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Effects of human disturbance on risk-taking behavior in painted turtles

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Abstract

Animals are exposed to high levels of anthropogenic disturbance, which has profound consequences for population persistence. Individuals can adjust their behavior plastically when faced with perturbations in their environment and may show consistent differences in the way they perceive and respond to risky situations. Over time, this variability among individuals in response to risk can affect the dynamics of populations exposed to human disturbance. Thus, understanding how animals cope behaviorally with human disturbance is important, especially for species vulnerable to human perturbations, such as turtles. In this context, we evaluated whether risk-taking behaviors are consistent within individual painted turtles (Chrysemys picta) and assessed how these behaviors are related to the extent of human disturbance along the Rideau Canal, Ontario, Canada. Specifically, we conducted repeated measurements of the number of active defensive behaviors used during handling and the time taken to escape a floating platform for 730 painted turtles (1117 observations) from 22 sites varying in human disturbance along the canal. We also quantified the emergence of the turtles from the water after escaping the platform. First, individual painted turtles showed consistent differences in all risk-taking behaviors. Second, painted turtles in areas with high boat activity displayed more active defensive behaviors, while turtles from sites in proximity to more houses with access to the canal used fewer. Our study highlights the importance of studying animal behavior to better understand the impact of human activities on animal populations.

KEYWORDS

among-individual variance, boldness, human activities, recreational boating, repeatability, risktaking propensity

INTRODUCTION 1 |

Human activities impact wildlife in most ecosystems (Barnosky et al., 2012; Ceballos et al., 2015; Foley et al., 2005). In fact, only 5% of the Earth's terrestrial lands are still untouched (Kennedy et al., 2019). Animals are now exposed to frequent and varied anthropogenic disturbances (e.g., pedestrian/vehicle traffic, outdoor recreation, and noise pollution) that can negatively affect important fitness-related activities (e.g., reproduction and foraging; Larson et al., 2016; Price, 2008; Steven et al., 2011) and thus threaten the

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persistence of wild populations (Dirzo et al., 2014). Therefore, the ability of animals to adjust to these perturbations is crucial to persist in human-impacted landscapes (Lowry et al., 2013).

To cope with human disturbance, the initial response of animals is often to alter their behavior (Lowry et al., 2013; Tuomainen & Candolin, 2011; Wong & Candolin, 2015). By adjusting their behavior to the new conditions prevailing in their environment, animals may improve their probability of surviving and reproducing in the short term (reviewed in Lowry et al., 2013; Tuomainen & Candolin, 2011; Wong & Candolin, 2015). For example, animals exposed to frequent human disturbance are more often in vigilance postures, at the expense of other activities (e.g., feeding and sleeping), to assess and respond better to potential threats (Ciuti et al., 2012; McBlain et al., 2020). Changes in activity and feeding patterns to avoid disturbed areas are other common behavioral modifications that help reduce animal exposure to stressful conditions (Tuomainen & Candolin, 2011). For instance, two studies conducted on over 50 species of mammals showed that they are less active, less vagile, and more nocturnal near human disturbance (Gaynor et al., 2018; Tucker et al., 2018). In contrast, some species (e.g., Peregrine falcons Falco peregrinus, Kettel et al., 2018; Raccoons Procyon lotor, Prange et al., 2003; Eastern chipmunks Tamias striatus, Lyons et al., 2017) often thrive in areas with high human density by benefiting from new food resources and reduced predation (Spotswood et al., 2021).

Individuals can adjust their behaviors to their environment and consistent differences in behavioral responses are often present among individuals within a single population (Dingemanse & Wolf, 2010). Many studies showed that individuals differ consistently over time and across contexts in the way they perceive and respond to risky situations by expressing different behaviors, referred to as animal personalities (McDougall et al., 2006; Réale et al., 2007; Sih, 2004). Regardless of context, some individuals are consistently more prone to take risks (i.e., bold) while others minimize their exposure to risky situations (i.e., shy; Koolhaas et al., 1999; McDougall et al., 2006; Réale et al., 2007; Sih, 2004). Therefore, behavioral consistency within individuals may affect how an individual perceives and copes with the changes in its environment (Dingemanse et al., 2004; Sih, 2004).

Among-individual variability in risk perception can affect the dynamics of populations exposed to human disturbance (Tuomainen & Candolin, 2011; Wong & Candolin, 2015). Environmental changes induced by human activities can alter selection pressures and individuals with specific behaviors can become favored in this new context, therefore shaping the population's behavioral response to human exposure (Miranda et al., 2013; Møller, 2008; Mueller et al., 2013; Sih et al., 2011). Alternatively, individuals can settle preferentially in habitats that better match their capacity to respond to risky situations, allowing them to reduce their stress level and avoid the need for behavioral adjustments (Cote et al., 2010; Holtmann, Santos, et al., 2017; Jacob et al., 2015; Martin & Réale, 2008). Over time, regardless of the underlying mechanism, an increase in interindividual differences in behavior should be observed among habitats exposed to different intensities of perturbations (Lowry et al., 2013; — ethology

Tuomainen & Candolin, 2011). Several studies showed that animals living in areas that were highly impacted by human activities differ behaviorally from their conspecifics located in less perturbed regions in that the former use more risk-taking behaviors (see Breck et al., 2019; Hardman & Dalesman, 2018; Holtmann, Santos, et al., 2017). For instance, Great tits (*Parus major*) that are consistently more prone to take risks are more common in areas with higher human frequentation (Sprau & Dingemanse, 2017). Given that variability in behavioral types could shape population dynamics, it is important to consider interindividual differences in risk-taking propensity when studying adaptation to human disturbance (Sprau & Dingemanse, 2017).

Evidence for how animal behavior is affected by human activities is accumulating for various taxa (reviewed in Lowry et al., 2013; Tuomainen & Candolin, 2011; Wong & Candolin, 2015). Early studies mainly focused on mammals and birds, but there is growing interest to study animal behavior in other taxa, such as turtles. Indeed, the propensity to take risks has been explored in turtles using various behavioral measurements. Diverse measures of latencies (e.g., latency for the head to emerge from the shell, latency to move) following a confinement or a simulated predator attack have been used as proxies for risk-taking propensity in several turtle species (Eastern box turtles Terrapene carolina, Carlson & Tetzlaff, 2020; Kashon & Carlson, 2018; Pich et al., 2019; Painted turtles Chrysemys picta, Roth et al., 2020; Red-eared slider turtles Trachemys scripta, Carter et al., 2016; Spanish terrapins Mauremys leprosa, Ibáñez et al., 2018; Ibáñez et al., 2013; Ibáñez et al., 2015). In particular, Pich et al. (2019) assessed risk-taking propensity in Eastern box turtles by adding the number of active defensive behaviors used during a simulated predator attack. Furthermore, the propensity to surface from the water was used by Allard et al. (2019) to evaluate risk-taking behavior in Blanding's turtles (Emydoidea blandingii) exposed to a simulated predator attack. By taking repeated measurements on individuals, these previous studies established that these behaviors were consistent within individuals, but the influence of human disturbance on these behavioral responses has yet to be assessed. A few studies indicated that turtles from areas highly frequented by humans seem to take more risks (i.e., shorter flight initiation distance to human approach and lower abandonment rate of basking sites after disturbance by boats; Polich & Barazowski, 2016; Selman et al., 2013). Given that turtles were not uniquely identified and not tested multiple times, the authors were unable to determine whether the different behavioral responses expressed toward human disturbance were consistent within turtles (Polich & Barazowski, 2016; Selman et al., 2013).

The scant information on how turtles adjust behaviorally to human disturbance is surprising considering their important ecological roles and that they are among the taxa most vulnerable to human activities (Böhm et al., 2013; Buhlmann et al., 2009; Gibbons et al., 2000; Lovich et al., 2018). In Canada, six out of 10 native freshwater turtles are considered at risk by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC, Species at risk public registry: www.canada.ca/en/environmentclimate-change/services/species-risk-public-registry). Freshwater WILEY- ethology

turtles are exposed to human perturbations both on land and in the water. On land, females can be disturbed while nesting (Moore & Seigel, 2006). In the water, recreational boating can perturb important activities, such as basking (Bulté et al., 2020; Moore & Seigel, 2006; Selman et al., 2013). Freshwater turtles can abandon nesting and basking sites for many hours after disturbance by a boat (Bulté et al., 2020; Moore & Seigel, 2006). Loss of basking opportunities can compromise thermoregulation, a critical behavioral mechanism to maintain body temperature in a range that optimizes reproductive success in turtles (Bulté & Blouin-Demers, 2010; Ernst & Lovich, 2009; Jain-Schlaepfer et al., 2017; Rollinson & Brooks, 2007).

In this study, we first determined whether risk-taking behaviors are consistent within individuals and different among individuals in painted turtles by estimating their repeatability. We took repeated measurements of three risk-taking behaviors: (i) the sum of active defensive behaviors used during handling, (ii) the escape latency, and (iii) the emergence of the turtle from the water after escaping. Then, we assessed the relationship between these behaviors and the extent of human disturbance along the Rideau Canal, Ontario, Canada. We quantified the level of human disturbance at each sampling site with several proxies for boat and human activities. We hypothesized that risk-taking behaviors in painted turtles are related to the level of human disturbance in the environment. More specifically, we predicted that individuals located in areas with higher human disturbance should be more prone to take risks. Our study was not designed to assess the mechanisms responsible for the observed changes, but we offer plausible explanations for our findings.

2 | METHODS

2.1 | Study species and system

Painted turtles occupy various aquatic habitats (e.g., swamps, marshes, rivers, and lakes) and are present in human-impacted habitats (DeCatanzaro & Chow-Fraser, 2010; Ernst & Lovich, 2009). Painted turtles inhabit the Rideau Canal, a 202-km slackwater canal located in southeastern Ontario, Canada, that connects the Ottawa River to Lake Ontario (Figure 1a). The Rideau Canal is composed of rivers, lakes, and excavated channels connected by 23 lockstations (Figure 1a). The canal is used extensively for recreational boating: there were over 60,000 vessel crossings recorded at lockstations in 2019 (Figure 1b), without counting the boaters that used the canal without going through the locks. Therefore, painted turtles are exposed to high levels of disturbance in some sections of the canal. Painted turtles have been assessed as a species of Least Concern by the International Union for Conservation of Nature (van Dijk, 2011), but populations in southeastern Ontario are considered of Special Concern by COSEWIC given their life-history traits (e.g., late sexual maturity and low juvenile survival) that make them vulnerable to the rapid human-induced changes currently occurring in their environment (COSEWIC, 2018).

2.2 | Sampling sites and turtle captures

We captured 730 painted turtles with fyke nets from May to August in 2019 and in 2020 at 22 sampling sites distributed approximately every 10km along the Rideau Canal (except two pairs of sampling sites, RR3-1 and RR3-2: 1.2 km apart, RR2-2-2019 and RR2-2020: 2.2km apart; Figure 1a; Table S1 in Appendix S1). We set our nets in areas suitable for painted turtles characterized by shallow water, weak currents, abundant aquatic vegetation, and presence of structures for basking (e.g., rocks, logs, and stumps). We deployed fyke nets for at least 1 week at each site and checked them every 24 h. During sampling, we moved nets within a given site to increase trapping success. We visited 10 sampling sites in both years (Table S1 in Appendix S1). We uniquely marked painted turtles by notching their marginal scutes according to the North American coding system developed for hard-shelled turtles to identify individuals (Nagle et al., 2017). We determined the sex of each turtle based on external morphological traits (e.g., tail and claw length, cloaca position on the tail, and shape of the shell). We also measured plastron length, carapace length, height, and width $(\pm .5 \text{ mm})$ with an aluminum caliper (Haglöf, Sweden).

2.3 | Risk-taking behaviors

We measured three behaviors related to risk-taking propensity: sum of active defensive behaviors used, escape latency, and emergence of the turtle from the water after escaping. We repeated all behavioral measurements at each capture to obtain multiple observations per individual (mean number of observations per turtle: 1.5: range=1-7 observations per turtle, see Table S2 in Appendix S1 for the number of painted turtles per number of trials). All turtles were tested individually and no visual contact with other turtles occurred during testing. The behavioral responses could be influenced by the experimenter's handling and measurement techniques, but we tried to minimize variation in handling by always performing our behavioral tests in the same way and order (i.e., sum of active defensive behaviors, escape latency, and emergence of the turtle after escaping). It was not possible to use a blinded method because our study involved behavioral measurements that required the release of focal turtles at their site of capture (see below in Escape latency and Emergence of the turtle after escaping). The experimenter was thus aware of the identity of the turtle tested and the location of capture. We controlled statistically for variation in testing conditions (e.g., order, time and day of the trial, and laboratory- vs. field-based tests) and individual characteristics (e.g., sex and carapace length) to minimize the possible effects of potential confounds related to the STRANGE framework (e.g., biases related to individual learning, habituation, and natural behavioral changes over time; Webster & Rutz, 2020) on the relationship between human disturbance and risk-taking behaviors (see section 2.8 in section 2). No information was available on individual history prior to the first capture given that turtles were captured from the wild. All turtles sampled during



FIGURE 1 (a) Map of the Rideau Canal Waterway, Ontario, Canada, and the 22 sites (dots) sampled in 2019 and 2020. Solid bars (dark blue) represent the lockstations with their respective numbers used as reference for (b). Urban areas (i.e., building and roads) are depicted in red (dark gray) based on the Southern Ontario Land Resource Information System (SOLRIS) V.3 (OMNRF, 2019). The star shows the location of the Queen's University Biological Station where the behavioral measurements in a controlled environment occurred. The map was built using ArcGIS® software by ESRI (www.esri.com) (b) Mean daily number of vessel crossings at each lockstation in 2019 based on Parks Canada records. The dashed line represents the mean across all lockstations. The numbers used to identify each lockstation are the reference numbers from (a). (c) Image of a painted turtle (Chrysemys picta) on the floating platform during the platform test. (d) Image of a painted turtle that emerged from the water after escaping from the floating platform.

the study were used in the analyses (see Table S1 in Appendix S1 for more details on the sample sizes).

Sum of active defensive behaviors used 2.3.1

During measurements of the four morphological traits, we noted whether the turtle used the following active defensive behaviors: (i) trying to escape (movement of the legs), (ii) trying to bite (the turtle

closes and opens the mouth with its neck stretched), (iii) hissing (gaping of the mouth when retracting the head in the shell, thus expulsing air), and (iv) defecating and/or urinating. We then calculated the number of active defensive behaviors used during the test ranging from 0 (no active defensive behaviors used) to 4 (all four active defensive behaviors used). Turtles were not handled prior to this test. This test was adapted from Pich et al. (2019) (see Appendix S2 for an example of the test). We considered that a turtle that used more active defensive behaviors was more prone to take risks. Uniquely

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among vertebrates, turtles have the possibility to withdraw in their shell, a passive strategy that is their main protection against predation (Greene, 1988). Thus, we considered the use of alternative active defensive behaviors to be a riskier strategy than hiding in the shell.

2.3.2 | Escape latency

After the morphological measurements, we measured surface temperature (±1°C) of the turtle with an infrared laser thermometer (UEi test instruments, United States) pointed at the middle of the plastron because latency behaviors in turtles are affected by plastron temperature (see Pich et al., 2019). We then put the turtle in the center of a floating platform (Figure 1c) and kept it under a black pail for 1 min. The floating platform consisted of a $.6m \times .6m$ plywood mounted on rigid polystyrene and covered with white adhesive vinyl (Figure 1c). The platform was held away from the boat with a 1-m wooden dowel attached to the platform with a hinge. After the 1-min wait, we lifted the pail with a stick from the boat and timed the latency to escape as the time until the turtle touched the water for a maximum of 10 min. The maximum time (i.e., 10-min latency) was recorded if a turtle did not escape. We estimated wind speed with the Beaufort scale during the platform test as wind can affect water turbulence and, thus, turtle escape behavior. Head emergence and movement latency were also measured during the platform test, but were not kept for analyses given their strong positive correlations with escape latency (Pearson's r correlations >.60; see Table S3 in Appendix S1 for the correlation coefficients between behavioral measurements), as observed in previous studies (see Carlson & Tetzlaff, 2020). We considered that a turtle that left the platform rapidly was more prone to take risks. As suggested by Ibáñez et al. (2018), turtles that take more time to move could be considered more cautious given that they are taking more time to get visual information about their environment and to analyze risk cues. In addition, the pace-of-life syndrome hypothesis suggests that risk-averse individuals explore more thoroughly their environment compared to risk-prone individuals (Réale et al., 2010).

2.3.3 | Emergence of the turtle after escaping

After the turtle escaped the platform, we surveyed the water surface around the platform for 30 s to see whether the turtle emerged from the water (No=0, Yes=1; Figure 1d). Individuals who did not escape from the platform after the 10-min period were not considered for this test. We considered that a turtle that emerged from the water after escaping was more prone to take risks that a turtle that remained submerged. We acknowledge that turtles could emerge far from the platform and several minutes after the test was performed. However, we were not interested in monitoring distant and late emergence from the platform given that we wanted to measure the level of risk-taking. Turtles that emerged close to the platform (i.e., the risky environment) were more prone to take risks than those that emerged far from the platform or much later.

2.4 | Behavioral measurements in a controlled environment

To secure repeated behavioral measurements on several individuals, we brought 122 painted turtles (2019=50; 2020=72) to the Queen's University Biological Station (Figure 1a). Turtles were kept for a maximum of 4 days in outside tanks (940L; 1.3m×1m [diameter×depth]) filled with water from the canal in groups consisting of a maximum of 10 individuals from the same sampling site. The same three behavioral measurements described above were made every day on each turtle. The platform test, used to measure escape latency and the emergence of the turtle after escaping, was performed in the tank (Appendix S2). On the last day of captivity, we performed all behavioral tests one last time prior to release at the sites of capture. Sampling occurred daily in the field and newly captured turtles were brought every day at the station until we reached the end of sampling period at a given site of capture (i.e., approximately 1 week). Thus, the number of days in captivity varied between turtles leading to different numbers of repeated behavioral measurements per turtle (see Table S2 in Appendix S1 for the number of painted turtles per number of trials for each behavioral test in the controlled environment).

The measurements made in the controlled environment were combined with those made in the field for the analyses. We statistically controlled for the testing environment (i.e., tests performed in the field or in the controlled environment), allowing us to quantify the impact of the environment on each risk-taking behavior. Measuring behavioral responses in both settings also allowed us to document the context-dependency of the behavioral tests by comparing repeatability estimates and estimating the correlations between laboratory- and field-based behavioral measurements (see section 2.6 and section 2.8 in section 2).

2.5 | Ethics statement

All protocols were approved by animal care committees at the University of Ottawa (protocol BL-3008) and Queen's University (protocol 2018-1836). All fieldwork was conducted under a Parks Canada Agency research and collection permit (number RIC-2018-29178) and Wildlife Scientific Collector's Authorizations from the Ontario Ministry of Natural Resources (numbers 1089358, 1092637 and 1095459). Prior to handling, turtles were kept under constant supervision in large containers away from direct sunlight with a small amount of canal water. Turtles that were temporarily kept in tanks at the Queen's University Biological Station had access to rocks for hiding and logs for basking. Food (e.g., lettuce and worms according to the recommendations made by the University of Ottawa Animal Care Committee) was distributed in each tank every 2 days and the tank water was changed 3-4h after feeding. The health status of each turtle was visually verified every day for the turtles in captivity and prior to their release at the capture sites.

2.6 | Repeatability and correlations between risktaking behaviors and testing environments

All statistical analyses were conducted with R 3.6.2 (R Core Team, 2019; RRID:SCR_001905). We used mixed models to assess the consistency of behavioral measurements. Prior to analyses, we explored the distribution of each behavioral measurement (response variable) to select the best distribution to use for our models. We fitted the sum of active defensive behaviors with a Gaussian distribution and an identity link function, the emergence of the turtle after escaping with a Binomial distribution and a logit link function, and the escape latency with a Gaussian distribution and an identity link function, after normalizing the variable using a log (x+1) transformation. In all models, we included turtle identity as a random effect and assessed among and within-individual variance for each behavioral measurement. Individual repeatability corresponds to the proportion of phenotypic variance attributed to differences among individuals (Nakagawa & Schielzeth, 2010). A high repeatability indicates that the variance of a repeated measurement within an individual is smaller than the variance among individuals (Lessells & Boag, 1987). We only used observations from individuals tested more than once and from sampling sites with more than five individuals sampled (N=202 turtles from 15 sampling sites; see Tables S1 and S2 in Appendix S1). We used the rpt function implemented in the rptR package (Stoffel et al., 2017) and adjusted our models for among-individual differences using sex. order of the trial, testing environment (i.e., made in the controlled environment or in the field), and sampling year as fixed effects. We included sampling site identity as a random effect to control for the non-independence of observations from the same location. We also fitted unadjusted models with only turtle identity as a random effect. We calculated 95% confidence intervals (95% CI) of repeatability estimates and raw variance components using likelihood ratio tests (LRTs) with 1000 parametric bootstrap iterations. We also assessed repeatability separately for behavioral measurements made in the field and in the controlled environment. Finally, we calculated Pearson's and Spearman's correlations between each pair of behaviors (and their respective *p* values) by using the mean values of each behavior for each individual tested (entire dataset, N=730) with the R Hmisc packages (Harrell, 2020; RRID:SCR_022497). We also assessed correlations between laboratory- and field-based measurements for each behavior with the first measurement of each individual tested in both environments (N = 122).

2.7 | Quantifying human disturbance

We used ArcGIS version 10.7.1 (ESRI, 2019; RRID:SCR_011081) and Python version 2.7.16 (Python Software Foundation, 2019;

RRID:SCR_008394) to perform all spatial analyses. We used four variables to quantify the intensity of human disturbance at each sampling site: (i) mean number of daily vessel crossings during the operational period of the canal, (ii) shortest aquatic distance (in m) to the navigation channel, (iii) number of houses with access to the canal within various buffers (see below), and (iv) proportion of urban area within various buffers (see below).

We calculated the mean daily number of vessel crossings at each lockstation based on Parks Canada counts made during the operational period (i.e., May (Canadian Victoria Day) to October (Canadian Thanksgiving); see Table S4 in Appendix S1; Figure 1b). Given the lower frequentation and late opening of the Rideau Canal in 2020 due to the COVID-19 pandemic, we only used the number of vessel crossings from 2019 to be more representative of boat traffic during a typical year and given that we were interested in the intersite variation in boating activity (Table S4 in Appendix S1). We used the mean daily number of vessel crossings from the upstream and downstream lockstations of each sampling site to calculate the mean daily number of vessel crossings. We considered that sampling sites in proximity to lockstations with high mean daily numbers of vessel crossings should have more boat activity.

We calculated the shortest aquatic distance of each sampling site to the navigation channel with the *Generate near table* tool in ArcMap. The channel was digitized by Parks Canada from digital navigation charts. We considered that sampling sites closer to the navigation channel should have more boat activity.

We used ArcGIS world imagery online basemap (ESRI, 2021) to identify each house with access to the Rideau Canal (e.g., presence of a dock on the property or at least one side of the property with access to the canal). We calculated the number of houses with access to the canal using buffer distances that ranged from 100m to 1000m at 100-m increments with the *Spatial Join* tool in ArcMap (based on the work of Čapkun-Huot et al., 2021; Fyson & Blouin-Demers, 2021). We considered that sampling sites close to numerous houses with access to the canal should have more boat activity.

Based on the same buffer distances as above, we determined the proportion of urban area around each sampling site based on the Southern Ontario Land Resource Information System (SOLRIS) V.3 with 15-m resolution (OMNRF, 2019; Figure 1a). We used the *Tabulate Area 2* tool from the Spatial Analyst Supplemental Tools v1.3 in ArcMap to calculate the number of cells of each land cover class inside each buffer distance. Then, we calculated the proportion of urban area (i.e., transportation, built-up area-pervious, and built-up area-impervious land cover classes) over the total buffer area (Figure 1a). We considered that sampling sites in proximity to higher proportion of urban area should have more human activity.

Finally, we determined the distance at which the number of houses with access to the canal and the proportion of urban area had the maximum effect on the three behavioral measurements separately. The scale of maximum effect was attributed to the buffer distance at which the variable had the highest Pearson's correlation coefficient with each behavioral measurement (see Appendix S3). We only kept the scale of maximum effect for each variable for -WILEY-ethology

further analyses. Similar techniques were used in other taxa to determine the scale of maximum effect of landscape variables (see Čapkun-Huot et al., 2021; Courtois et al., 2021; Fyson & Blouin-Demers, 2021; Martin et al., 2020; Wilkin et al., 2006).

2.8 | Relationships between risk-taking behaviors and human disturbance

The same distributions and link functions described above for repeatability analyses were used here. We used (generalized) linear mixed models to assess the relationships between human disturbance and risk-taking behaviors from measurements made on 730 painted turtles (Tables S1 and S2 in Appendix S1) with the Ime4 package (Bates et al., 2015; RRID:SCR_015654). In all models, we used the behavior as the response variable and different predictor variables to assess the variance related to testing conditions (e.g., order of the trial and laboratory- vs. field-based tests) and individual characteristics (e.g., sex and carapace length), as well as the variables quantifying human disturbance (see Tables S5 and S6 in Appendix S1 for a list and description of all the variables included). All continuous predictor variables were standardized (mean zero, unit variance) before model selection (Table S6 in Appendix S1). We removed from initial models all variables that were highly correlated (r > .8) or with high generalized variance inflation factors ($GVIF^{(1/(2^*df))} > 2$) to avoid multicollinearity (see Tables S5 and S7 in Appendix S1). We simplified models with a backward selection procedure (α =.05) until all remaining variables were significant and the inclusion/deletion of each variable was confirmed with a LRT (Crawley, 2007). We also included turtle and sampling site identity as random effects to respectively control for the repeated behavioral measurements on individuals and individuals from the same location. Turtle identity was significant (according to LRTs) and kept in all models, while sampling site identity was only significant in the sum of active defensive behaviors model. We visually verified model assumptions of each initial model by checking residual distributions and their relationships with fitted values. We calculated the estimates and 95% CI for all predictor variables from the final models fitted with restricted maximum likelihood (Zuur et al., 2009). We estimated marginal and conditional variance explained (R^2) by the final models with the MuMIn package (Bartoń, 2020). We generated final model predictions with the ggeffects package (Lüdecke, 2018; RRID:SCR_022496) and built figures with the ggplot2 package (Wickham, 2016; RRID:SCR_014601).

3 | RESULTS

3.1 | Description of risk-taking behaviors in painted turtles

Combining tests performed in the controlled environment and in the field, we made 1117 observations of the number of active defensive behaviors used during manipulations on the 730 turtles captured. In

30% of observations, no active defensive behaviors were used (340 observations; mean = 1.08 active defensive behaviors used, standard deviation (SD) = .92). Only three turtles used all four active defensive behaviors during the same trial. We made 1115 observations of escape latency and turtles escaped within 30s 82% of the time (929 observations; mean = 66s, SD = 118). During the platform test, 23 turtles (29 observations) had not escaped after 10min. Finally, for the 1071 observations of emergence after escaping, turtles did not emerge from the water 70% of the time (750 observations; see Table S1 in Appendix S1 for more details on the sample sizes).

3.2 | Repeatability and correlations between risktaking behaviors and testing environments

We obtained repeated behavioral measurements both from the controlled environment and in the field for 202 individuals, representing 28% of the total number of turtles tested (N=730; Table S2 in Appendix S1). We found statistically significant adjusted repeatability estimates for sum of active defensive behaviors (.363 (95% CI = .263-.458)), escape latency (.387 (95% CI = .286-.490)), and emergence of the turtle after escaping (.365 (95% CI=.129-.630)) (Table 1). There were slight differences between adjusted and unadjusted repeatability estimates for all behavioral measurements: when our models were adjusted with the fixed effects and sampling site identity as a random effect, repeatability estimates for escape latency and emergence of the turtle after escaping increased, while it decreased for the sum of active defensive behaviors used (Table 1). For all behavioral measurements, however, the 95% CI of the unadjusted and adjusted repeatability estimates overlapped (Table 1). In each testing environment separately, repeatability estimates were significant for all risk-taking behaviors and similar to those we obtained with the combined dataset (Table S8 in Appendix S1). We found slightly higher repeatability estimates in the field for the sum of active defensive behaviors used and escape latency, while it was the opposite for the emergence of the turtle after escaping the platform (Table S8 in Appendix S1). However, the 95% CI of repeatability estimates from field and controlled environment all overlapped (Table S8 in Appendix S1).

Painted turtles that used more active defensive behaviors escaped from the floating platform sooner (Pearson's *r* correlation = -.24, p < .01; Table S3 in Appendix S1) and emerged from the water more often after escaping (r=.26, p < .01; Table S3 in Appendix S1). Turtles that took more time to escape from the platform emerged less often from the water after escaping (r= -.19, p < .01; Table S3 in Appendix S1). We obtained similar results with a multivariate mixed model that included the three behavioral measurements as response variables with the MCMCglmm package (Hadfield, 2010; Table S9 in Appendix S1). Painted turtles tested in the controlled environment used fewer active defensive behaviors during handling and emerged less often from the water after escaping (Table 2). Lastly, for all risk-taking behaviors, we obtained significant positive correlations between measurements made in the field and those made in the

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TABLE 1 Sources of variance (V_G: group-level variance; V_R: residual variance) and repeatability estimates (R) for three risk-taking behaviors in painted turtles (*Chrysemys picta*): sum of active defensive behaviors, escape latency, and emergence of the turtle after escaping.

	Nb. ID (Nb. Entries)	V _{G-individual}	V _{G-site}	V _R	R _{individual}	R _{site}	R ² _{fixed}	
Sum of active defer	nsive behaviors							
Unadjusted	202 (569)	.374 [.275492]	-	.430 [.374499]	.465 [.371–.549]	-	-	
Adjusted	196 (553)	.292 [.206388]	.103 [.014234]	.411 [.349473]	.363 [.263458]	.128 [.020254]	.06	
Escape latency								
Unadjusted	199 (574)	.506 [.338681]	-	.916 [.796-1.045]	.356 [.258442]	-	-	
Adjusted	193 (558)	.506 [.352682]	.081 [.000226]	.723 [.619817]	.387 [.286490]	.062 [.000154]	.10	
Emergence of the turtle after escaping								
Unadjusted	196 (543)	1.679 [.521–2.484]	-	4.565 [4.298-5.065]	.257 [.107317]	-	-	
Adjusted	190 (527)	3.185 [.813-4.928]	2.325 [.226-4.553]	4.576 [4.152-6.137]	.365 [.129630]	.267 [.008555]	.20	

Note: The unadjusted repeatability estimates only included turtle identity as random effect, while the adjusted repeatability estimates also included sex, trial order, testing environment (i.e., made in the controlled environment or in the field), and year as fixed effects, and sampling site identity as a random effect (V_{G-site} and R_{site}). Significance [95% confidence intervals] of the variances and repeatability estimates were determined with likelihood ratio tests. The coefficient of determination (R^2) of the fixed effects included in the adjusted repeatability estimates was calculated. Sources of variances for the emergence of the turtle after escaping were estimated from the link-scale approximation and repeatability estimates from the original scale. The number of individuals tested (Nb. ID) with the total number of observations (Nb. Entries) for each behavior is provided.

controlled environment ($r_{active defensive behaviors} = .40$; $r_{escape latency} = .39$; $r_{emergence} = .33$; p < .01; Table S10 in Appendix S1).

3.3 | Relationships between risk-taking behaviors and human disturbance

We found significant relationships between some measurements of human disturbance and the sum of active defensive behaviors used, but no relationships for escape latency and emergence of the turtle after escaping (Table 2). Painted turtles from sites closer to the navigation channel (Table 2; Figure 2a) and with more daily vessel crossings (Table 2; Figure 2b) used more active defensive behaviors. In contrast, painted turtles from sites with more houses with access to the canal within 200m used fewer active defensive behaviors (Table 2; Figure 2c). Model estimates and their 95% CI for all predictor variables included in our models are provided in Table 2.

4 | DISCUSSION

Understanding how animals adjust behaviorally to perturbations in their environment is crucial to better evaluate the impact of human disturbance on wildlife populations, especially for species particularly vulnerable to human activities. We observed that risk-taking behaviors of painted turtles were repeatable and consistent among the different tests and the two testing environments. Painted turtles from sites with more boat activity used more active defensive behaviors, while turtles from sites in proximity to more houses with access to the canal used fewer. These findings add to the limited information currently available on the impact of human disturbance on risk-taking behaviors in turtles.

4.1 | Painted turtles show consistent differences in risk-taking behaviors

All three risk-taking behaviors of painted turtles were repeatable, as observed in other studies (Bell et al., 2009; Holtmann, Lagisz, & Nakagawa, 2017). Across taxa, approximately 40% of the phenotypic variation of behavioral responses reflects among-individual variance, similar to our estimates (Bell et al., 2009; Holtmann, Lagisz, et al., 2017). In previous studies of turtles, repeatability estimates of risk-taking behaviors were slightly higher than ours (mean~.5; see Table S11 in Appendix S1). In these studies, however, repeated measurements were generally only obtained in controlled environments, over short periods of time (i.e., a few hours to several weeks), and on a small number of individuals (i.e., fewer than 30 turtles; Table S11 in Appendix S1). Repeatability estimates are generally higher when measurements are made temporally close to each other and in stable conditions (Bell et al., 2009; Holtmann, Lagisz, et al., 2017). The use of only one sampling technique (i.e., fyke nets) in our study, however, could have led to more conservative repeatability estimates (see also section 4.3). Estimating repeatability over a longer period and from a large dataset collected in the field, as in our study, is probably more realistic and representative of the long lifespan of turtles and the environmental

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TABLE 2 Summary statistics for the final (generalized) linear mixed models with risk-taking behaviors in painted turtles (*Chrysemys picta*) as the response variable: sum of active defensive behaviors used, escape latency, and emergence of the turtle after escaping.

Variables	Estimate	SE	t-value	p-value	[95% CI]	
Sum of active defensive behaviors	714 individuals (10	91 observations); R^2	– marginal: .08; R ² – cor	ditional: .52		
Intercept	.853	.074	11.544	<.001	[.708 to .998]	
Number of houses within 200 m	134	.058	2.316	.031	[247 to021]	
Distance to navigation channel	122	.057	2.122	.047	[234 to009]	
Mean daily number of vessel crossings	.194	.065	2.986	.008	[.067 to .321]	
Sex (Male)	.327	.070	4.687	<.001	[.191 to .464]	
Testing environment (controlled setting)	218	.068	3.228	.001	[350 to086]	
Carapace length	.112	.037	3.014	.003	[.040 to .186]	
Turtle temperature	.003	.046	.077	.939	[087 to .094]	
Julian Day	012	.061	.197	.845	[132 to .107]	
Hour	.016	.035	.462	.644	[053 to .086]	
Year (2020)	.040	.073	.555	.579	[102 to .183]	
Order of the trial	.043	.027	1.573	.116	[010 to .096]	
Escape latency	596 individuals (919 observations); R^2 – marginal: .10; R^2 – conditional: .44					
Intercept	3.401	.044	76.525	<.001	[3.314 to 3.488]	
Order of the trial	231	.036	6.415	<.001	[302 to161]	
Julian Day	.141	.053	2.645	.008	[.036 to .245]	
Turtle temperature	199	.047	4.245	<.001	[291 to107]	
Carapace length	.167	.042	4.013	<.001	[.085 to .248]	
Wind scale (Beaufort scale)	176	.036	4.899	<.001	[246 to106]	
Sex (Male)	.005	.093	.053	.958	[177 to .186]	
Distance to navigation channel	.025	.052	.475	.635	[077 to .126]	
Number of houses within 400m	.032	.053	.602	.548	[072 to .137]	
Mean daily number of vessel crossings	028	.041	.681	.496	[108 to .052]	
Year (2020)	087	.088	.995	.320	[260 to .085]	
Proportion of urban areas within 200 m	.094	.060	1.547	.123	[025 to .212]	
Testing environment (controlled setting)	.244	.144	1.692	.091	[039 to .527]	
Hour of the platform test	039	.039	.990	.322	[115 to .038]	
Emergence of the turtle after escaping	704 individuals (10	071 observations); R ²	– marginal: .12; R ² – cor	ditional: .49		
Intercept	-1.135	.208	5.464	<.001	[-1.543 to728]	
Testing environment (controlled setting)	-2.318	.417	5.558	<.001	[-3.135 to -1.500]	
Julian Day	.994	.182	5.473	<.001	[.638 to 1.350]	
Carapace length	323	.131	2.473	.013	[579 to067]	
Sex (Male)	072	.242	298	.767	[545 to .402]	
Turtle temperature	.082	.135	.606	.545	[183 to .348]	
Hour of the platform test	.080	.128	.627	.531	[170 to .331]	
Year (2020)	.299	.231	1.293	.196	[154 to .751]	
Distance to navigation channel	188	.138	1.361	.173	[459 to .083]	
Number of houses within 300 m	160	.134	1.196	.232	[423 to .102]	

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TABLE 2 (Continued)					
Variables	Estimate	SE	<i>t</i> -value	p-value	[95% CI]
Mean daily number of vessel crossings	.196	.121	1.620	.105	[041 to .433]
Order of the trial	.167	.107	1.570	.116	[042 to .376]

Note: All continuous predictor variables were scaled (mean zero and unit variance) before model selection. Reference factors are in parentheses for categorical predictor variables. Turtle and sampling site identities were included as random effects in the model for sum of active defensive behaviors, while only turtle identity was included in the two other models. For each model, we provided for each significant predictor variable: the estimate, the standard error (SE), the *t*-value (*z*-value for the binomial model), the *p*-value, and the 95% confidence interval (95% CI). Statistically significant effects (*p*-value <.05) are in bold. The marginal and conditional coefficient of determination (R^2) are provided for each model as well as the number of unique painted turtles tested with the total number of observations in parentheses.



FIGURE 2 Relationships between the number of active defensive behaviors used by painted turtles (*Chrysemys picta*) and three proxies of human disturbance in the Rideau Canal, Ontario, Canada: (a) shortest aquatic distance to the navigation channel, (b) mean daily number of vessel crossings, and (c) number of houses with access to the canal within 200 m of the sampling site. Predictor variables were standardized (mean zero, unit variance). Each dot represents an observation (*N*=1091). Dots were jittered to avoid overlap. Gray areas represent 95% confidence intervals of the model-predicted effect (black line).

context in which they live. Given that risk-taking behaviors are partially consistent within individuals, it allows evaluating the effect of human disturbance on the variation observed in risk-taking behaviors.

We observed consistency among our three measures of risk-taking propensity. Painted turtles that escaped sooner from the floating platform used more active defensive behaviors and emerged more often from the water after escaping: these turtles may be considered more risk prone. Our three behavioral tests seem to measure the same underlying risk-taking propensity. Previous studies in turtles also indicated consistent boldness under alternative tests (Pich et al., 2019; Roth et al., 2020). Behavioral consistency among tests could indicate a behavioral syndrome (i.e., suite of correlated behavioral measurements) in painted turtles where individuals use different behavioral strategies (i.e., pace-of-life continuum: proactive vs. reactive individuals; Réale et al., 2010; Sih, 2004). Measurements in different contexts (e.g., simulated predation attack vs. human presence) or along other axes of behavior (e.g., exploration, aggressivity, and sociability) are needed to confirm the presence of a behavioral syndrome in painted turtles.

Risk-taking behaviors were positively correlated between testing environments indicating consistency across contexts. Risktaking behaviors were also repeatable in each testing environment indicating consistency in among-individual differences regardless of the context (Rudin, Simmons, & Tomkins, 2018). These results indicate that behavioral measurements obtained in a controlled environment could predict risk-taking level in the field. On the other hand, painted turtles used fewer active defensive behaviors and emerged less often from the water after escaping in the controlled environment. Painted turtles reacted slightly differently between testing environments. In the controlled environment, turtles were not exposed to external cues and might have perceived it as a novel environment while turtles tested in the field had access to cues from their surroundings with which they were familiar (Mouchet & Dingemanse, 2021; Rudin, Simmons, et al., 2018; Rudin, Tomkins, & Simmons, 2018). Turtles tested in the controlled environment may also have different behavioral responses to the tests given their short-term captivity. Our findings highlight the importance of performing behavioral tests in different contexts, especially in natural environments, and to control statistically for testing conditions given their potential impacts on behavioral responses. We lacked enough repeated measurements in the field to calculate correlations between contexts by partitioning among- and within-individual variances and to completely evaluate cross-context consistency, which would be useful in future analyses (Mouchet & Dingemanse, 2021).

4.2 | Painted turtles from sites with high boat activity take more risks

Painted turtles from sites more exposed to boat activity were more prone to take risks, as indicated by their use of more active defensive

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behaviors, suggesting that human presence influences behavioral responses. Previous studies documented similar relationships. For instance, more risk-prone turtles (i.e., shorter flight initiation distance to human approach and lower abandonment rate of basking sites after boating disturbance) were observed in areas with more frequent human disturbance (Polich & Barazowski, 2016; Selman et al., 2013). To our knowledge, our study is the first to relate the use of active defensive behaviors to human disturbance, making comparisons with other studies impossible. While shorter flight initiation distances and lower abandonment rates in areas with higher exposure to human activities reflect a higher tolerance toward human disturbance, the use of more active defensive behaviors suggests the opposite (Bejder et al., 2009). We need to understand how these various behaviors are related to each other and to human disturbance.

It is unclear how the use of active defensive behaviors can be advantageous in human-altered environments considering that turtles have the opportunity to withdraw in their shell, a possibly safer strategy for protection. A previous study by Kashon and Carlson (2018) found that risk-prone Eastern box turtles (i.e., low movement latencies) had more shell injuries, suggesting a higher exposure to risky situations such as predation. Thus, risk-prone turtles may use alternative active defensive behaviors (i.e., stronger antipredator behaviors) to compensate for the risks of not hiding in risky situations (Pascual & Senar, 2014; Pich et al., 2019). While risk-averse individuals (i.e., those that use fewer active defensive behaviors and greater propensity to hide) are more cautious and may have a lower mortality rate (Smith & Blumstein, 2008), they may miss many feeding, reproductive, and basking opportunities compared with riskprone individuals by avoiding areas with high human disturbance (Dugatkin & Alfieri, 2003; Dyer et al., 2009; Griffin et al., 2017; Réale et al., 2009). Risk-prone individuals resume activities more rapidly after exposure to an unknown threat, suggesting that the loss of opportunities can be limited compared to risk-averse individuals (Cole & Quinn, 2014). Therefore, the capacity to cope better with risky situations, suggested by the use of more active defensive behaviors, may allow painted turtles to coexist with boating activities in the canal and to persist in a human-altered environment.

We observed that painted turtles from sites with more houses with access to the canal used fewer active defensive behaviors. This result is unexpected because we predicted that all our proxies of human disturbance would be similarly related to risk-taking behavior. One possible explanation is that this relationship is simply spurious. The scale of maximum effect occurred at 200m and the effect size was small, at least partly because of limited variance in the predictor variable (Table S6 in Appendix S1). It is also possible that the number of houses within 200m is a poor predictor of the level of recreational boating. The response of wildlife to human disturbance can be complex depending on the type and intensity of perturbations (Gaynor et al., 2018; Larson et al., 2016; Tablado & Jenni, 2017; Tucker et al., 2018). The behavioral response can also depend on the predictability of perturbations and, thus, the capacity of the animal to predict risk level (Nickel et al., 2020). Therefore, risk-averse turtles (i.e., that use fewer active defensive behaviors) could avoid areas with high boat activity where risk level is less predictable, whereas the number of houses may reflect a more permanent and constant human disturbance (i.e., predictable), leading to different behavioral responses to these different proxies of human disturbance.

While our study was not designed to assess the mechanisms responsible for the observed changes, our findings still provide insights into which mechanisms may play a role in the relationship observed between human disturbance and the number of active defensive behaviors used. For instance, the use of a higher number of active defensive behaviors in larger turtles (i.e., long carapace; Table 2) that are likely older (Wilson et al., 2003) suggests a long-term behavioral plasticity where turtles may adapt their behavior according to their past experiences. We cannot exclude that the behavioral responses observed in this system could be the result of multiple mechanisms. Indeed, new selection pressures could have appeared during canal construction leading to the selection of risk-prone turtles and followed by a long-term behavioral plasticity of the individuals that have persisted in these new conditions. The construction of the canal is relatively recent (e.g., between 1826 and 1832) in terms of painted turtle generation time (~30-45 years; COSEWIC, 2018), and it could be too short for selection to occur. Another possibility is that painted turtles, after exposure to new environmental conditions caused by the canal construction, have dispersed and selected habitats better adapted to their behavior at some point during their lifetime. Longterm monitoring of these populations would be necessary to achieve a better understanding of the mechanisms driving the behavioral responses of painted turtles toward human disturbance.

4.3 | Possible limitations of the study and STRANGEness of animals sampled

We are aware of the potential lack of independence between nearby sampling sites along the canal and that risk-taking behaviors could be spatially autocorrelated. To quantify the potential presence of spatial autocorrelation, we estimated Moran's I statistic for different distances (i.e., from 5 to 130km) for each risk-taking behavior. We detected positive spatial autocorrelation for the sum of active defensive behaviors and the emergence of the turtle after escaping in the water (positive and significant Moran's I statistic, respectively, under 5 and 27 km; see Table S12 in Appendix S1). Given that we did not find a significant effect of sampling site identity and human disturbance on the emergence of the turtle after escaping, it was only relevant to evaluate the effect of spatial autocorrelation on the results obtained for the sum of active defensive behaviors. We modified the variable representing sampling site identity by grouping together observations from sampling sites located less than 5 km apart (i.e., RR3-1 with RR3-2 and RR2-2-2019 with RR2-2020). By fitting a new model with this adapted version of sampling site identity that considers spatial autocorrelation as a random effect, we found that the variance explained by sampling site identity was very similar to

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vulnerable to human activities through the creation of conservation plans that are better adapted to minimize the negative effects of human disturbance on wildlife. AUTHOR CONTRIBUTIONS Audrey Turcotte: Conceptualization; writing - original draft; methodology; formal analysis; investigation; data curation; project administration; validation; visualization; supervision. Dany Garant: Conceptualization; supervision; funding acquisition; writing review and editing; resources; validation. Gabriel Blouin-Demers: Conceptualization; supervision; funding acquisition; writing - review and editing; resources; validation. ACKNOWLEDGMENTS We thank all field assistants who helped with data collection. Vincent Fyson helped with spatial analyses. Valerie Minelga and Chantal Vis from Parks Canada Agency provided data on lockage activities and the digitized navigation channel of the Rideau Canal. We thank Catherine Čapkun-Huot for interesting discussions on animal behavior. Pictures from Figure 1c,d were provided by Audrey Turcotte. This work was supported by a Natural Sciences and Engineering Research Council of Canada (NSERC) Strategic Project Grant focused on the Rideau Canal Waterway and the Ottawa Field-Naturalists' Club. AT was supported by a postgraduate NSERC scholarship. 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 Zenodo Digital Repository: https://doi.org/10.5281/zenodo.7795750.

CONSENT TO PARTICIPATE AND PUBLISH

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

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that in the model that did not consider spatial autocorrelation (without correction for spatial autocorrelation: variance=.051, SD=.226; with the correction: variance=.053, SD=.229). We also obtained the same significant predictors in the final model after model selection (Table S13 in Appendix S1).

We only used one sampling technique (i.e., fyke nets), which may have led to the capture of turtles that are not representative of the entire population in their behaviors according to the STRANGE framework (Webster & Rutz, 2020). Nets could have been avoided by risk-averse individuals leading to the trapping of more risk-prone individuals and, thus, to the underestimation of the range of behavioral responses. Less diversity in behavioral types, however, should have led to more conservative repeatability estimates by reducing among-individual variances. It should also have reduced our capacity to identify how human disturbance is related to risk-taking behaviors, which did not appear to be the case, possibly because our high sampling effort at a large spatial scale may have minimized these biases. In addition, by combining data collected in two testing environments, we obtained a large sample size that allowed us to control statistically and quantify the effects of multiple confounding factors related to testing conditions (e.g., order of the trial and laboratory- vs. field-based tests) and individual characteristics (e.g., sex and carapace length; see Table 2 for a list of all the variables included in models and their respective effect sizes). By measuring behaviors in the field, however, we could not control for spatiotemporal variations in the testing environment. In addition, our ability to detect the emergence of the turtle after escaping could potentially vary between testing environments. Positive correlations and similar repeatability estimates between testing environments indicate that our behavioral tests seem appropriate to assess risk-taking level in both contexts. In addition, repeating the analyses separately for turtles tested in the controlled environment and in the field, and for turtles tested more than once, gave qualitatively similar results (see Tables S14 and S15 in Appendix S1). Thus, we are confident that our analyses are robust and that the results obtained reflect how human disturbance is related to risk-taking behaviors in painted turtles.

5 | CONCLUSION

Overall, we found that painted turtles show consistent differences in risk-taking behaviors and that their behavioral response to risky situations is influenced by the level of human disturbance in the Rideau Canal. Our study adds to the current research on turtle behavior and is one of the first to assess how risk-taking behavior is related to human disturbance in this group. There is a need to assess the impact of human activities on other types of behaviors and to identify the mechanisms driving the differences observed in behavioral responses according to the level of human disturbance. It would also be beneficial to assess how the behavioral responses are related to fitness and survival (see Allard et al., 2019; Germano et al., 2017). A better understanding of the consequences of behavioral changes would allow better management of species WILEY - ethology

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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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