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Demographic evidence that development is not compatible with sustainability in semi-urban freshwater turtles

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Abstract

Balancing urban development with environmental sustainability is a major challenge that is increasingly recognized in planning decisions. Urban development proposals are often approved with the expectation that deleterious impacts on native species will be constrained, but this assumption is rarely tested over sufficient timelines to confirm its validity for long-lived, at-risk species. We tracked changes in Blanding's turtle (*Emydoidea blandingii*) habitat availability and demography over 10 years near Ottawa, ON, Canada, to determine whether urban development and associated mitigation measures were sufficient to ensure long-term population persistence. Suitable turtle habitat declined by 10% during the study, and wetland corridors were essentially lost. Habitat loss coincided with a marked reduction in adult turtle apparent survival, resulting in a 70% decline in population size. Adult females experienced the greatest decline, and despite wildlife fencing and culvert placement as conditions of project approval, turtle road mortality likely was the primary cause of the decline. Deterministic population viability analysis revealed that ~4 adult female road mortalities (of an initial 56 females) per year produced a comparable decline to that observed in our population estimates; at this rate, the population will likely breach its quasi-extinction threshold (4 females) in under a decade. Accordingly, we infer that in our study area, approved urban development was not compatible with at-risk turtle population viability. Our findings imply that urban development approval conditions, even when conducted in the context of seemingly robust species-at-risk protection, can be inadequate to ensure sustainability. We contend that if environmental sustainability is to be prioritized, urban development projects in areas occupied by at-risk species must be subject to more stringent oversight during the planning, approval and implementation phases.

Introduction

Land-use change is the main driver of biodiversity loss worldwide (Sala *et al.*, 2000), with urban development being an important source of decline for many native species occurring in proximity to humans (Czech, Krausman, & Devers, 2000; Aronson *et al.*, 2017). Urban development can have direct impacts on species' mortality and productivity, as well as indirect effects arising through changes in resource availability, altered system dynamics and restricted gene flow (e.g. Shochat *et al.*, 2006; Fusco, Pehek, & Munshi-South, 2021). Collectively, these impacts may lead to marked shifts in species distribution and abundance, as well as changes in populations, communities and ecosystem structure and functions. However, factors determining the speed and severity of these impacts are not well studied. For example, a primary, proximate outcome of urbanization on wildlife species can be higher mortality from increased rates of vehicle collisions, but if impacts on population size and distribution are variable across demographic groups, population-level outcomes can range in severity (e.g. Gibbs & Steen, 2005; Dorcas, Willson, & Gibbons, 2007). Some impacts of urban development on biodiversity are detectable during the initial disturbance phase, whereas others may only be discernible after a prolonged period of activity (e.g. Carlson, 2000; Harju *et al.*, 2010). It follows that predicting how species and systems will respond to disturbance is particularly challenging, especially among cryptic or long-lived species with complex life histories. Therefore, properly quantifying the effects of urban development on environmental sustainability remains an important challenge that is not being fully addressed (Bull *et al.*, 2016; Theis *et al.*, 2020).

To reduce environmental impacts of urban development, projects may receive approval on the condition that mitigation measures are enacted. Mitigation can take a variety of forms, including efforts to reduce impacts on sensitive species and habitats during urban development and after the work is completed. Although it is widely recognized that effective planning may require adoption of mitigation measures, often these measures lack rigorous testing and are implemented without quality assurance (van der Grift *et al.*, 2013). This limitation is especially relevant when responses to mitigation may be subtle and only discernible after prolonged monitoring that extends beyond the scope of most impact assessments. Indeed, assessing long-term effects of urban development and the efficacy of mitigation measures is usually beyond the scope of activities or timelines mandated by the development approval process (Vasconcelos & Calhoun, 2006; Pickett *et al.*, 2013).

Freshwater turtles living in semi-urban areas may be particularly vulnerable to development-related disturbance. Owing to their long generation times, delayed age to maturity and naturally low nest survival, freshwater turtles are vulnerable to new disturbances but may only exhibit clear demographic responses after a prolonged period of exposure (Congdon, Dunham, & Van Loben Sels, 1993). Most turtle populations require high adult female survival to compensate for naturally low recruitment rates; however, this can be problematic in an urbanized environment where road mortality associated with inter-wetland movement or use of roadsides for nesting is common (Steen *et al.*, 2006; Enneson & Litzgus, 2008). Furthermore, even with higher mortality among adult females, it is not inconceivable that compensatory effects through higher immigration or recruitment could mask direct impacts of urban development. Longer-term studies are needed to track demographic responses to urban development and assess whether approved protocols are sufficient to ensure population viability. To date, such studies have not spanned sufficiently long time periods or adequately modelled different disturbance scenarios for robust assessment of either impact of urban development or mechanisms underlying observed demographic responses (Beaudry, Demaynadier, & Hunter, 2010; Howell & Seigel, 2019; Ross, Thompson, & Dreslik, 2020).

Here, we investigate the effects of recent urbanization on the structure and viability of a population of Blanding's turtles (*Emydoidea blandingii*) in Ottawa, Ontario, Canada. Blanding's turtles can be strongly affected by land-use changes (Mui *et al.*, 2017; Rhodin *et al.*, 2018), especially by the compounding effects of habitat loss and road mortality (Beaudry, Demaynadier, & Hunter, 2010; Howell & Seigel, 2019). We use 10 years of field data to reconstruct changes in population size and structure that we combine with population viability and habitat analysis to assess possible mechanisms for the observed changes. We focus on how residential and road development has altered turtle habitat availability and connectivity in the area, affecting their population size and trajectory. We expected: (1) loss of habitat deemed suitable for turtles and (2) reduced habitat connectivity between turtle sub-populations, leading to (3) a decline in the estimated turtle population size. All freshwater turtles are vulnerable to vehicle collisions, but road mortalities seem disproportionately skewed towards females because of their propensity to travel over land (Aresco, 2004, 2005). Thus, we also expected (4) a more pronounced numerical decline in females, leading to (5) unsustainable rates of road mortality, despite mitigation measures (fencing, culverts) established specifically to protect turtles. More broadly, our investigation is a case study of the robust assessment of impacts of urbanization on a sensitive, long-lived species.

Materials and methods

Study area and population

We studied Blanding's turtles in the South March Highlands in Ottawa, Ontario, Canada (45°20′N, 75°56′W). The study site (~1000 ha) includes the protected South March Highlands conservation forest (SMH) in the north and a provincially significant wetland (Kizell Cell Wetland) in the south and is bounded by roads and residential areas (Figure S1). The study site has been impacted by substantial urban development during the past 40 years, including extending Terry Fox Drive, a major arterial route that now bisects the area, and development of two residential zones in the centre of the area (Figure S1). Following development beginning in 2008, several mitigation measures were established with the intent to protect at-risk turtles, including: ~2 km of wildlife fencing along Terry Fox Drive (2008), construction of 10 road culverts to allow turtle passage from SMH to Kizell Cell Wetland (2008) and construction of one artificial turtle nesting area (0.3 ha) and two artificial ponds (2017; total area = 0.5 ha) (Dillon Consulting Limited 2013; DST Consulting Engineers 2015). The turtle population was previously monitored by the City of Ottawa (2010–2013, Hasler *et al.*, 2015; Dillon Consulting Limited 2013) and we compare contemporary (2017–2020) site features and turtle demography to those observed by Hasler *et al.* (2015), allowing our study to span 10 years.

Turtle captures

During both study periods, turtles were captured between May and September using baited hoop nets or by hand, assigned age classes (hatchling, juvenile and adult) based on body size and mass (Congdon & van Loben Sels, 1991; Hasler *et al.*, 2015), sexed based on secondary sexual characters (Congdon & van Loben Sels, 1991; Hamernick, 2000) and individually marked with carapace notches (Cagle, 1939). Because the 2010–2013 study included a site to the north of the study area that was not sampled in 2017–2020 (*c.* 110 ha), we excluded data (n = 9 turtles) from that site. Our 2017–2020 capture effort (i.e. number of traps and person-hours trapping) was ~50% of the earlier study; this disparity in effort was integrated into population models. All animals were handled in accordance with Canadian Council on

Animal Care (CCAC) (2005) guidelines and procedures were approved by Trent University Animal Care Committee (Protocol No. 24729) and the Ministry of Natural Resources and Forestry (MNRF, Permit No. KV-C-002-14).

Tracking and survival

Between 2011 and 2013, 92 Blanding's turtles were captured, of which 21 were equipped with VHF radio-transmitters and tracked for survival and location on average every 4 days (Hasler *et al*., 2015; Dillon Consulting Limited 2013). During 2017–2020, we captured 36 Blanding's turtles and equipped 31 adults with GPS (AxyTrek, Technosmart, Rome, Italy; GPS accuracy ±17.4 m, A. Auge, unpubl.) and VHF transmitters (SI-2, Holohil, Carp, Canada) (both <10% of turtle body mass). We retrieved GPS data from 28 turtles. We lost the VHF signal of three turtles due to unknown causes, and an additional two turtles were fitted with VHF transmitters only. GPS devices recorded locations hourly, which we then rarefied to one location per 4 days for comparison with less extensively sampled VHF locations from 2010 to 2013 (see Mills, Patterson, & Murray, 2006). We tracked turtles using VHF telemetry weekly and determined their survival (and cause of death when mortalities were detected) either visually (2017–2019) or using a motion-based mortality sensor (2020). Additionally, we searched for dead turtles by driving and walking along the primary roads daily, and other roads surrounding the study area 3–4× per week. We considered the recovery rate of tagged road-killed turtles as a crude carcass detection rate because turtle carcass recovery from road surveys likely underestimates the true number of road mortalities as injured animals may move off the road before they die or road-killed turtles may be removed by scavengers or residents (DeGregorio, Moody, & Myers, 2020).

Change in habitat and connectivity

We developed habitat maps of the study area to quantify 2010–2020 change in aquatic (open water, swamp and marsh) and terrestrial (forest, grassland) habitat and settlement area (see Table S1). We assessed habitat loss at two spatial scales: (1) within the entire study area and (2) within the combined home ranges of turtles that were observed in the central part of the study area (2010–2013, including developed areas). We applied a least-cost path model to estimate change in connectivity between Category 1 habitat (defined as turtle nest and overwintering sites including 30 m buffer), using the habitat map as a resistance layer (lower resistance values in aquatic habitats; see Table S2) (Mui *et al*., 2017). Corridor modelling and mapping were performed in ArcGIS Pro 2.4.0 (Esri Inc., Redlands, CA, USA, 2019) (see Appendix S1).

Statistical analyses

We compared male-to-female sex ratios and juvenile to adult ratios in the captured turtles between 2010–2013 and 2017–2020 using a χ^2 goodness-of-fit test. We calculated turtle home ranges as 95% minimum convex polygons (MCP) (Row & Blouin-Demers, 2006) and compared their size between study periods using Welch's two-sample t test (Moser & Stevens, 1992). Based on 2017–2020 data, we used realized GPS fix rate to estimate proportion of time that turtles were on land (obtained GPS locations/scheduled GPS locations), assuming that most missed fixes occurred when animals were submerged in water. We used ArcGIS to calculate distance of each turtle's GPS location to the nearest road. We compared proportion of time on land and mean distance to roads during 2017–2020 nesting seasons (June to mid-July; A. Auge, unpubl.) across sexes using Student's t tests (Kim, 2015). We collected survival data for tracked animals during both study periods, and for the 2017–2020 period, we calculated 30-day survival probability during the turtle active season (May–September) using Kaplan–Meier estimates (Murray & Bastille-Rousseau, 2020). Low sample sizes precluded calculating continuous time survival rates during 2010–2013. Female and male survival rates were compared using a Cox proportional hazard (CPH) model; we confirmed the model fit of the proportional hazards assumption using Schoenfeld residuals (Murray & Bastille-Rousseau, 2020). Survival analysis was performed using the *survival* package (Therneau 2021) in R version 4.0.2 (R Development Core Team, Vienna, Austria, 2020).

Population size estimation

We estimated adult and juvenile turtle population size for each monitoring year (2010–2020) with Jolly–Seber (JS) models (POPAN formulation) (Schwarz & Arnason, 1996), using turtle capture histories from all eight sampling years. Jolly–Seber models assume an open population, where deaths, emigration and immigration can occur (Schwarz & Arnason, 1996; Pledger, Pollock, & Norris, 2010). We assumed that weak connectivity with both the closest Blanding's turtle population outside our study area (Carp River System, *c*. 3 km from our study area, see Dillon Consulting Limited 2013) and the northern portion of the study area that was not sampled during the 2017–2020 period meant that migration was possible but unlikely. Our assumption was supported by the low estimated probability of entry into the population (P_{ent}, see Results, but also Schwarz & Arnason, 1996). Note that JS models are designed for open population estimation, but can serve to estimate apparent survival (Φ) in populations with negligible probability of immigration (e.g. Cross *et al*., 2021; Kiss, Hamer, & Vörös, 2021). Thus, JS models provided an alternate calculation of turtle survival probability, with JS estimates being the product of true (year-round) survival and site fidelity, and explicitly considering imperfect detection (Lebreton *et al*., 1992). We constructed multiple JS models ranging from those with all parameters being constant to others varying by sex, time and sampling period, and chose the best-fit model using Akaike information criterion (AIC) (Burnham & Anderson, 2002). Differences in sampling effort across study periods were factored into the JS models as a covariate. We estimated

Table 1 Demographic estimates used in a population viability analysis of Blanding's turtles (*Emydoidea blandingii*) in Ottawa, ON, Canada

Parameter	Value	Source
Breeding structure	Polygamous	Ernst & Lovich, 2009
Female reproductive age	14	Congdon et al., 1983; Congdon, Dunham, & Van Loben Sels, 1993; Congdon & van Loben Sels, 1991
% Females at birth	50	Beaudry, deMaynadier, & Hunter, 2008; Midwood *et al*., 2015
Number of eggs per clutch	11.7	Beaudry, Demaynadier, & Hunter, 2010
Female hatchling survival rate	0.2610	Congdon, Dunham, & Van Loben Sels, 1993
Female juvenile survival rate	0.7826	Congdon, Dunham, & Van Loben Sels, 1993
Female adult survival rate	0.9600	Congdon, Dunham, & Van Loben Sels, 1993
Quasi-extinction level	4 females	Enneson & Litzgus, 2008
Initial adult population size	55.6 females	This study
Initial juvenile population size	17.1 females	This study
Initial adult sub-population size (SMH)	21.9 females	This study
Initial juvenile sub-population size (SMH)	5.3 females	This study
Initial adult sub-population size (Kizell)	7.1 females	This study
Initial juvenile sub-population size (Kizell)	1.0	This study
% Adult females breeding	60	This study

Values were taken from the literature when they could not be determined from our study.

population sizes first for the entire population and then separately for the northern conservation forest and southern wetland. Population size modelling was conducted using the R packages *marked* (Laake, Johnson, & Conn, 2013) and *RMark* (Laake, 2013).

Population viability analysis (PVA)

The impact of urban development on Blanding's turtle population viability was evaluated using demographic projection models (Morris & Doak, 2002; Legendre, 2020). Based on the 2010 adult female and juvenile turtle population size estimate from our JS models, we populated a three-stage Leftkovich matrix representing turtle life stages (hatchlings [age 0–1], juveniles [age 1–14] and adults [age 14+]). Our base model was parameterized mostly using estimates from studies on Blanding's turtle populations subjected to few anthropogenic effects, to establish potential demographic conditions prior to the 2010 pulse in urban development. In particular, annual baseline survival rates were derived from a long-term Blanding's turtle study in Michigan with low human access (Congdon, Dunham, & Van Loben Sels, 1993; Congdon, Kinney, & Nagle, 2011), productivity rates came from a study in Maine (Beaudry, Demaynadier, & Hunter, 2010) and initial population sizes and proportion of breeding females were estimated from our data (see Table 1). Because sex of juvenile Blanding's turtles was not determined, for simplicity we assumed the juvenile and adult sex ratios were similar to those at the start of the study (see below). Based on the number of eggs per clutch, proportion of reproductive females per year and adult survival rate, we calculated fecundity to be 3.37 female eggs per female per year.

Population projections included only females, as they tend to be most important in the demography of long-lived and polygamous species (Doak, Kareiva, & Klepetka, 1994; Caswell, 2001). In addition, we focused on the effects of adult female survival on population projections because of the apparent high loss of adult females during this study (see below) and adult female survival being the key demographic parameter influencing population growth rate in our population, as opposed to other population parameters such as migration (see below). Turtle PVA was conducted using the R package *popbio* (Stubben, & Milligan, 2007), with populations projected deterministically over 50 years. We used probability of the population breaching a quasi-extinction threshold of four adult female turtles as our measure of population viability (Enneson & Litzgus, 2008; Howell & Seigel, 2019), and explored the impact of anthropogenic disturbance as different road impact scenarios by changing age-specific annual mortality rates and assessing their correspondence with observed changes in adult female turtle population size during our study. Apart from our baseline model (which assumes no additional mortality), we modelled: (1) one adult female mortality per year for the first 10 years, based on the approximate number of observed adult female roadkills observed during the duration of the monitoring study (see below); (2) two adult female mortalities per year for the first 10 years, assuming 50% road mortality detection rate during road surveys; and (3) increased adult female mortality to 3 and 4 per year, in an effort to reproduce the 2010–2020 population size changes estimated from the JS model. Additionally, (4) we modelled a constant reduction in adult female survival rate by 1.8% per year, which conservatively, represents the mean observed number of roadkills as a proportion of the 2010 female population size; and (5) a decrease in adult female survival rate by 3.6% per year, representing two road mortalities proportional to the 2010 population size. (6) We explored how female survival probability via female-biased road mortality could produce the observed decline in females by incrementally reducing adult female survival (compared to the baseline annual survival of 0.96) until projected population sizes were comparable to those observed during our study. To explore the maximum level of adult female mortality that would be sustainable above the quasi-extinction threshold by 2030 and 2060 (20 and 50 years after the beginning of the study, respectively), (7) we reduced annual female survival rates incrementally until the population size was ≤ 4 adult females. Lastly, to explore the potential consequences of habitat fragmentation on population dynamics, (8) we conducted projections on two distinct sub-populations (northern SMH conservation forest and southern Kizell wetland) starting with estimated sub-population sizes from 2013 (the period prior to the recent development pulse). We projected sub-population dynamics with one and two female mortalities per year only in the northern sub-population and assessed adult female survival rate necessary to reproduce observed decline in sub-population sizes. Note that population projections were deterministic and focused exclusively on female survival because our goal was to quantify impacts of different road mortality rates on population viability, rather than forecast demographic responses according to stochastic variation. Finally, we conducted elasticity analyses to assess the importance of each demographic parameter to population growth rate (Morris & Doak, 2002; Legendre, 2020).

Results

During 2010–2013, 92 Blanding's turtles were captured and marked in the study area, of which 19.6% were juveniles.

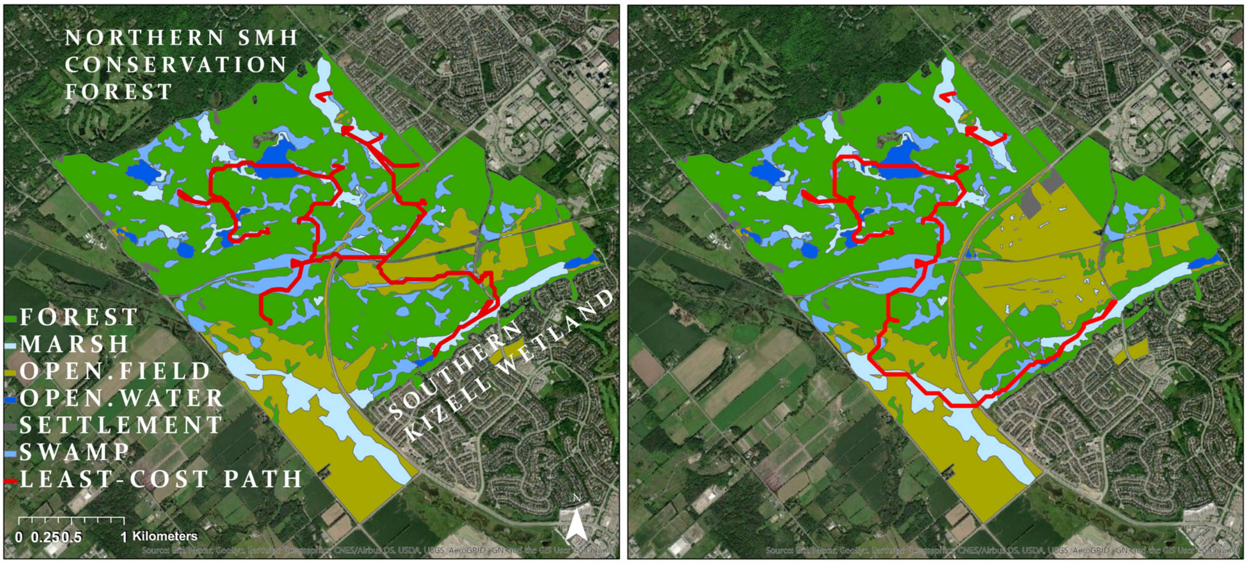

Figure 1 Blanding's turtle (*Emydoidea blandingii*) habitat in the study area in Ottawa, ON, Canada. Changes in available habitat and least-cost paths (red) connecting Category 1 habitat in the northern conservation forest and southern wetlands in the study area before (left, 2010–2013) and after (right, 2017–2020) initiation of two major development projects. The northern conservation area and southern sub-populations are, respectively, to the north and south of the main road bisecting the site.

Among adults, 68.9% of the population was female. In contrast, during 2017–2020, we caught 36 turtles, of which 1.3% were juveniles and 48.6% were adult females. Thus, based on this capture history, the turtle population experienced both lower recruitment ($\chi^2_1 = 6.46$, $P = 0.011$) and an increased skew towards males ($\chi^2_1 = 6.75$, $P = 0.009$) since the beginning of this study (2010).

Habitat changes and connectivity

Compared to 2010, by 2020, urban development in the study area had caused a 10.0% loss in forest area, 16.8% loss in swamps and no change in marsh area (Fig. 1). Availability of Category 1 habitat decreased by 10.1% during the 10-year period. The study area gained 1.2% open water area due to the creation of two artificial ponds in 2017 as part of required mitigation. As a result of land clearing, open area covered by grassland increased by 40.5% and developed area increased by 131.4%, compared to 2010. Urban development occurred almost exclusively within the area occupied by turtles tracked during the 2010–2013 study. Specifically, there was an 18.9% loss in forest and 34.2% loss of swamps in areas initially occupied by turtles; ultimately, development resulted in a 93.6% increase in grassland.

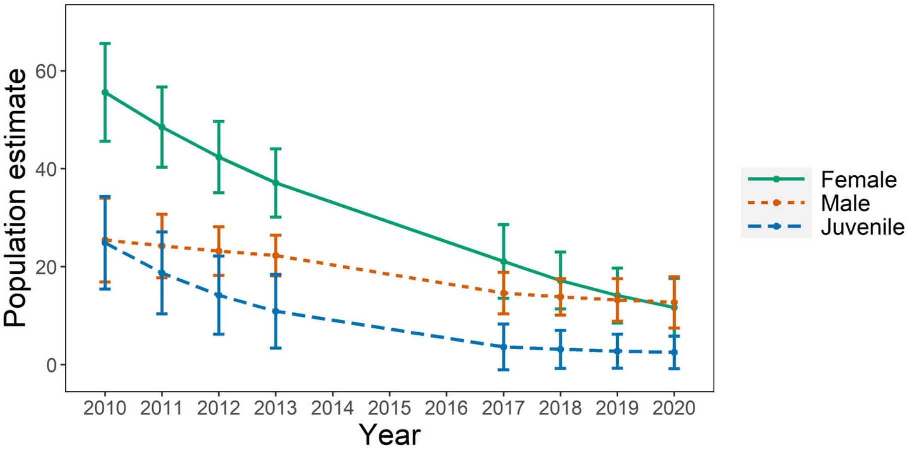

Figure 2 Estimated Blanding's turtle (*Emydoidea blandingii*) population size (with 95% CI) in Ottawa, ON, Canada, including both the northern conservation area and southern sub-populations. Estimates were calculated from a Jolly–Seber population model (POPAN formulation).

Table 2 Estimated population parameters for the adult Blanding's turtle (*Emydoidea blandingii*) population in Ottawa, ON, Canada, including both the northern conservation area and southern sub-populations

	Entire population			SMH			Kizell		
	Estimate	Lower 95% CI	Upper 95% CI	Estimate	Lower 95% CI	Upper 95% CI	Estimate	Lower 95% CI	Upper 95% CI
Capture probability	0.478	0.412	0.545	0.516	0.406	0.625	0.419	0.312	0.533
Super-population size[a]	8.1	4.1	15.8	6.3	2.8	13.9	0.3	0.0	54.5
Apparent survival									
2010–2013	0.860	0.809	0.899	0.808	0.743	0.860	0.944	0.848	0.980
2017–2020	0.805	0.643	0.904						
Probability of immigration									
Females	0.009	0.001	0.080	0.016	0.002	0.100	<0.001	<0.001	1
Males	0.052	0.029	0.091	0.062	0.035	0.106			
Female population size									
2010	55.6	45.6	65.6	37.3	27.5	47.1	8.2	6.7	9.8
2020	11.7	5.8	17.6	7.6	3.4	11.8	5.0	2.4	7.6
Male population size									
2010	25.4	16.9	34.0	15.4	8.6	22.3	9.2	7.7	10.8
2020	12.7	7.5	17.9	8.0	4.5	11.6	5.6	2.7	8.5

Parameters were derived from Jolly-Seber estimation for the whole population and for the northern (SMH) and southern (Kizell) sub-populations separately. Sex- or study period-specific parameters are shown where appropriate. Where only one estimate is shown, the parameter was estimated to be constant through time and for both sexes.

[a] Super-population = the total number of individuals available for entry into the sampled population (Schwarz & Arnason, 1996).

Largely due to a decrease in low-resistance wetlands (mostly swamps) and increase in high-resistance habitat (settlement and grassland) within the central region of the study area, availability of least-cost paths linking the northern and southern wetlands declined, with the shortest paths being entirely lost by 2017–2020 and the single remaining corridor being 480 m (15.1%) longer than the previous least-cost path and following a more convoluted trajectory involving traversing wetland, forest and some open-field habitat, as well as roads (Fig. 1).

Population size estimation

We estimated that turtle population size was 81.0 animals (95% CI: 62.5–99.6) in 2010, declining to 24.4 (95% CI: 13.3–35.5) in 2020. The overall estimated population decline (69.9%) was not consistent between sexes, with females declining >4-fold from 55.6 (95% CI: 45.6–65.6) to 11.7 (95% CI: 5.8–17.6) (79.0%) and males declining from 25.4 (95% CI: 16.9–34.0) to 12.7 (95% CI: 7.5–17.9) (50.0%). The greater loss of females shifted the population from being female-biased in 2010 (68.6% female) to sex ratio parity (48.0% female) in 2020 (Fig. 2, Table 2). The best-fit JS population estimation model had constant capture probability ($\rho = 0.48$; 95% CI: 0.41–0.55) and number of individuals ($N_s = 8.1$; 95% CI: 4.1–15.8) available to enter the population (2010–2020). The best-fit JS model estimated the same apparent annual survival (Φ) for both sexes, which was 0.86 (95% CI: 0.81–0.90) during 2010–2013 and 0.81 (95% CI: 0.64–0.90) during 2017–2020 (Table 2). Probability of entry into the population (P_{ent}) was low, estimated as 0.052 (95% CI: 0.029–0.091) for males and 0.009 (95% CI: 0.001–0.080) for females (Table 2). Furthermore, we estimated that the juvenile cohort decreased by 90.0% from 24.9 (95% CI: 15.4–34.3) in 2010 to 2.5 (95% CI: 0.0–5.8) in 2020, with an estimated apparent annual survival rate of 0.78 (95% CI: 0.63–0.88) and a capture probability of $\rho = 0.20$ (95% CI: 0.12–0.31) (Fig. 2, Table S3).

When considering only the sub-population of adult turtles in the northern SMH conservation forest, we estimated a 70.4% population decline from 52.7 (95% CI: 46.1–69.4) to 15.6 turtles (95% CI: 7.9–23.4) between 2010 and 2020. Specifically, females in this sub-population experienced a greater decline (79.6%) than males (48.1%; Figure S2, Table 2). In this sub-population, adult apparent annual survival (Φ) was 0.81 (95% CI: 0.74–0.86) and probability of immigration for males ($P_{\text{ent}} = 0.062$; 95% CI: 0.035–0.106) was low but nevertheless >3 times higher than that for females (Table 2). In this sub-population, estimated number of juveniles declined from 16.2 (95% CI: 6.1–26.4) in 2010 to 2.4 (95% CI: 0.0–5.6) in 2020 (Figure S2, Table S3). In contrast, the adult population model exclusive to the southern wetland revealed relatively high apparent survival ($\Phi = 0.94$, 95% CI: 0.85–0.98), but markedly low probability of entry for both sexes ($P_{\text{ent}} < 0.001$). In this analysis, the total adult sub-population declined by 40.2% from 17.4 (95% CI: 14.4–20.6) to 10.6 (95% CI: 5.1–16.1), with declines in females (39.0%) and males (39.1%) being comparable (see Figure S2, Table 2). Juveniles in the southern sub-population apparently declined from 2.3 (95% CI: 0.8–3.9) in 2010 to 0.4 (95% CI: 0.0–2.0) in 2020 (Figure S2, Table S3).

Home ranges and locations

Mean home range area of monitored turtles was 19.7 ha (95% CI: 5.3–34.1) in 2010–2013 compared to 13.8 ha (95% CI: 4.6–23.02) in 2017–2020 ($t_{28.9} = 0.73$, $P = 0.47$; $n = 36$ turtles). During the 2017–2020 nesting seasons, 33.1% of female turtle GPS locations and 21.3% of male turtle locations were within 200 m of roads ($t_{25} = 0.68$, $P = 0.51$; $n = 27$ turtles). On average, females were located 260.5 m (95% CI: 117.7–403.3) (44.3%) closer to roads than males ($t_{25} = 3.75$, $P < 0.001$; $n = 27$). Moreover, the proportion of realized GPS fixes was twice as high for females ($t_{25} = 2.12$, $P = 0.043$), indicating that they likely spent more time on land when transmitter signals were detectable via satellite. Turtle GPS trajectories showed that 5 (4 females, 1 male) of the 35 tagged turtles in 2017–2020 crossed the major road that bisects the study area, but GPS data resolution was not sufficient to determine if these crossings occurred through culverts or via fence openings along the road.

Mortalities

During 2010–2013, of 21 radio-tagged turtles, 9.5% ($n = 2$ turtles) died during the May to September monitoring period. A single known adult female died from a vehicle collision, with the other succumbing to an unknown cause. During 2017–2020, a single male (2.9%, $n = 33$) died from a vehicle collision. Based on telemetry, estimated 30-day turtle survival probability during summers 2017–2020 was 0.96 (95% CI: 0.89–1.0) and 1.0 for male and female turtles, respectively, with 4 of 33 turtles succumbing to unknown fate (and thus censored in survival estimation). Our CPH model revealed no hazard ratio differences between the sexes ($P = 0.99$).

Untagged turtles were found dead on the road during both 2010–2013 ($n = 5$, only one could be identified as an adult female) and 2017–2020 ($n = 3$, 2 of which were identified as adult females, the other could not be sexed). Note that during 2018 and 2019, an additional four road mortalities were detected by local observers unaffiliated with our project, two of which were identified as adult females and two as juveniles (D. Seburn, CWF, pers. comm.). Thus, we infer that at a minimum one adult female per year was killed on the road. However, we consider that because the single road mortality of a tagged turtle in 2020 would not have been detected without telemetry, and because additional road mortalities may have been removed prior to our road survey, estimated road mortality rates are likely considerably higher than our reported estimates. Notably, 92.9% of observed road mortalities occurred on roads surrounding the northern conservation forest and 78.6% were found on the primary road through the area and in proximity to known breaches in the roadside fence.

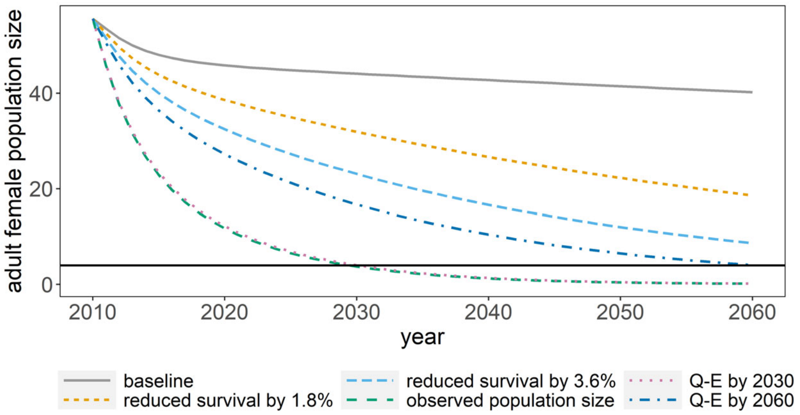

Figure 3 Population viability analysis (PVA) of the adult female Blanding's turtle (*Emydoidea blandingii*) population in Ottawa, ON, Canada, starting with the estimated female adult population size in 2010. Projected scenarios are as follows: Baseline in the absence of road mortality; with road mortality scenarios similar to roadkill observations (1.8% and 3.6% reduced female annual survival rate), with a survival rate of 0.82 that recreated observed female population size in 2020, and survival rates with which quasi-extinction (Q-E) threshold of four female adults were breached by 2030 and 2060 (survival rates: 0.83 and 0.91, respectively). The horizontal line represents the quasi-extinction threshold.

Population viability analysis

In the baseline projection, the turtle population experienced a stable finite growth rate throughout the 50 years ($\lambda = 0.997$). Adult female survival was the parameter with the highest elasticity (80%), with remaining parameters having lower contributions (all <11%, Table S4). When one and two additional female mortalities per year were modelled, projected adult female population size in 2020 was 37.0 and 28.2, respectively, which was considerably larger than our estimated population size of 11.7 (95% CI: 5.8–17.6) females from the JS model. When female mortality was increased to 3 and 4 per year, projected adult female population size in 2020 was 19.3 and 10.5, respectively. Thus, four adult female mortalities per year match closely to our estimated decline in the adult female cohort. When annual female survival rate was reduced proportionally by 1.8% for 50 years (representing 1 of the 56 initially estimated adult females in 2010), λ was 0.982 and estimated population size in 2020 was 38.6 adult females (Fig. 3, Table S5); when female survival rate was reduced by 3.6% (representing 2 of 56 females in 2010), total population growth rate declined further ($\lambda = 0.968$) and the 2020 population size was projected as 32.5 females (Fig. 3, Table S5). Note that these projected female population sizes were 3.3 and 2.7 times larger, respectively, than our estimated population size from the JS model. In fact, we found that an adult female annual survival rate of 0.82 was needed to produce the female population size estimated by the JS model (Fig. 3, Table S5). With a female survival rate of 0.82, the population experienced a finite growth rate of $\lambda = 0.922$ and likely would breach the quasi-extinction threshold of four females before 2030 (see Fig. 3, Table S5). Likewise, annual female survival of 0.75 and 0.86 would recreate the lower ($n = 5.8$ females) and upper 95% confidence limit ($n = 17.6$ females) of the population size estimate respectively (Table S5). Lastly, to sustain a population size above the quasi-extinction threshold ($n = 4$ females) by 2030 and 2060, the adult female survival rate would have to be ≥0.82, or ≥0.91, respectively, starting in 2010 (Fig. 3, Table S5).

When modelled as two sub-populations and adding one female road mortality per year to the northern sub-population (as suggested from our road mortality observations), the projected 2020 sub-population size was 12.1 adult females. When two female road mortalities were added per year, projected 2020 population size was 5.7 adult females (Table S6). This provided an estimated number of 7.6 (95% CI: 3.4–11.8) adult females in the sub-population, with a survival probability of 0.84 being needed to recreate the observed decline in females in this sub-population. With this survival rate, the northern sub-population experienced a growth rate of $\lambda = 0.904$ (see Figure S3). In contrast, in the southern wetland adult females likely experienced a higher annual survival rate (0.94), leading to the observed sub-population size of 5.0 (95% CI: 2.4–7.6) adult females and a population growth rate of $\lambda = 0.977$ (see Figure S3).

Discussion

Consistent with our expectations, current urban development in our study area near Ottawa, Ontario, Canada, is not compatible with Blanding's turtle population viability. Over the decade of intensive urban development, the study area experienced a substantial loss of turtle habitat and connectivity, likely promoting two smaller sub-populations of turtles. Habitat loss coincided with a decline in adult turtle survival and population size, which was especially pronounced in females and ultimately shifted population sex ratio and likely led to low juvenile recruitment. Turtles were killed by vehicles and females spent more time on land and were closer to roads than males. Our estimated adult female survival rate (0.82) is not sustainable. Our results show that despite efforts to offset habitat loss and road mortality through mitigation measures that were mandated for project approval, urban development is not compatible with freshwater turtle population viability in our study area. Generally, our work shows that development approval conditions, even when involving accommodations for at-risk species, can be insufficient to prevent population declines for some species and that such impacts may only be revealed through long-term monitoring spanning pre- and post-development phases.

We show that urbanization can dramatically alter animal population size and structure, primarily through reduced habitat availability and higher road mortality. We suspect that additional mortality, especially road mortality, is the major contributor to the observed population decline in our study population. Survival estimates in our area were markedly lower than those observed in undisturbed Blanding's turtle populations (e.g. Congdon, Dunham, & Van Loben Sels, 1993), and while sex-biased road mortality is not universally recognized in freshwater turtles (e.g. see Carstairs, Dupuis-Desormeaux, & Davy, 2019) and often not considered explicitly in turtle population management, several studies highlight that roads can have varied effects, with potentially strong impacts on mortality risk to females (Beaudry, Demaynadier, & Hunter, 2010; Howell & Seigel, 2019). For example, high road mortality resulted in an >80% decline and increased male bias in common snapping turtle (*Chelydra serpentina*) populations (Piczak, Markle, & Chow-Fraser, 2019). Our detections of road mortality combined with estimates of time spent on land and in proximity to roads (see also Aresco, 2005; Steen *et al.*, 2006) support that females were at higher risk of vehicle collisions. Thus, our results highlight the influence of roads on total turtle population size and especially on females (Tuberville, Gibbons, & Greene, 1996; Ernst & Lovich, 2009). Adult female survival is critical in long-lived species that experience low recruitment rates (Morris & Doak, 2002), and coinciding with the decline of adult females, we found lower juvenile recruitment over the last decade. While there is no evidence that Blanding's turtles show sex bias depending on trapping methods (Gibbs & Steen, 2005; Browne & Hecnar, 2007), juvenile turtles may experience lower detection probabilities compared to adults (Pike *et al.*, 2008). However, we used identical capture methods in 2017–2020 and 2010–2013, and conducted extensive visual surveys of the area and, thus, surmise that the observed decline in juveniles is representative of demographic changes in our study population.

It is understood that habitat loss due to urbanization often works in tandem with other anthropogenic disturbances, leading to aggravated impacts on wildlife populations (Romero-Muñoz *et al.*, 2020; Paterson *et al.*, 2021). In our case, loss of a portion of turtle habitat and reduced connectivity between sub-populations could have forced animals into the proximity of roads, where permeable fencing failed to prevent vehicle collisions. In addition to direct impacts of roads on turtle mortality, increased turtle nest predation by suburban predators such as raccoons (*Procyon lotor*) could also contribute to low recruitment, especially if nests are placed in accessible roadside locations (Karson, Angoh, & Davy, 2018). Such responses could compound the impact of roads on freshwater turtle population viability. These results emphasize the need to consider potentially compounding effects of urban development when considering management plans to limit impacts on urban wildlife populations.

Our study population likely cannot sustain current rates of adult road mortality, a phenomenon seen in other systems where wildlife population sustainability has been sought during rapid urban development (e.g. Howell *et al.*, 2019; Stokes *et al.*, 2021). Developers are often required to apply a hierarchy of mitigative measures to limit impacts, and if these successively fail it may be necessary to directly offset environmental impacts via reducing the development footprint and related activities. However, guidelines to inform such decisions are lacking (Gardner *et al.*, 2013; Marshall *et al.*, 2020). Approval of urban development projects often also assumes that unproven and hypothetical mitigation measures will alleviate impacts (Doebeli *et al.*, 2021; Gannon, 2021), and often, artificial turtle nest sites and hibernacula are developed despite being untested (Jochimsen *et al.*, 2004; Lesbarrères & Fahrig, 2012). In our study area, artificial turtle nest sites and hibernacula were constructed mostly ad hoc and with limited oversight and quality assurance (A. Auge, unpubl., see also McLaughlin *et al.*, 2012), leading to the concern that these resources should have been strategically directed towards more beneficial mitigation measures. It is understood that newly created habitats frequently fail to fully restore ecosystem function (Moreno-Mateos *et al.*, 2012) or else require years to become established (Vesk *et al.*, 2008), which can lead to poor success (Moilanen *et al.*, 2009; Pickett *et al.*, 2013). In principle, fences and wildlife passages can help sustain populations by reducing road mortalities and compensating for low connectivity (Jarvis, Hartup, & Petrovan, 2019), but these measures have also failed elsewhere (Cunnington *et al.*, 2014; Gilhooly *et al.*, 2019). For freshwater turtles, these measures have had mixed success (Baxter-Gilbert *et al.*, 2015). Thus, our results highlight the need to adopt mitigation measures that are proven to be effective in sustaining populations and communities in urban environments (Edwards *et al.*, 2019; Ghisbain *et al.*, 2020). In the present case, obvious steps that could alleviate impacts of development on the turtle population include no additional road development, and restoration of turtle habitat in the region (see Phalan *et al.*, 2018), but these changes seem unlikely to be supported by city planners or other officials. Less effectively, roadside fences can be monitored and maintained to reduce gaps, fence ends can be altered to redirect animals away from the road (Baxter-Gilbert *et al.*, 2015; Read & Thompson, 2021) and seasonal signs or speed reductions in turtle-crossing hotspots can occur during times of high risk of road mortality (Beaudry, Demaynadier, & Hunter, 2010). However, we suspect that none of these measures will reverse the ongoing decline in the study population.

Long-lived species with delayed maturity and low natural recruitment often have a larger minimum viable population size, slower population growth rate (Wang *et al.*, 2019) and thus limited ability to recover from mortality associated with anthropogenic disturbance (Hamilton *et al.*, 2018; Richards, Cooke, & Bates, 2021). Although some proximate effects of urban and road development can be detected over a short time span (e.g. loss of nesting sites, increased predation and direct mortality through vehicle collisions), demographic consequences may only be revealed after an extended period and following intensive monitoring. If long-lived species are already in slow decline prior to development activities, it can be more challenging to evaluate actual impacts and merits of mitigation (Pike *et al.*, 2010). However, approval of urban development proposals rarely requires the level of pre-development baseline data that would inform, for example, change in habitat availability or demography for long-lived species (Kilgour *et al.*, 2007; Thorn, Hobbs, & Valentine, 2018). Lack of baseline data implies that assessments of wildlife responses to urban development almost always suffer from crucial data deficiencies, which precludes both rigorous assessment of responses and the ability to use such information to make adaptive refinements to mitigation measures (Frick, Kingston, & Flanders, 2020; Hattam *et al.*, 2021). Considering the extent and rate of land-use change happening worldwide, there is an urgent need for a more rigorous framework to assess impacts of urbanization on natural systems, prior to development approval (Lin & Fuller, 2013; Cortinovis & Geneletti, 2018). Indeed, a minimum of 10–15 years of monitoring is often needed to adequately track population trajectory (Morris & Doak, 2002; White, 2019), meaning that current urban development planning and approval timelines are inadequate to ensure that population-level responses can be effectively tracked.

In the present age of widespread biodiversity loss, urban sprawl and environmental change, the onus is on legislators and planners to devise better strategies for allowing urban development while ensuring protection of native species. This obligation should be especially important for at-risk species, which has been highlighted by the responses of Blanding's turtles to urban development in our study area. Ultimately, conserving urban greenspace should be as important as conserving natural landscapes, and contemporary principles in urban planning highlight the benefits of this balance (Shanahan *et al.*, 2015). We need to rethink how we approach urban development and conservation to ensure the sustainability of biodiversity in an increasingly disturbed, urbanized environment.

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Author contribution

A.-C. Auge, G. Blouin-Demers and D. L. Murray conceived the ideas and designed methodology; A.-C. Auge collected the data; C. T. Hasler provided data. A.-C. Auge conducted fieldwork, analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Conflict of interest

The authors declare that they have no competing interests.

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Supporting information

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

Figure S1. Blanding's turtle (*Emydoidea blandingii*) study area in Ottawa, ON, Canada, where intensive development was initiated in the early 2000s and has continued to 2020. The study area includes the South March Highlands Conservation Forest in the north und the Kizell Wetland in the south, which is adjacent to the area being developed since 2017.

Figure S2. Estimated population size (with 95% CI) of adult female and male and juvenile Blanding's turtles (*Emydoidea blandingii*) in each sub-population (northern South March Highlands conservation forest ("SMH") and southern Kizell Cell Wetland ("Kizell") in the South March Highlands, Ottawa, between 2010 and 2020. Estimates were calculated from a Jolly-Seber population model (POPAN formulation).

Figure S3. Population viability analysis (PVA) of the South March Highlands Blanding's turtle (*Emydoidea blandingii*) population treated as two distinct sub-populations, starting with estimated population sizes in the northern SMH conservation forest and southern sub-populations in 2013. Shown are population projections over 50 years since 2013 for the two sub-populations, modelled with baseline conditions, and with the female adult annual survival rates necessary to recreate observed changes in the sub-populations (female survival rate in north: 0.84, south: 0.94).

Table S1. Definitions of habitat types in the study area that were used in the habitat suitability analysis.

Table S2. Resistance values for variables used in the connectivity analysis. Habitat resistance values are mean Blanding's turtle specific values for spring and summer resistance reported by Mui et al. (2017) (0 = least resistance, 100 = highest resistance).

Table S3. Estimated population parameters for the juvenile Blanding's turtle population near Ottawa, ON, Canada, including both the northern SMH conservation area and southern Kizell cell sub-populations. Parameters were derived from Jolly-Seber estimation for the whole population and for the northern and southern sub-populations separately.

Table S4. Sensitivity and elasticity of demographic parameters used for the population viability analysis (PVA) for the female Blanding's turtle (*Emydoidea blandingii*) population in Ottawa, ON, Canada.

Table S5. Population viability analysis (PVA) results for each simulated scenario of the Blanding's turtle (*Emydoidea blandingii*) population in Ottawa, ON, Canada, starting with initial population size from 2010 (n = 55.6 female adults, n = 17.1 female juveniles) and recreating estimated adult female population size in 2020 (n = 11.7 females, 95% CI: 5.8–17.6) as estimated by the Jolly-Seber model.

Table S6. Population viability analysis (PVA) results for each simulated scenario of the two Blanding's turtle (*Emydoidea blandingii*) northern conservation area and in the southern sub-populations in Ottawa, ON, Canada, starting with initial population sizes from 2013 (SMH: n = 21.9 female adults, n = 5.3 female juveniles; Southern: n = 7.1 female adults, n = 1.0 female juveniles) as estimated by the Jolly-Seber model, and assuming 70% females in the juvenile cohort.