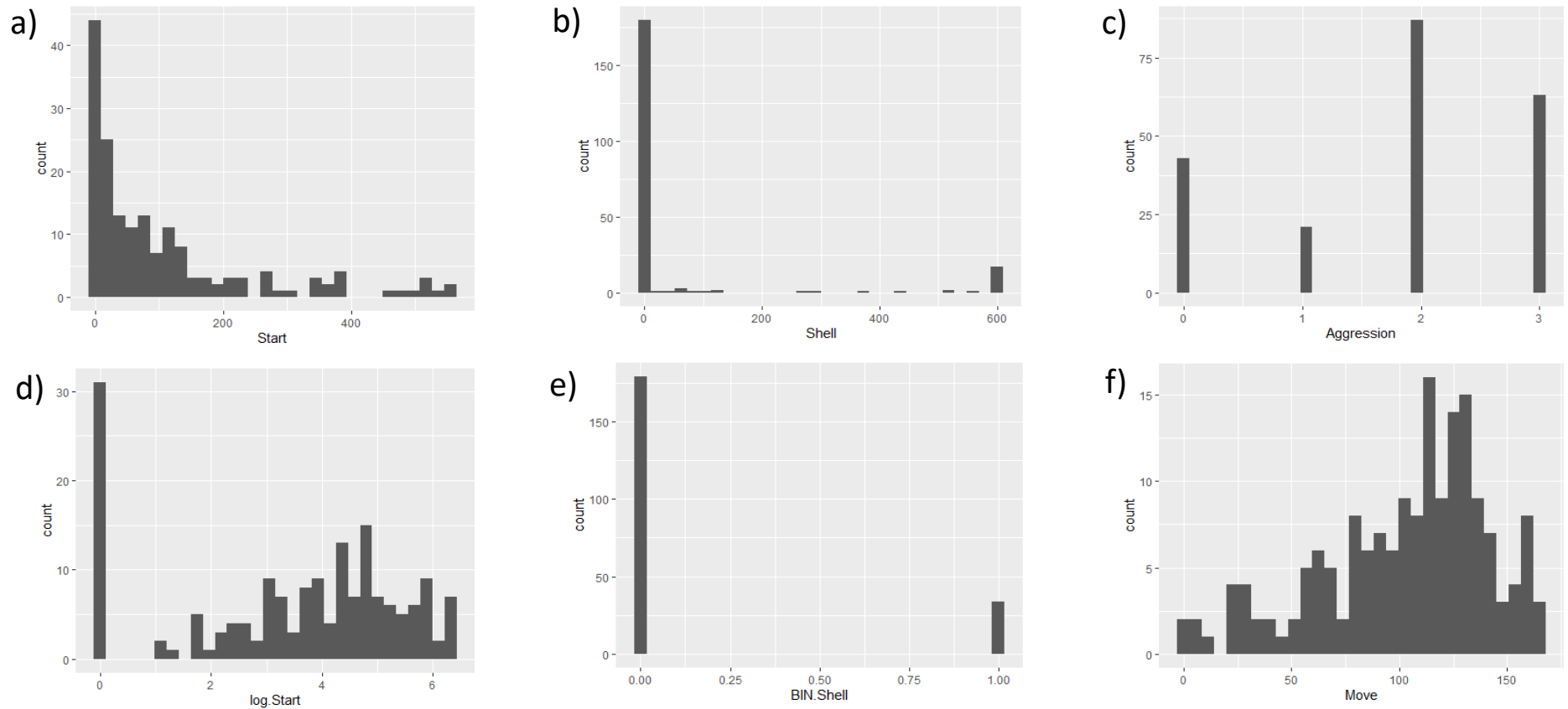
Supplemental Figure 2. Count plots of the distributions of observations across different behaviours measured in painted turtles in the field. a) Time of initial movement (Start), b) time of shell emergence (Shell), c) handling reactions (Aggression), d) log(x+1) transformed version of time of initial movemet (log.Start) e) binary version of time of shell emergence (BIN.Shell), f) total time spent moving (Movement).
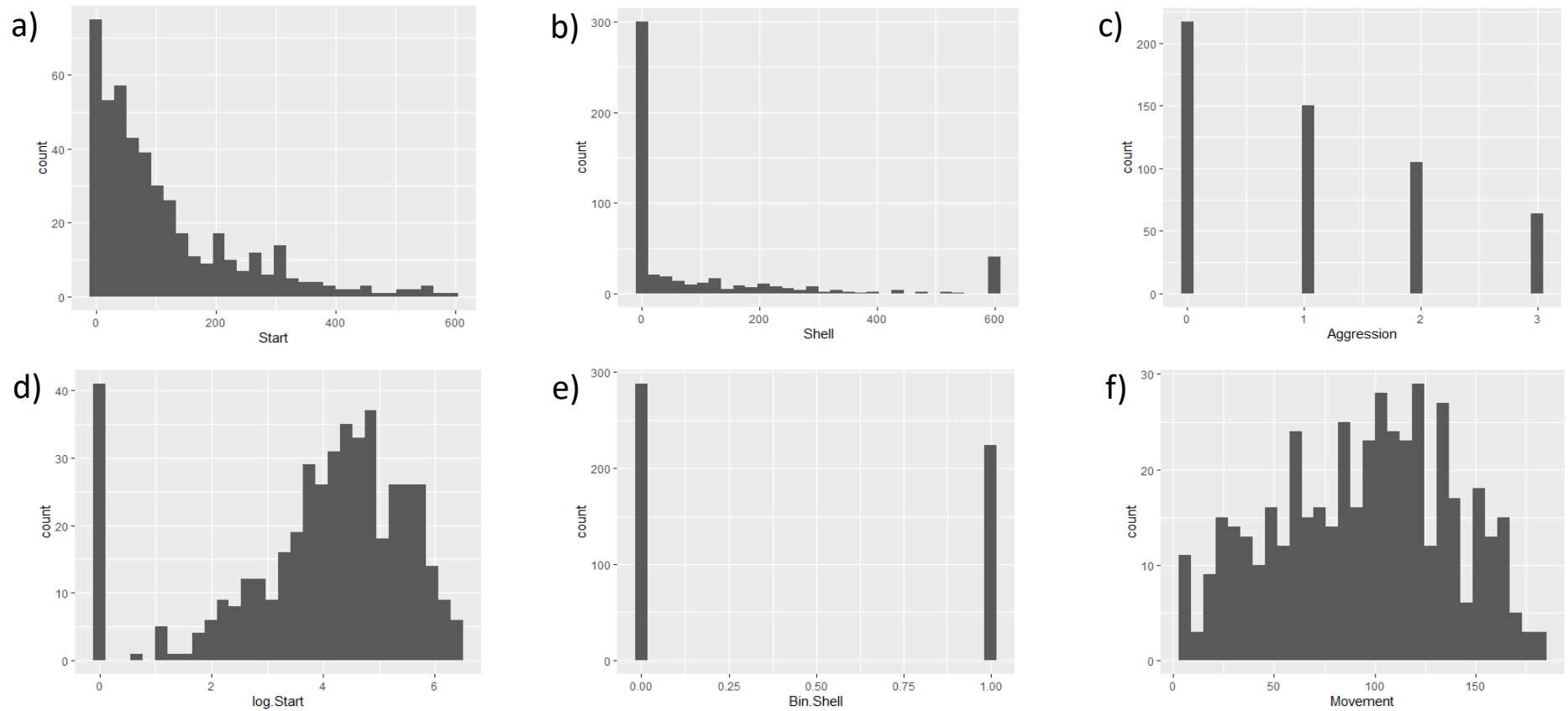
Supplemental Figure 3. The proportion of urban area at 1000 m for each of the testing sites. The proportion of urban ranged from 0 to 0.918 (mean = 0.341, 95% CI = [0.2313 to 0.4523]). The dotted line represents the mean proportion of urban area.