# Landscape composition predicts the local abundance of painted turtles (*Chrysemys picta*)

Catherine Čapkun-Huot<sup>1,\*</sup>, Vincent K. Fyson<sup>1</sup>, and Gabriel Blouin-Demers<sup>1</sup>

**Abstract.** Urbanisation and agriculture are paradigmatic cases of habitat loss, degradation, and fragmentation that imperil wildlife. Anthropogenic landscape modifications can harm species such as freshwater turtles that rely on both aquatic and surrounding terrestrial habitats to survive and reproduce. We tested the hypothesis that the local abundance of painted turtles (*Chrysemys picta*) in wetlands depends on the composition of the surrounding landscape. We predicted that there would be fewer turtles in wetlands in more modified landscapes (i.e., urban and agricultural) with higher road densities. From repeated visual surveys of 34 wetlands around Ottawa, Canada, we found that there were more painted turtles in wetlands that were larger and surrounded by more forest. Therefore, proper management of forested lands and green areas in urban landscapes are needed to protect turtles cohabiting with humans.

Keywords. Urbanisation, Agriculture, Habitat, Wetland, Forest, Road

## Introduction

Our epoch is often defined as the Anthropocene, an era dominated by *Homo sapiens* (Lewis and Maslin, 2015) where only 5 % of Earth's terrestrial area remains unmodified by human activities (Kennedy et al., 2019). Humans are driving a major biodiversity crisis with one million species currently threatened with extinction (IPBES, 2019) and an expected species loss of up to 50 % by 2050 (Koh et al., 2004); we are in the midst of the sixth mass extinction (Thomas et al., 2004; Ceballos et al., 2015). Globally, reptiles are one of the most endangered groups and freshwater turtles are highly threatened (Böhm et al., 2013).

Many factors may cause the plight of reptiles, and particularly of turtles, including habitat loss and degradation (Gibbons et al., 2000). Habitat loss and degradation have many implications for wildlife, including an increase in habitat fragmentation, which in turn increases isolation (Meffe and Carroll, 1997) and predation pressure (Oehler and Litvaitis, 1996). Indeed, fragmentation may elevate predation rates via an increase in predator abundance (Oehler and Litvaitis, 1996) due to a human-induced increase in food supply (Baxter-Gilbert et al., 2015). Fragmentation therefore results in an increase in the mortality rate and the probability of extinction of many species (Shepard et al., 2008). While wetlands are recognised as critical habitat for freshwater turtles and other wildlife, the rate of wetland loss is three times higher than the rate of forest loss worldwide (Ramsar Convention on Wetlands, 2018). In Canada, southern Ontario is no exception: large numbers of wetlands have been drained or filled to accommodate urbanisation and agriculture (Ontario Ministry of Natural Resources and Forestry (OMNRF), 2017), which has resulted in the loss of 72 % of the original wetland area (Ontario Biodiversity Council, 2010, 2015). Over the years, therefore, freshwater turtles have lost an important part of their habitat in Ontario.

One human-made habitat modification particularly impedes wildlife movements and fragments the habitat: roads. Roads can have indirect effects on turtles, such as isolating populations, but they can also affect turtles directly through roadkill (Shepard et al., 2008). Indeed, Gibbs and Shriver (2002) estimated that large-bodied turtle mortality increases when road density exceeds 2 km/km<sup>2</sup>. Turtles are thought to be particularly vulnerable to the effects of roads because they are long-lived and late-maturing species that depend on high adult survivorship to counterbalance naturally high egg, hatchling, and juvenile mortality (Howell and Seigel, 2019). Therefore, population viability is highly sensitive to additive adult mortality caused by roadkill (Heppell, 1998; Litzgus, 2006).

<sup>&</sup>lt;sup>1</sup> Department of Biology, University of Ottawa, Ottawa K1N 6N5, Canada.

<sup>\*</sup> Corresponding author. E-mail: ccapk060@uottawa.ca

<sup>© 2021</sup> by Herpetology Notes. Open Access by CC BY-NC-ND 4.0.

Urbanisation is a paradigmatic case of habitat loss, degradation, and fragmentation which intensively and irreversibly modifies ecological processes (Stokeld et al., 2014). Urbanisation, as well as agriculture, can indeed radically change a landscape. Landscape-level factors are important for freshwater turtles because they use both aquatic and surrounding terrestrial habitats. Terrestrial habitats are needed for dispersal, nesting, and, in some species, aestivation (Buchanan et al., 2019). Terrestrial habitats can be important refuges (Roe and Georges, 2007) and can be essential in case of drought (Winchell and Gibbs, 2016). Landscape modifications via urbanisation or agriculture can therefore have a profound impact on turtle populations.

The painted turtle (*Chrysemys picta*) is found across North America (Ernst and Lovich, 2009). Even though painted turtles are considered globally stable by the IUCN (van Dijk, 2011), they are considered Special Concern by the Committee on the Status of Endangered Wildlife in Canada, in part because of road mortality and habitat loss caused by human activities (COSEWIC, 2018).

We tested the hypothesis that the local abundance of painted turtles (*Chrysemys picta*) in wetlands depends on the composition of the surrounding landscape. We predicted that there would be fewer turtles in wetlands located in more modified landscapes (i.e., urban and agricultural) with higher road densities. Indeed, more natural landscapes should be less isolated, less fragmented, and less conducive to roadkill than more urban landscapes, resulting in higher habitat quality.

## **Materials and Methods**

**Study area.** We assessed painted turtle abundance in 34 wetlands in Ottawa, Canada. We selected wetlands to span a gradient of urbanisation. To minimise potential dispersion between sites and spatial auto-correlation (Stokeld et al., 2014), we selected wetlands that were at least 1.5 km apart. This distance was chosen because it is beyond the dispersal abilities of most painted turtles (Christens and Bider, 1987; Marchand and Litvaitis, 2004; Steen and Gibbs, 2004; Patrick and Gibbs, 2010). Importantly, we did not select wetlands on the basis of their expected suitability for turtles. Wetlands varied in size, ranging from 0.12 ha to 19.57 ha, with a mean area of 4.12 ha.

**Visual surveys.** We counted the number of painted turtles present at a wetland by scanning with binoculars and a spotting scope from different locations until as much of the wetland perimeter and potential basking sites as possible were scrutinised. The probability of turtle detection is highly related to basking behaviour. As this behaviour is very sensitive to environmental conditions, we used the ambient air temperature, wind, and cloud cover to control for their potential effects on our observations. We retrieved the ambient air temperature from hourly data reports from an Environment Canada weather station in Ottawa (https://climat.meteo.gc.ca/). Wind speed, based on the Beaufort wind force scale, and cloud cover were estimated visually by the same person (CČH).

Surveys were conducted from 30 May to 27 August 2019 on days with no rain. Each site was visited nine times. In general, all 34 sites were sampled consecutively before revisiting a site and the order of visits was changed so that sites were not surveyed at the same time of day for the nine visits.

Landscape composition. We conducted landscape analyses in ArcMap version 10.6 (ESRI, 2018; http://www.esri.com) using the Ontario Land Cover Compilation (OLCC) v.2.0 layer. Although the original file contained 29 land cover classes, we condensed them to five cover types (open water, wetland, forest, anthropogenic, agriculture). We manually delineated wetland edges at a scale of 1:3000 using orthophotos to obtain wetland area. Buffers were created from the perimeters of the wetlands, excluding the wetland itself, from 50 m to 2,000 m in 50-m increments (Fig. 1). Land cover was measured as a percentage of the total buffer area for each cover type. We calculated correlations (Pearson's correlation coefficient) between the number of turtles observed at each site and the percentage of each land cover type for each buffer distance, and retained only the buffer distance at which the correlation was maximal for further statistical analyses. Although land cover types are correlated to each other because the sum of their proportions equals one, their highest correlation with turtle abundance were all at different buffer distances. We also measured road densities as road length per unit of area and we selected the buffer distance (50 m - 2,000 m) at which the correlation with painted turtle abundance was the highest for use in our statistical models.

**Statistical analyses.** To investigate the effect of survey conditions on turtle counts (i.e., survey duration, wind speed, cloud cover, mean temperature during survey, and wetland area), we used a mixed model with a Poisson distribution and incorporated wetland ID as a random factor, which takes into account the non-independence of the nine visits to each wetland. We added a random variable to the model that allocates a unique number



**Figure 1.** Buffers were created from 50 m to 2,000 m (at 50m increments) from the wetlands' perimeter to measure land cover. The wetland perimeter is delineated in black and the first two buffer distances (50 m and 100 m from the wetland's perimeter) are shown in yellow.

to each observation to control for overdispersion of the data (Elston et al., 2001). To estimate the effect of land cover variables on local abundances, we used a generalised linear model. For this second model, we considered the highest count for a site as the best approximation of local abundance. Selecting the highest counts confers several advantages: (1) it removes some noise in the data, (2) it is appropriate for a seasonal time frame, and (3) it reduces the variation in ambient temperature during surveys among sites because all maximum number of observations happened in a narrower range of temperatures that are more suitable for basking. A follow-up analysis revealed that using the mean or the sum of painted turtle counts for each wetland did not change the statistical conclusions. We used a quasi-Poisson distribution to control for overdispersion in the data. Due to low power caused by our modest sample size (n = 34 wetlands), we had to reduce the number of variables included in this model. Therefore, we selected only the two land cover types for which the univariate correlation with turtle abundance was over 0.3. We also added wetland area to the model. As explained above, using the highest count for each site removed the necessity to include temperature as a covariate. All statistical analyses were completed in R version 3.5.3 (R Core Team, 2019) using the ImerTest package (Kuznetsova et al., 2017).



Figure 2. Maximum number of painted turtles observed during one visit at each wetland (N = 34) around Ottawa, Ontario, Canada.

## Results

We found painted turtles in 88% of the wetlands we surveyed (30/34), ranging from one to 415 observed individuals, all visits combined (n = 1895 observations, mean maximum abundance of  $16.2 \pm 4.8$  turtles per wetland) (Fig. 2).

Sampling conditions influenced the number of turtles observed. Indeed, more turtles were observed during longer sessions on cool days with few clouds (all p values < 0.01; Table 1), but the turtle count was unaffected by wind speed (p = 0.93) or wetland area (p = 0.17). However, wetland area is highly correlated with sampling duration (r = 0.53). Larger wetlands generally take more time to sample, which results in a higher number of turtles observed.

We obtained the scale of maximum effect for each land cover type through correlations between the number of turtles detected and the land cover proportions (Fig. 3). The highest correlations were at a buffer distance of 900 m for water cover (r = 0.24), 200 m for wetland cover (r = 0.27), 600 m for forest cover (r = 0.35), 100 m for anthropogenic cover (r = -0.21), and 700 m for agricultural cover (r = -0.30).

All variables considered for the second model evaluating land cover effect on turtle abundance showed moderate to high correlations between each other, the highest correlation being between forest cover and road density (r = -0.58). However, all variables included in the model had variance inflation factors (VIF) below 3. More turtles were detected in larger wetlands surrounded by more forest (p values < 0.01; Table 2). For instance, a 10% increase from the mean in forest cover in the landscape surrounding the wetland results in six more turtles being detected in the wetland, when all other variables are set at the mean (Fig. 4). Wetland proportion (p = 0.18) and road density (p = 0.46), however, were not significant predictors of local turtle abundance.

#### Discussion

**Painted turtle presence.** We found painted turtles in a surprisingly large variety of wetlands, from the most secluded ones to ponds located in crowded parks or golf courses in the centre of the city. This observation is consistent with the literature which proposes that painted turtles can live in highly human-altered wetlands and seem to be the most tolerant turtle species to anthropogenic changes (DeCatanzaro and Chow-Fraser, 2010). Tolerance to habitat alteration corroborates the understanding of painted turtles as a generalist species **Table 1.** Mixed model investigating the effects of sampling conditions on the number of painted turtles observed in wetlands around Ottawa, Ontario, Canada (N = 34 wetlands surveyed a total of 306 times). All variables except wind speed (which is a categorical variable) were standardised. Significant p values for  $\alpha = 0.05$  are in bold.

Variables	Estimate	Degrees of freedom	p value
Intercept	0.4636	1	0.496
Sampling duration	7.4351	1	0.006
Wind speed	1.2673	5	0.938
Cloud cover	9.0100	1	0.003
Mean temperature	9.1270	1	0.003
Wetland area	1.8986	1	0.168

**Table 2.** Generalised linear model investigating the effects of land cover and road density on the number of painted turtles observed in wetlands (N = 34) around Ottawa, Ontario, Canada. All variables were standardised. Significant p values for  $\alpha = 0.05$  are in bold. The buffer distance used to measure land type proportion and road density was variable for each predictor (forest: 600 m; wetland: 200 m; road density: 300 m).

Variables	Estimate	Standard error	t value	p value
Intercept	2.3627	0.2611	9.049	< 0.001
Forest cover	0.7391	0.2464	3.000	0.006
Wetland cover	0.2352	0.1707	1.378	0.179
Road density	0.2651	0.3564	0.744	0.463
Wetland area	0.5918	0.1659	3.566	0.001



**Figure 3.** Correlations between the maximum number of turtles observed and the proportion of the five landscape cover types at various buffer distances (from 50 m to 2,000 m at 50-m intervals). The highest absolute value is at 900 m for water cover, 200 m for wetland cover, 600 m for forest cover, 100 m for anthropogenic cover, and 700 m for agricultural cover.



**Figure 4.** Maximum number of painted turtles predicted to occupy a wetland based on the forest proportion (**A**; %), the wetland proportion (**B**; %), the wetland area (**C**; ha), and the road density (**D**; km/km<sup>2</sup>) when all other predictors are set to the mean. Only the forest cover and the wetland area are statistically significant predictors of the number of turtles. The points displayed represent the actual data points (N = 34). The light blue cloud represents the 95 % confidence interval. The buffer distance used to measure land type proportion and road density was variable for each predictor (forest: 600 m; wetland: 200 m; road density: 300 m).

with a wide niche breadth (Swihart et al., 2006; Stokeld et al., 2014; Buchanan et al., 2019).

Although human-modifications of a habitat are often detrimental to wildlife, in part because they fragment the area, isolate the populations, and increase mortality through roadkill (Shepard et al., 2008; Stokeld et al., 2014), developed areas could benefit turtles in two ways (DeCatanzaro and Chow-Fraser, 2010): they may provide (1) new nesting sites through the creation of canopy gaps (e.g., residential lawns, roadside banks; Baldwin et al., 2004; Marchand and Litvaitis, 2004) and (2) more abundant food sources as water bodies may have become more eutrophic and thus have an increased productivity (Knight and Gibbons, 1968; Buchanan et al., 2019). High turtle abundances observed in disturbed areas could also be due to low emigration rates, as expected in large isolated patches. Indeed, urban turtle populations have been isolated from others by wetland loss and human disturbance, which could result in reduced dispersion outside of the wetland and a high population size (Thomas et al., 2000; Rizkalla and

Swihart, 2006; DeCatanzaro and Chow-Fraser, 2010).

The four unoccupied wetlands in our study were young (formed between 2007-2017) or had dried up in the past few years, which indicates that painted turtles just may not yet have had time to colonise these new habitats. Buchanan et al. (2019) suggested that painted turtles have a great ability to disperse and colonise created wetlands, but the probability of colonisation depends on many factors such as isolation, habitat quality, wetland area, and wetland inundation levels (Cosentino et al., 2010). Unfortunately, we do not have sufficient data to estimate these probabilities.

**Painted turtle detection.** Sampling conditions had a significant effect on turtle detection. More turtles were observed during longer sessions and when it was cooler with few clouds. The increase in the number of turtles detected with increased sampling duration is trivial for two main reasons: (1) in general, as sampling effort increases, the number of individuals sampled increases; and (2) wetlands take longer to sample usually because they are larger, and, all else being equal, larger suitable

patches of habitat can sustain larger populations. Moreover, the effect of environmental conditions on turtle counts was also expected because turtles were mainly observed while they were basking. Basking is highly related to environmental conditions such as temperature and cloud cover. Indeed, the need for basking at 30 °C should be much less than at 15 °C, as the preferred body temperature of painted turtles ranges between 21.3 and 25.0 °C (Edwards and Blouin-Demers, 2007).

Turtle detection may increase in less developed areas because there is less human activity taking place around the wetland. Even though we tried to minimise our impact on turtle detection at each visit through attenuation of the noise we made when approaching wetlands and limited proximity with wetland edges, some factors were outside and beyond our control. For instance, in more developed areas some sites were visited before us by hikers, bikers, swimmers, or dog owners. Turtles may have been disturbed before we could see them. However, because developed areas are generally more visited, disturbed more frequently and over a longer period of time, turtles may have become habituated to human presence and may no longer be disturbed by their activities in those areas. Benign encounters with humans are indeed thought to result in habituation to human presence in turtles (Bateman et al., 2014). This mechanism could therefore compensate for the effects of increased disturbance in developed areas.

Landscape predictors of turtle abundance. The main goal of our study was to test the hypothesis that local abundance of painted turtles depends on landscape composition. Our hypothesis was partly supported, with some landscape cover types (e.g., forest cover) being better predictors of local turtle abundance than others (e.g., wetland cover).

We predicted that there would be fewer painted turtles in more disturbed landscapes. We found that there were more painted turtles when there was more forest surrounding the wetland. In fact, when every other parameter is set to the mean, the number of turtles predicted to be observed in a wetland increases by 90 individuals for an associated increase from 0 to 65% of forest cover in a 600-m buffer area around the wetland. This result was also found in similar studies (Patrick and Gibbs, 2010; Quesnelle et al., 2013; Buchanan et al., 2019), which confirms the importance of forest cover in the surrounding terrestrial habitat of turtles. However, it is difficult to assess directly the effect of human-altered landscapes since agricultural and anthropogenic covers

were excluded from our model because their univariate effects were weak. Urbanisation and agriculture have certainly led to important forest losses over time and still do. Forest cover was indeed highly negatively correlated with anthropogenic and agricultural cover. Bearing in mind that forest did have a positive significant effect on turtle populations, we can assume that, in turn, urbanisation and agriculture may have negative effects. Conversion of forested land into agricultural land may cause fragmentation, degradation, and affect wetland hydrology (Findlay and Houlahan, 1997). Therefore, this suggests that lower turtle abundances should be observed in more urbanised or agricultural areas.

In the literature, the effects of human-modified habitats on abundance are mixed. Human-modified areas can have negative effects on amphibians (Griffin et al., 2017) and turtles (Karunarathna et al., 2017; Stratmann et al., 2020) or can have no effects (Bowen and Janzen, 2008; Eskew et al., 2010; Stokeld et al., 2014). It is possible that the potential gain in nesting sites and food availability associated with disturbed areas (DeCatanzaro and Chow-Fraser, 2010) compensates for the loss of refuges and connectivity (Meffe and Carroll, 1997; Roe and Georges, 2007). Unfortunately, the results of our study do not allow us to shed light on this uncertainty in the scientific literature, in part because the effect is most certainly species-specific and context-specific.

**Roads.** We predicted that there would be fewer turtles in wetlands surrounded by high road densities because such infrastructures fragment the area (Shepard et al., 2008) and can cause high adult mortality (Crawford et al., 2014). We found no effect of road density on painted turtle abundance. This result is unexpected given that forest cover positively affected turtle abundance and that there is a high negative correlation between road density and forest cover. The correlation between those variables was in fact the highest between all variables in our model (r = -0.58) and, thus, the effect of road density could have been masked by its high correlation with forest cover. Masking seems improbable, however, because all variables had variance inflation factors (VIF) bellow 3 (Zuur et al., 2010).

The absence of correlation between road density and painted turtle abundance could be explained by at least two factors. (1) Wildlife often exhibits a lagged response to habitat modification (Reese and Welsh, 1998). It could take several decades before we observe the effects of roads on reptiles (Findlay and Bourdages, 2000), especially on long-lived species such as turtles. If indeed roads have an effect on turtle populations, our results suggest that it simply cannot be detected yet. Over the past 50 years, the Ottawa road landscape has dramatically changed, with more and bigger roads being built. Since turtles have long generation times (Vanek and Glowacki, 2019), it is possible that those changes are too recent for their effects to be observed. (2) Our study may not have enough power to detect the effect of roads on turtle populations because of our modest sample size and the small variation in road density among sites. We combined all road types into one variable and tested its effect at only one buffer size (at which the correlation was maximised; 300 m). We had to reduce the number of variables tested because our sample size was too modest to build more complex models. However, some studies have found that road mortality varies with road types and traffic volumes (Findlay and Houlahan, 1997; Gibbs and Shriver, 2002; Szerlag and McRobert, 2006; Winchell and Gibbs, 2016), with high road density and low traffic volumes causing low mortality. In residential areas, where most of the urban sites in our study were located, low traffic volumes combined with low speed limits could explain a low mortality rate and the absence of correlation between road density and turtle abundance (Eskew et al., 2010; Winchell and Gibbs, 2016). Yet, not all studies have used different road categories in their analyses, but they still found significant effects of road density on turtle populations (e.g., DeCatanzaro and Chow-Fraser, 2010). In any case, the amalgamation of road types and traffic volumes into one broad variable could explain, at least partially, the absence of significant correlation in our data.

In the literature, the evidence is mixed, with studies that have found effects of roads on reptiles (Findlay and Houlahan, 1997; DeCatanzaro and Chow-Fraser, 2010) and others that have not (Quesnelle et al., 2013; Dorland et al., 2014). Once again, the conflicting results found in the literature may be symptomatic of context specificity.

**Conclusion.** Our study emphasises that biodiversity critically depends on terrestrial habitat surrounding wetlands (Semlitsch and Bodie, 2003). Protecting larger areas around wetlands, especially forested ones, could be crucial to turtle population persistence.

Potentially synergistic effects of urbanisation are worrisome. For example, the effect of forest loss could be aggravated by roadkill (Patrick and Gibbs, 2010). This may seem improbable in our case because we found no negative effects of roads on painted turtle populations. However, the absence of immediate response in population abundance to habitat modification at the landscape level can be misleading. Indeed, there is a potential delay in turtles' response to changes in the habitat (Reese and Welsh, 1998; Marchand and Litvaitis, 2004). We should also bear in mind that a high abundance does not imply that the population is stable (Winchell and Gibbs, 2016). Only a long-term monitoring study could assess the trajectories of the populations.

The conservation-minded management of urban greenspaces could provide suitable habitat for turtles (Colding et al., 2006) and could even complement nature reserves (Winchell and Gibbs, 2016). Anecdotally, we noticed that wetlands located in golf courses and parks sustained relatively large painted turtle populations compared to sites in more industrialised areas, surrounded by small amounts of vegetation. This reiterates the need for protection and proper management of wetlands in urban areas through effective incentive programs for private landowners.

Acknowledgements. We thank the landowners and golf course managers who gave us access to their lands. We acknowledge the support of the Natural Sciences and Engineering Research Council of Canada for funding C.Č.-H. and G.B.-D.

## References

- Baldwin, E.A., Marchand, M.N., Litvaitis, J. (2004): Terrestrial habitat use by nesting painted turtles in landscapes with different levels of fragmentation. Northeastern Naturalist 11: 41–48.
- Bateman, P.W., Fleming, P.A., Jones, B.C., Rothermel, B.B. (2014): Defensive responses of gopher tortoises (*Gopherus polyphemus*) are influenced by risk assessment and level of habituation to humans. Behaviour **151**: 1267–1280.
- Baxter-Gilbert, J.H., Riley, J.L., Lesbarrères, D., Litzgus, J.D. (2015): Mitigating reptile road mortality: Fence failures compromise ecopassage effectiveness. PLoS ONE 10: 1–15.
- Böhm, M., Collen, B., Baillie, J.E.M., Bowles, P., Chanson, J., Cox, N., et al. (2013): The conservation status of the world's reptiles. Biological Conservation 157: 372–385.
- Bowen, K.D., Janzen, F.J. (2008): Human recreation and the nesting ecology of a freshwater turtle (*Chrysemys picta*). Chelonian Conservation and Biology 7: 95–100.
- Buchanan, S.W., Buffum, B., Puggioni, G., Karraker, N.E. (2019): Occupancy of freshwater turtles across a gradient of altered landscapes. Journal of Wildlife Management 83: 435–445.
- Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M., Palmer, T.M. (2015): Accelerated modern human-induced species losses: Entering the sixth mass extinction. Science Advances 1: 9–13.
- Christens, E., Bider, J.R. (1987): Nesting activity and hatching success of the painted turtle (*Chrysemys picta marginata*) in Southwestern Quebec. Herpetologica 43: 55–65.
- Colding, J., Lundberg, J., Folke, C. (2006): Incorporating greenarea user groups in urban ecosystem management. AMBIO: A Journal of the Human Environment 35: 237–244.

- Committee on the Status of Endangered Wildlife in Canada (COSEWIC). (2018): COSEWIC assessment and status report on the Midland Painted Turtle *Chrysemys picta marginata* and the Eastern Painted Turtle *Chrysemys picta picta* in Canada. Ottawa, Canada.
- Cosentino, B.J., Schooley, R.L., Phillips, C.A. (2010): Wetland hydrology, area, and isolation influence occupancy and spatial turnover of the painted turtle, *Chrysemys picta*. Landscape Ecology 25: 1589–1600.
- Crawford, B.A., Maerz, J.C., Nibbelink, N.P., Buhlmann, K.A., Norton, T.M. (2014): Estimating the consequences of multiple threats and management strategies for semi-aquatic turtles. Journal of Applied Ecology 51: 359–366.
- DeCatanzaro, R., Chow-Fraser, P. (2010): Relationship of road density and marsh condition to turtle assemblage characteristics in the Laurentian Great Lakes. Journal of Great Lakes Research 36: 357–365.
- van Dijk, P.P. (2011): *Chrysemys picta* (errata version published in 2016). The IUCN Red List of Threatened Species 2011.
- Dorland, A., Rytwinski, T., Fahrig, L. (2014): Do roads reduce painted turtle (*Chrysemys picta*) populations? PLoS ONE 9: e98414.
- Edwards, A.L., Blouin-Demers, G. (2007): Thermoregulation as a function of thermal quality in a northern population of painted turtles, *Chrysemys picta*. Canadian Journal of Zoology 85: 526–535.
- Elston, D.A., Moss, R., Boulinier, T., Arrowsmith, C., Lambin, X. (2001): Analysis of aggregation, a worked example: Numbers of ticks on red grouse chicks. Parasitology **122**: 563–569.
- Ernst, C.H., Lovich, J.E. (2009): Turtles of the United States and Canada. Second Edition. Baltimore, Maryland, USA, John Hopkins University Press.
- Eskew, E.A., Price, S.J., Dorcas, M.E. (2010): Survivorship and population densities of painted turtles (*Chrysemys picta*) in recently modified suburban landscapes. Chelonian Conservation and Biology 9: 244–249.
- ESRI (2018): ArcGIS, version 10.6. Redlands, California, USA, Environmental Systems Research Institute.
- Findlay, C.S., Houlahan, J. (1997): Anthropogenic correlates of species richness in Southeastern Ontario wetlands. Conservation Biology 11: 1000–1009.
- Findlay, C.S., Bourdages, J. (2000): Response time of wetland biodiversity to road construction on adjacent lands. Conservation Biology 14: 86–94.
- Gibbons, J.W., Scott, D.E., Ryan, T.J., Buhlmann, K.A., Tuberville, T.D., Metts, B.S., et al. (2000): The global decline of reptiles, déjà vu amphibians. BioScience 50: 653–666.
- Gibbs, J.P., Shriver, W.G. (2002): Estimating the effects of road mortality on turtle populations. Conservation Biology 16: 1647– 1652.
- Griffin, L.P., Brownscombe, J.W., Gagné, T.O., Wilson, A.D.M., Cooke, S. J., Danylchuk, A.J. (2017): Individual-level behavioral responses of immature green turtles to snorkeler disturbance. Oecologia 183: 909–917.
- Heppell, S.S. (1998): Application of life-history theory and population model analysis to turtle conservation. Copeia 1998: 367–375.
- Howell, H.J., Seigel, R.A. (2019): The effects of road mortality on

small, isolated turtle populations. Journal of Herpetology 53: 39-46.

- Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES). (2019): Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. Díaz, S., Settele, J., Brondízio, E.S., Ngo, H.T., Guèze, M., Agard, J., Arneth, A., Balvanera, P., et al. Eds. IPBES secretariat, Bonn, Germany.
- Karunarathna, S., Amarasinghe, A.A.T., Henkanaththegedara, S., Surasinghe, T., Madawala, M., Gabadage, D., Botejue, M. (2017): Distribution, habitat associations and conservation implications of Sri Lankan freshwater terrapins outside the protected area network. Aquatic Conservation: Marine and Freshwater Ecosystems 27: 1301–1312.
- Kennedy, C.M., Oakleaf, J.R., Theobald, D.M., Baruch-Mordo, S., Kiesecker, J. (2019): Managing the middle: A shift in conservation priorities based on the global human modification gradient. Global Change Biology 25: 811–826.
- Knight, A.W., Gibbons, J.W. (1968): Food of the painted turtle, *Chrysemys picta*, in a polluted river. The American Midland Naturalist 80: 558–562.
- Koh, L.P., Dunn, R.R., Sodhi, N.S., Colwell, R.K., Proctor, H.C., Smith, V.S. (2004): Species coextinctions and the biodiversity crisis. Science **305**: 1632–1634.
- Kuznetsova, A., Brockhoff, P., Christensen, R. (2017): ImerTest package: Tests in linear mixed effects models. Journal of Statistical Software 82: 1–26.
- Lewis, S.L., Maslin, M.A. (2015): Defining the Anthropocene. Nature **519**: 171–180.
- Litzgus, J.D. (2006): Sex differences in longevity in the spotted turtle (*Clemmys guttata*). Copeia 2006: 281–288.
- Marchand, M.N., Litvaitis, J.A. (2004): Effects of habitat features and landscape composition on the population structure of a common aquatic turtle in a region undergoing rapid development. Conservation Biology 18: 758–767.
- Meffe, G.K., Carroll, C.R. (1997): Principles of conservation biology. Second edition. Sunderland, Massachusetts, USA, Sinauer Associates, Inc.
- Oehler, J.D., Litvaitis, J.A. (1996): The role of spatial scale in understanding responses of medium-sized carnivores to forest fragmentation. Canadian Journal of Zoology 74: 2070–2079.
- Ontario Biodiversity Council (OBC). (2010): State of Ontario's biodiversity 2010: A report of the Ontario Biodiversity Council. Peterborough, Ontario, Canada.
- Ontario Biodiversity Council (OBC). (2015): State of Ontario's biodiversity 2015: A report of the Ontario Biodiversity Council. Peterborough, Ontario, Canada.
- Ontario Ministry of Natural Resources and Forestry (OMNRF). (2017): A wetland conservation strategy for Ontario 2017–2030. Queen's Printer for Ontario, Toronto, Ontario, Canada.
- Patrick, D.A., Gibbs, J.P. (2010): Population structure and movements of freshwater turtles across a road-density gradient. Landscape Ecology 25: 791–801.
- Quesnelle, P.E., Fahrig, L., Lindsay, K.E. (2013): Effects of habitat loss, habitat configuration and matrix composition on declining wetland species. Biological Conservation 160: 200–208.

- R Core Team. (2019): R: A language and environment for statistical computing. Vienna, Austria.
- Ramsar Convention on Wetlands. (2018): Global wetland outlook: State of the world's wetlands and their services to people. Gland, Switzerland, Ramsar Convention Secretariat.
- Reese, D.A., Welsh, H.H. (1998): Comparative demography of *Clemmys marmorata* populations in the Trinity River of California in the context of dam-induced alterations. Journal of Herpetology **32**: 505–515.
- Rizkalla, C.E., Swihart, R.K. (2006): Community structure and differential responses of aquatic turtles to agriculturally induced habitat fragmentation. Landscape Ecology 21: 1361–1375.
- Roe, J.H., Georges, A. (2007): Heterogeneous wetland complexes, buffer zones, and travel corridors: Landscape management for freshwater reptiles. Biological Conservation 135: 67–76.
- Semlitsch, R.D., Bodie, J.R. (2003): Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. Conservation Biology 17: 1219–1228.
- Shepard, D.B., Kuhns, A.R., Dreslik, M.J., Phillips, C.A. (2008): Roads as barriers to animal movement in fragmented landscapes. Animal Conservation 11: 288–296.
- Steen, D.A., Gibbs, J.P. (2004): Effects of roads on the structure of freshwater turtle populations. Conservation Biology 18: 1143–1148.
- Stokeld, D., Hamer, A.J., Van Der Ree, R., Pettigrove, V., Gillespie, G. (2014): Factors influencing occurrence of a freshwater turtle in an urban landscape: A resilient species? Wildlife Research 41: 163–171.

- Stratmann, T.S.M., Floyd, T.M., Barrett, K. (2020): Habitat and history influence abundance of bog turtles. Journal of Wildlife Management 84: 331–343.
- Swihart, R.K., Lusk, J.J., Duchamp, J.E., Rizkalla, C.E., Moore, J.E. (2006): The roles of landscape context, niche breadth, and range boundaries in predicting species responses to habitat alteration. Diversity and Distributions 12: 277–287.
- Szerlag, S., McRobert, S.P. (2006): Road occurrence and mortality of the northern diamondback terrapin. Applied Herpetology 3: 27–37.
- Thomas, C.D., Baguette, M., Lewis, O.T. (2000): Butterfly movement and conservation in patchy land. In: Behaviour and Conservation, p. 85–104. Gosling, L.M., Sutherland, W.J., Ed., Cambridge, UK, Cambridge University Press.
- Thomas, J.A., Telfer, M.G., Roy, D.B., Preston, C.D., Greenwood, J.J.D., Asher, J., et al. (2004): Comparative losses of British butterflies, birds, and plants and the global extinction crisis. Science **303**: 1879–1881.
- Vanek, J.P., Glowacki, G.A. (2019): Assessing the impacts of urbanization on sex ratios of painted turtles (*Chrysemys picta*). Diversity 11: 1–13.
- Winchell, K.M., Gibbs, J.P. (2016): Golf courses as habitat for aquatic turtles in urbanized landscapes. Landscape and Urban Planning 147: 59–70.
- Zuur, A.F., Ieno, E.N., Elphick, C.S. (2010): A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution 1: 3–14.