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Large-scale collaboration reveals landscape-level effects of land-use on turtle demography

H. Patrick Roberts

University of Massachusetts Amherst, h.patrick.roberts@gmail.com

Michael T. Jones

Massachusetts Division of Fisheries and Wildlife

Lisabeth L. Willey

Antioch University

Thomas S. B. Akre

Smithsonian Conservation Biology Institute

Paul R. Sievert

University of Massachusetts Amherst

See next page for additional authors

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Authors

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Large-scale collaboration reveals landscape-level effects of land-use on turtle demography

H. Patrick Roberts^{a,*}, Michael T. Jones^b, Lisabeth L. Willey^{c,d}, Thomas S.B. Akre^e, Paul R. Sievert^a, Phillip deMaynadier^f, Katharine D. Gipe^g, Glenn Johnson^h, John Kleopferⁱ, Michael Marchand^j, Joshua Megyesy^j, Steven Parren^k, Edward Thompson^l, Chris Urban^g, Derek Yorks^f, Brian Zarate^m, Lori Erb^b, Angelena M. Rossⁿ, Jeffrey Dragon^e, Lori Johnson^b, Ellery Lassiter^e, Elliot Lassiter^e

^a Department of Environmental Conservation, University of Massachusetts Amherst, 204 Holdsworth Hall, Amherst, MA 01003, USA

^b Natural Heritage and Endangered Species Program, Massachusetts Division of Fisheries and Wildlife, 1 Rabbit Hill Road, Westborough, MA 01581, USA

^c Department of Environmental Studies, Antioch University New England, 40 Avon St., Keene, NH 03431, USA

^d American Turtle Observatory, 90 Whitaker Rd., New Salem, MA 01355, USA

^e Smithsonian Conservation Biology Institute, Front Royal, VA 22630, USA

^f Maine Department of Inland Fisheries and Wildlife, 650 State Street, Bangor, ME 04401, USA

^g Pennsylvania Fish and Boat Commission, 595 E Rolling Ridge Drive, Bellefonte, PA 16823, USA

^h Biology Department, State University of New York, 44 Pierrepont Ave, Potsdam, NY 13676, USA

ⁱ Virginia Department of Game and Inland Fisheries, 3801 John Tyler Highway, Charles City, VA 23030, USA

^j New Hampshire Fish and Game Department, 11 Hazen Drive, Concord, NH 03301, USA

^k Vermont Fish and Wildlife Department, 111 West Street, Essex Junction, VT 05452, USA

^l Maryland Department of Natural Resources, P.O. Box 68, Wye Mills, MD 21679, USA

^m New Jersey Division of Fish and Wildlife, PO Box 394, Lebanon, NJ 08833, USA

ⁿ New York State Department of Environmental Conservation, Potsdam, NY, USA

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ABSTRACT

Freshwater turtles and tortoises are declining worldwide and currently represent one of the most imperiled major vertebrate groups. Identifying the conditions that promote long-term viable populations is a critical conservation need. However, for most species, there is relatively little or no empirical information about the factors influencing population demographics. Large-scale population monitoring efforts necessary to acquire such information remain rare due to the logistic challenges associated with low and variable detectability, which generally preclude large monitoring initiatives by any single entity. The development of collaborative population monitoring programs represents one potential strategy for overcoming these challenges. Our goal was to leverage partnerships to identify the potential factors and relevant scales affecting wood turtle (*Glyptemys insculpta*) population demographics. Through a large-scale collaborative multi-institutional monitoring effort, we conducted 983 spring stream surveys at 293 sites across the northeastern United States. Wood turtle abundance was negatively associated with agriculture (300 m and 5500 m) and road traffic (5500 m) and positively associated with mature forest (5500 m). Juvenile proportion displayed strong negative relationships with stream gradient and imperviousness (300 m). Sex ratios were more male-skewed with higher mature forest cover (90

* Correspondence to: University of Massachusetts Amherst, 204 Holdsworth Hall, Amherst, MA 01003, USA.

E-mail address: hprobert@umass.edu (H.P. Roberts).

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m) and road density (5500 m) and less undeveloped land (300 m). These findings suggest that effective conservation of demographically robust turtle populations will require consideration of multiple spatial scales. Landscape-level conservation may be particularly important for ensuring long-term viable populations. This study highlights the valuable role that collaboration across institutions and jurisdictions can play in the conservation of cryptic taxa.

1. Introduction

Turtles are one of the most imperiled major vertebrate groups in the world with over half of species currently vulnerable to extinction (Lovich et al., 2018). Although successful for hundreds of millions of years, a life history strategy characterized by delayed sexual maturity, extreme longevity, and iteroparity has proven disadvantageous in a world shaped by rapid anthropogenic change (Heppell, 1998; Stanford et al., 2020). Globally, freshwater turtles face a common array of threats including land conversion for agriculture and urbanization, road mortality and collection for the food, medicine and pet trades (Gibbons et al., 2000; Stanford et al., 2020). While these threats are well established and frequently cited (Rhodin et al., 2018), there is a notable lack of published research that identifies and describes the precise combination of threats facing individual species. Moreover, for most species, there is relatively little or no empirical evidence indicating the relative severity of known threats, the nature of their effect on populations, or their most relevant spatial scales — key pieces of information needed to guide effective conservation of long-term viable populations. Studies that have made progress in addressing these questions have primarily focused on select species with life histories more conducive to anthropogenic environments (e.g., early sexual maturity, multivoltinism) that are relatively common and abundant, and therefore a lower conservation priority (e.g., Steen and Gibbs, 2004; Bowne et al., 2018). To improve the effectiveness of conservation practice, and more efficiently focus limited resources, there is an urgent need to develop more precise understandings of the primary stressors affecting declining freshwater turtle species. However, this task is made inherently difficult by the cryptic nature and life history of many species.

The paucity of detailed information about threats to individual turtle species is undoubtedly due in part to the difficulty of sampling turtle populations. Many species exhibit low and variable detectability and inhabit environments that are difficult for humans to navigate. These challenges increase logistic and monetary constraints associated with sampling, which in turn reduce the potential for collecting sufficient sample sizes across broad geographic areas. As a result, case study findings of individual (or few) populations are often the primary source of information about species threats (e.g., Saumure et al., 2007). While single-population studies can contribute important information about factors affecting cryptic turtles, confident extrapolation of threats to the broader species range requires systematic, standardized sampling across large geographic extents that encompass relevant ecological and environmental variation. For most species, this level of population monitoring will require the development of strategies that mitigate the inherent challenges of turtle sampling.

Assessing threats to turtle species is further complicated by the reality that common metrics used to assess species-environment relationships, such as abundance, are potentially misleading when applied to turtles. Due to extreme longevity and high site fidelity of many species, populations may be functionally extinct despite remaining abundant for decades if recruitment is suppressed by a lack of suitable nesting habitat or high juvenile mortality (Gibbs and Amato, 2000). Populations might also be abundant with detectable recruitment, but suffer sexually disparate mortality rates (Gibbs and Steen, 2005) that skew sex ratios and eventually lead to a long-term loss of genetic diversity and population decline. Thus, effective turtle conservation will require an understanding of the factors influencing not only population size, but also other important demographic parameters. Efforts to simultaneously elucidate the drivers of different demographic parameters are very rare for turtles and have primarily occurred for a single relatively abundant and observable species (e.g., Bowne et al., 2018). Acquiring such information for cryptic and declining species represents an important, yet elusive conservation priority.

Anthropogenic land-use can directly affect turtle population demographics by increasing mortality rates and altering the quality, quantity, and configuration of resources on the landscape (Garber and Burger, 1995; Marchand and Litvaitis, 2004b; Steen and Gibbs, 2004; Browne and Hecnar, 2007). Roads in particular are thought to negatively affect most turtle populations by both increasing overall adult mortality via car collisions and destabilizing population sex ratios by disproportionately elevating female mortality due to increased vulnerability during nesting excursions (Steen and Gibbs, 2004). Interestingly, despite the prevalence of road mortality in turtle populations around the world, few, if any, studies have successfully linked lower turtle abundance to road density (Quesnelle et al., 2013). Further, studies examining the effect of roads on sex ratio have produced conflicting results, even within the same species (Marchand and Litvaitis, 2004a; Dorland et al., 2014; Bowne et al., 2018), highlighting the risk of extrapolating such relationships to different landscape contexts and species without appropriate sampling. Further research, particularly involving broad geographic sampling for species underrepresented in the literature, is clearly needed to better understand the complex effects of anthropogenic land-use on turtles as a taxon.

The North American wood turtle (*Glyptemys insculpta*) is a semi-terrestrial fluvial specialist that overwinters in streams (Harding and Bloomer, 1979), but spends the majority of the summer up to 300 m from flowing water in the surrounding upland (Kaufmann, 1992). This amphibious annual activity cycle, and extensive terrestrial activity in particular, makes wood turtles highly vulnerable to urbanization and human land use. Collisions with vehicles and agricultural machinery are considered major threats throughout the species range, although there is a notable lack of empirical evidence across multiple populations (Jones and Willey, 2015). Females often make extensive terrestrial nesting excursions and tend to dwell further from streams than males (Jones, 2009), making this

species a valuable candidate for testing the link between roads and anthropogenic land-use on sex ratio. The wood turtle is listed as endangered by the International Union for the Conservation of Nature (IUCN; van Dijk and Harding, 2011), threatened by the Committee on the Status of Endangered Wildlife in Canada (Committee on the Status of Endangered Wildlife in Canada COSEWIC, 2007), and currently under review for listing under the Endangered Species Act in the United States (U.S. Fish and Wildlife Service, 2016). Individual population declines have been documented (Saumure et al., 2007 among other studies), but no large-scale population assessments have occurred, presumably due to its cryptic nature and broad geographic range.

Collaborative initiatives that leverage the resources of multiple entities increase the potential to reveal large-scale population trends that otherwise would not be possible (Yoccoz et al., 2001). In North America there are large monitoring programs for taxa that are readily observable during portions of the year (e.g., North American Breeding Bird Survey), but similar monitoring networks are uncommon or nonexistent for many cryptic taxa, such as reptiles. By distributing the workload among participating partners, collaborative monitoring programs have the potential to overcome the challenges of turtle sampling and ultimately generate the robust sampling needed to elucidate the complex assortment of factors that affect the long-term viability of freshwater turtle populations.

The overarching goal of this study was to leverage partnerships in order to identify the conditions that promote long-term viable wood turtle populations throughout the species range. Specifically, our objective was to identify and describe the factors that may influence wood turtle abundance, sex ratio, and juvenile recruitment. To accomplish this task, we undertook a multi-institutional and jurisdictional collaborative population monitoring program involving federal, state, academic, non-profit, and volunteer biologists across 12 states throughout the northeastern United States. We hypothesized a priori that wood turtle abundance would be negatively associated with agriculture and roads, male-biased sex ratios would be positively related to roads, and juvenile recruitment would be negatively related to impervious surface (a proxy for urbanization) due to corresponding increases in human-subsidized predator abundance. We also surmised that the relationship between wood turtle demographics and land-use would be scale-dependent, although we made no a priori hypotheses.

2. Materials and methods

2.1. Study area

We conducted this study within the wood turtle species range in the northeastern United States from Virginia and West Virginia to Maine (USFWS Region 5). To prevent use of spatially-explicit information for illegal collection, we have not provided a map of survey locations or any site-specific information.

2.2. Collaborative network

We conducted wood turtle surveys in association with the Northeast Wood Turtle Working Group (NEWTWG), a collaborative network of state, federal, academic, and nonprofit biologists, among others, that was formed in 2009 in conjunction with Northeast Partners in Amphibian and Reptile Conservation (NEPARC; northeastparc.org). During this study, the NEWTWG had no formal by-laws; however, one or two individuals were tasked with leading monthly conference calls and tracking objectives during funded periods. State agency biologists as well as select nonprofit and academic representatives served as the primary coordinators of surveys throughout the study area, although we encouraged volunteers to conduct surveys at their own discretion, contingent upon land access permission and appropriate permits. NEWTWG held in-person meetings at annual NEPARC conferences as well as survey protocol (northeastturtles.org) trainings periodically throughout the region.

2.3. Site selection

Participants selected survey locations that primarily fell into 3 categories: known populations, suitable habitat (as assessed by experts), or data-deficient areas. Due to the competing goals of concurrent projects as well as logistic constraints, we could not randomly select survey locations along a priori variable gradients, but attempted to maximize geographic dispersion, representation of watersheds, and representation of land cover types including mature forest, human development, and agriculture. Sampling intensity varied by state depending upon available resources.

2.4. Visual encounter surveys

We conducted visual encounter surveys for wood turtles along stretches of streams and rivers throughout the northeastern United States (Virginia to Maine) from 2012 to 2017. Surveys consisted of multiple observers (1–4 recommended) searching for wood turtles along the stream channel, bank, and surrounding floodplain (typically < 10 m) at a target speed of approximately 1 km/h. Survey segments were restricted to 1 km whenever possible. We conducted 3 surveys per site per year and restricted all surveys to the spring season, which we defined as between overwintering emergence and 28 May (approximate onset of nesting). We applied this temporal restriction because adult and juvenile wood turtles are typically most detectable in spring (Jones and Willey, 2015) and sex ratios are likely least biased during this time because all turtles emerge from in-stream overwintering sites during this period. Before each survey, we assigned each observer a number corresponding to the order in which they would search along the stream (i.e., observer 1 would lead each survey searching ahead of all other observers, followed by observer 2 and so on). We encouraged individual observers to survey as many different locations as possible and to alternate lead observers among surveys to reduce observer bias. Surveyors marked

individual turtles with a unique identification code by filing notches into marginal carapace scutes using an established notching system (primarily the system established by Ernst et al., 1974). We used either the presence (male) or absence (female) of a plastron concavity to determine sex of adult turtles (Vega and Stayton, 2011).

We prioritized conducting surveys when air temperatures were 9–24 °C and water temperatures were 7–20 °C. To reduce temporal bias, we discouraged surveying sites on consecutive days, except when temporally spacing surveys was logistically unfeasible. We recorded time of day, date, cloud cover (clear skies, partly cloudy, mostly cloudy, overcast, light rain, or heavy rain), air temperature, and water temperature.

2.5. Landscape analysis

We obtained a range of land cover, stream-based, and climate covariates hypothesized to influence wood turtle abundance or population structure. Land cover covariates included road density (km/ha), mean traffic, mean imperviousness, proportion undeveloped land, proportion mature forest cover, proportion early-successional cover, and proportion agricultural land. We estimated road density using U.S. Census Bureau TIGER/Line® road Shapefiles. We obtained or derived the remaining variables listed above from regional 30-m cell size data layers developed by the North Atlantic Landscape Conservation Cooperative (NALCC) Designing Sustainable Landscapes (DSL) project (http://www.umass.edu/landeco/research/dsl/products/dsl_products.html). The NALCC DSL traffic metric combines distance to roads and traffic rate to estimate the relative effect of road traffic intensity for every cell on the landscape. We used the NALCC DSL Land Cover layer to represent the general land cover variables. We combined the Formation types “Northeastern Upland Forest” and “Boreal Upland Forest” to represent mature forest cover. We used “Grassland” and “Shrubland” to represent early-successional cover. We calculated land cover variables at 90-m (riparian), 300-m (annual movement), and 5500-m (landscape) scales around each survey segment. We used 90 m because a majority of wood turtle movements occur within this distance (Jones and Willey, 2015). We used 300 m because > 95% of movements occur within 300 m of overwintering streams (Jones and Willey, 2015). We used 5500 m because this scale has been shown to be potentially predictive of relative wood turtle population size (Jones and Willey, 2015). We calculated variables related to land cover using the “raster” package (Hijmans, 2019) in the R software environment (R version 3.1.1).

Stream-based covariates included stream segment length, gradient, sinuosity, and flow accumulation, which we calculated in ArcGIS (Environmental Systems Research Institute, Inc., Redlands, CA). We hand delineated all stream segments using start and end coordinates in conjunction with aerial imagery. We estimated stream gradient by dividing the change in elevation (derived from NALCC DSL Digital Elevation Model) from start to end of each segment by the length of the segment. We calculated a relative measure of stream sinuosity by dividing the segment length by the straight-line distance between the start and end of each segment. We extracted flow accumulation (NALCC DSL data layer) at the midpoint of each stream segment.

Climate covariates included solar incidence, annual precipitation (30-year normal), minimum annual temperature (30-year normal), July temperature (30-year normal), heat index (sum of maximum daily temperatures above 35 °C), and elevation. We extracted climate values from the mid-point of stream segments. We acquired all climate variables from NALCC DSL.

2.6. Statistical analyses

2.6.1. Abundance

We used N-mixture models (Royle and Dorazio, 2008) to relate wood turtle counts to land cover, stream, and climate variables. This modeling approach uses repeated surveys at sites to account for bias associated with detection to produce relative measures of abundance. We fit closed-population N-mixture models using the “unmarked package” (Fiske and Chandler, 2011) in R.

Detection covariates included total time spent searching, time of day, cloud cover, air temperature, number of observers, day of year, and an interaction between growing degree days and day of year (to account for variation in emergence phenology). We converted cloud cover to a numeric variable representing relative cloud cover, where “clear” = 0, “partly cloudy” = 1, “mostly cloudy” = 2, and “overcast” = 3. To facilitate model convergence, we scaled all continuous covariates such that mean (SD) = 0 (1).

We treated each year as a separate sampling unit and included year as a covariate in all models. We only used sites with more than two surveys in a given year. We randomly selected surveys from sites with > 3 surveys in a year to avoid potential bias associated with increased search effort that was directed toward priority populations. For sites that were sampled across multiple years, we randomly selected a single year for analyses. Because few surveys were conducted in 2014 and 2017, we removed surveys from these years to reduce the variable-sample size ratio. While this analysis potentially violated the model assumptions of no deaths, immigration, or emigration, we believe violations were minimized because wood turtle survival rates are generally very high (e.g. Compton, 1999) and we considered only surveys from a relatively narrow temporal window.

We used Akaike’s Information Criterion corrected for overdispersion (QAIC; Burnham et al., 2011) to assess the relative performance of candidate mixture models. To begin model selection, we first compared negative binomial and zero-inflated poisson error distributions with all 7 detection covariates as well as 5 uncorrelated ($r < 0.7$) arbitrarily selected site covariates. We included only a subset of the site covariates to avoid overfitting. Negative binomial performed better with respect to QAIC and therefore we used this error distribution in all subsequent models.

To determine the best performing detection covariates, we first fit all subsets of detection covariates using the MuMIn package (Barton, 2016) in R. To account for as much variation as possible without overfitting, we also included the same 5 site covariates that were used to select the error distribution as fixed covariates in all candidate detection models. We also limited the maximum number of detection variables in competing models to 5 and considered quadratic terms for all detection covariates. Similar to Smetzer et al.

(2014), we selected detection covariates with parameter 95% confidence intervals (CI) that did not overlap zero and appeared in models that performed better than the null model and had a $\Delta\text{QAIC} < 2$. We included detection covariates selected through this process in all subsequent models.

Next, we selected the best performing site covariates within each of 3 classes: stream, climate, and land cover covariates (see “Landscape Analysis”). July temperature, minimum temperature, and heat index were each correlated ($r > 0.7$), leading us to exclude heat index and July temperature from consideration because minimum temperature performed best in single variable models (lowest QAIC value). For each class of variable, we compared models using all variable subsets and selected top variables using the same criteria used for selecting detection covariates (variables with 95% CI that did not overlap zero and appeared in models that performed better than the null model and had a $\Delta\text{QAIC} < 2$). Because there were many land cover variables under consideration, we first divided the selection process for this variable class into sub-stages, where the top performing variables were selected within each spatial scale if 90% CI of parameter estimates did not overlap 0 and were not correlated ($r < 0.7$) with the best performing variable (lowest QAIC value) within the respective scale. We selected variables within each scale using the same all subsets approach described above.

After we selected the top performing variables for each variable class, we conducted a final model determination process where the best performing models ($\Delta\text{QAIC} < 2$) were identified within an all-subsets comparison. To avoid overfitting models we only considered models with < 6 site covariates. We assessed goodness-of-fit of all top models using a parametric bootstrap in the “unmarked” package in R.

2.6.2. Sex ratio and age structure

We used general linear mixed models (LMM) to relate both the proportion of captured adults that were male and the proportion of total captures that were juvenile (across all surveys) to land cover and stream variables. We compared the performance of models using Akaike’s Information Criterion corrected for small sample size (AICc). Following Gibbs and Steen (2005), we restricted our dataset to sites with ≥ 10 detections. With the exception of selecting detection variables (because LMMs do not account for detectability), we used the same variable and model selection process that was used for abundance models. We only considered models with < 6 variables. We included state (where surveys were conducted) as a random effect in all models because surveys were often conducted by the same observers in each state. We performed analyses using the glmmTMB package in R (Brooks et al., 2017). We assessed final models with Q-Q plots, uniformity, dispersion, and outlier tests with 2000 residual simulations using the “DHARMA” package (Hartig, 2019) in R.

3. Results

We recorded 2519 wood turtle detections during 983 surveys at 293 different survey sites throughout the northeastern United States from 2012 to 2017. Of these detections, 1035 were male (51% of adults), 983 were female, and 410 were juveniles or subadults. Surveys averaged 2.56 wood turtle detections per survey ($SD = 4.31$). Surveyors failed to detect a turtle during 364 (37%) individual surveys. Proportion of juveniles at sites with ≥ 10 total detections ($n = 76$) ranged 0–0.62. Proportion of adult males at sites with ≥ 10 adult detections ($n = 63$) ranged 0.09–1.0.

We surveyed streams in Maine (11% of surveys), New Hampshire (17%), Vermont ($< 1\%$), Massachusetts (29%), Connecticut (4%), New York ($< 1\%$), New Jersey (7%), Pennsylvania (13%), Maryland (3%), Delaware ($< 1\%$), West Virginia (1%), and Virginia (15%). Rhode Island was the only state within the species range in USFWS Region 5 that was not surveyed. In total, over 200 individuals participated in surveys. We estimate that non-profit organizations, academic institutions, state agency biologists led approximately 19%, 29%, and 52% of surveys respectively. Dozens of volunteers also assisted surveys.

Table 1
Parameter estimates of best performing models of wood turtle abundance throughout the northeastern United States.

Agriculture 300 ^{2a}	Agriculture 5500 ^{2a}	Traffic 5500 ^b	Forest 5500 ^c	Elevation	Elevation ^{2d}	Min. temp ^e	Solar ^{2f}	ΔQAIC^g	Weight ^h
	-0.142 ⁱ			0.358 ⁱ	-0.228 ⁱ	-0.207 ⁱ	-0.081 ⁱ	0	0.195
-0.125 ⁱ	-0.129 ⁱ	-0.486 ⁱ			-0.12 ⁱ		-0.079 ⁱ	0.82	0.13
-0.114 ⁱ			0.395 ⁱ		-0.144 ⁱ		-0.082 ⁱ	1.21	0.107
-0.113 ⁱ	-0.107 ⁱ	-0.403 ⁱ				-0.146	-0.079 ⁱ	1.48	0.093
-0.098	-0.117 ⁱ			0.324 ⁱ	-0.211 ⁱ	-0.179 ⁱ		1.52	0.091
-0.129 ⁱ			0.312 ⁱ	0.174	-0.201 ⁱ		-0.086 ⁱ	1.56	0.09
	-0.148 ⁱ	-0.397 ⁱ			-0.107	-0.148	-0.079 ⁱ	1.91	0.075
	-0.141 ⁱ			0.316 ⁱ	-0.21 ⁱ	-0.191 ⁱ		1.93	0.075
-0.144 ⁱ				0.366 ⁱ	-0.22 ⁱ	-0.221 ⁱ	-0.083 ⁱ	1.95	0.074

^a Quadratic terms for proportion agriculture within 300 and 5500 m.

^b Mean traffic rate within 5500 m.

^c Proportion mature forest within 5500 m.

^d Quadratic term for elevation.

^e Minimum annual temperature.

^f Quadratic term for solar incidence.

^g Difference in Akaike’s Information Criterion corrected for overdispersion and small sample sizes for models with $\Delta\text{QAICc} < 2$.

^h QAICc model weights.

ⁱ Parameter estimates with asterisks have 95% confidence intervals that exclude 0.

Wood turtle abundance ($n = 172$) displayed a strong negative quadratic (unimodal) relationship with agricultural cover at 300-m and 5500-m scales, strong positive relationship with mature forest cover within 5500 m, a strong negative relationship with traffic at 5500 m and mean minimum annual temperature, and strong negative relationships with quadratic terms for elevation and solar incidence (Table 1, Fig. 1). Best performing detection covariates included number of observers (positive), time spent searching (positive), and day-of-year (negative and quadratic). Goodness-of-fit tests indicated adequate fit for all top models.

Proportion of juveniles captured displayed strong negative relationships with mean imperviousness within 300 m and stream gradient (Table 2, Fig. 2). Proportion of adult males captured displayed strong positive relationships with percent forest cover within 90 m and road density within 5500 m as well as a strong negative relationship with undeveloped land within 300 m (Table 3, Fig. 3). Goodness-of-fit tests indicated adequate fit to the data.

4. Discussion

Lack of knowledge about cryptic organisms has hampered conservation at the global scale (Roll et al., 2017) and strategies that address the challenges of studying these taxa are urgently needed. Collaborative initiatives that distribute work among partners and emphasize standardized methodologies, have the potential to greatly increase our understanding of cryptic and imperiled species and in turn improve their conservation. By relying heavily upon a collaborative framework, we successfully amassed a large population monitoring dataset across much of the wood turtle species range, which increased our ability to make inferences about the conditions that promote long-term viable populations of this cryptic and increasingly threatened turtle.

Our findings indicate that effective conservation of abundant and demographically robust populations of semi-terrestrial turtles will require consideration of multiple biologically relevant spatial scales, even when considering individual demographic parameters. Notably, the landscape scale (5500 m), which was particularly important for predicting wood turtle abundance, is several times larger than the typical annual wood turtle home range (Jones and Willey, 2015), suggesting that interpopulation and landscape-level processes such as dispersal, connectivity, disturbance regimes, and/or overall ecosystem function may be important for supporting robust populations. For example, landscapes with minimal anthropogenic disturbance (e.g., dams or bank stabilization) may maintain low-intensity flood dynamics that sustain nesting beaches and early-successional riparian areas, but do not displace or kill individual turtles (Jones and Sievert, 2009; Spradling et al., 2010). We identify several landscape-level factors that may influence population demographics (agriculture, mature forest, traffic, and road density), highlighting the potentially complex and important role that the broader landscape likely plays in supporting populations. These findings suggest that frequently cited terrestrial land protection buffers for North American freshwater turtles (< 290 m; Semlitsch and Bodie, 2003) are likely not sufficient for comprehensive conservation of the wood turtle and possibly other semi-terrestrial species.

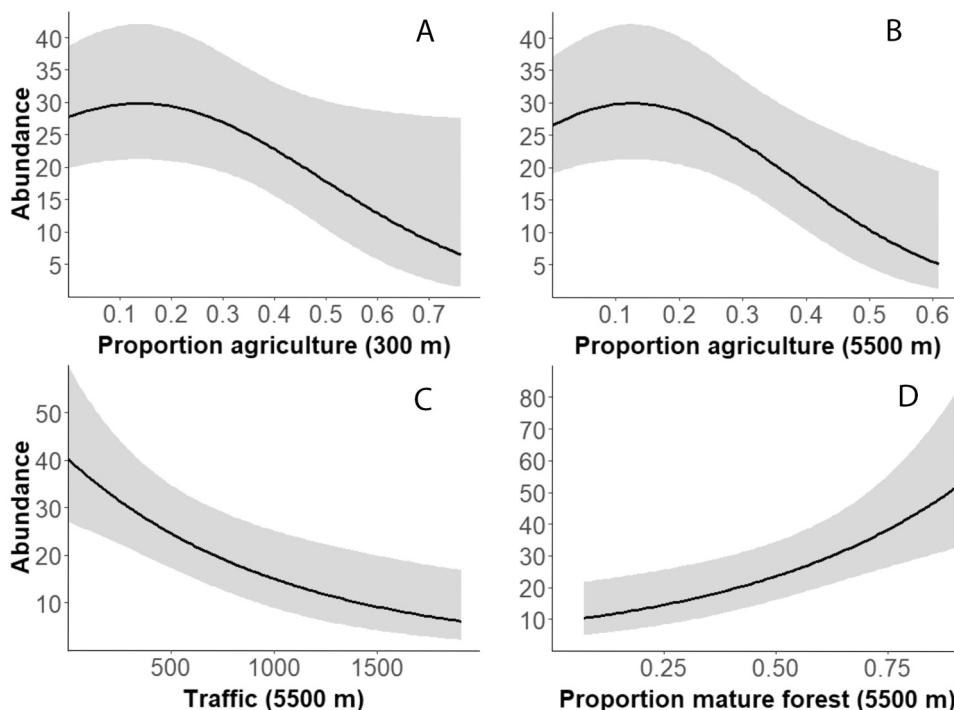


Fig. 1. Wood turtle abundance in relation to proportion agriculture within 300 m (A) and 5500 m (B), traffic within 5500 m (C), and proportion of mature forest within 5500 m (D). We show weighted-average model predictions for candidate models. Shaded areas represent 95% confidence intervals.

Table 2

Parameter estimates of best performing models of proportion of juvenile wood turtles detected during standardized surveys throughout the north-eastern United States.

Gradient ^a	Gradient ^{2a}	Impervious 300 ^b	Impervious 90 ^b	ΔAICc ^c	Weight ^d
-0.048 ^e		-0.032 ^e		0	0.342
-0.045 ^e			-0.027	0.98	0.21
	-0.018 ^e	-0.032 ^e		1.43	0.167
-0.046 ^e				1.61	0.152
-0.047 ^e		-0.024	-0.012	1.98	0.127

^a Linear and quadratic terms for stream gradient.

^b Mean percent impervious surface within 300 m and 90 m.

^c Difference in Akaike’s Information Criterion corrected for small sample sizes. We only show models with ΔAICc < 2.

^d AICc model weights.

^e Parameter estimates with asterisks have 95% confidence intervals that exclude 0.

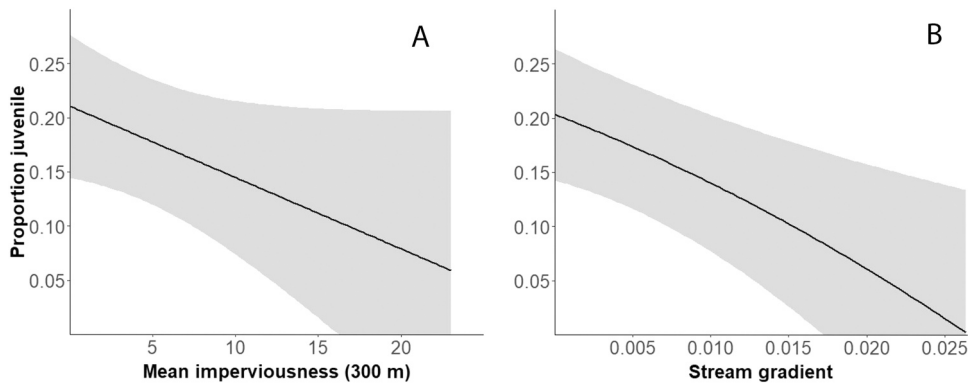


Fig. 2. Proportion of juvenile wood turtles in relation to mean imperviousness (A) and stream gradient (B). We show weighted-average model predictions for variables in candidate models. Shaded areas represent 95% confidence intervals for predictions.

Table 3

Parameter estimates of best performing models of the proportion of turtles that were male during standardized surveys throughout the northeastern United States.

Flow accumulation	Forest 90 ^a	Road density 5500 ^b	Undeveloped 300 ^c	ΔAICc ^d	Weight ^e
	0.487 ^f	0.036	-0.031	0	0.214
	0.041 ^f	0.048 ^f		0.11	0.203
-0.028	0.049 ^f		-0.046 ^f	1.06	0.126
	0.053 ^f		-0.046 ^f	1.06	0.126
-0.02	0.047 ^f	0.03	-0.034	1.4	0.106
-0.016	0.039 ^f	0.044 ^f		1.83	0.086

^a Mature forest within 90 m.

^b Road density within 5500 m.

^c Undeveloped land within 300 m.

^d Difference in Akaike’s Information Criterion corrected for small sample sizes. We only show models with ΔAICc < 2.

^e AICc model weights.

^f Parameter estimates with asterisks have 95% confidence intervals that exclude 0.

Our study provides strong support for the notion that agriculture can be detrimental for wood turtles (Saumure et al., 2007). While this relationship has been described at select populations (Saumure and Bider, 1998; Saumure et al., 2007) and watersheds (Jones, 2009), our study confirms what is primarily a negative relationship with wood turtle abundance throughout the northeastern United States. Moreover, our results show that agriculture likely exerts pressure on populations at multiple spatial scales, indicating that agriculture may not only cause direct mortality at the annual movement scale (300 m), but also disrupt or reduce other landscape-level processes such as dispersal and immigration (5500 m). Reduced movement rates have been linked to urbanization for more aquatic species (Patrick and Gibbs, 2010), but the effect of agriculture on connectivity of wood turtle populations remains unknown. Intensive agriculture may also indirectly affect habitat quality through erosion and sedimentation as well as nutrient and thermal pollution (Stanford et al., 2020).

While streams dominated by agriculture (> 60%) were associated with low abundance, streams with minimal levels of agriculture

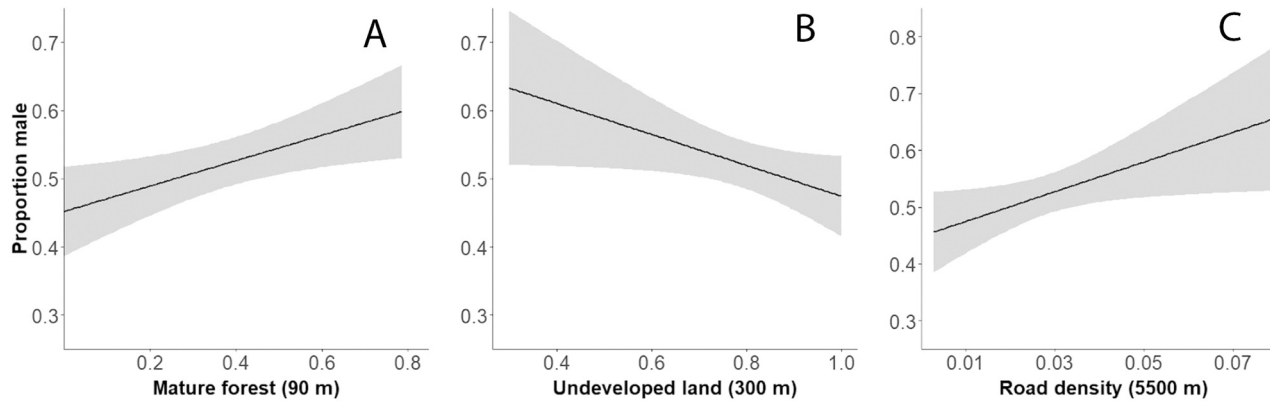


Fig. 3. Proportion of male wood turtles in relation to mature forest within 90 m (A), undeveloped land within 300 m (B), and road density within 5500 m (C). We show weighted-average model predictions for variables in candidate models. Shaded areas represent 95% confidence intervals for predictions.

(0–15%) were not necessarily characterized by a negative relationship between abundance and agriculture. Wood turtles are attracted to the early-successional conditions often fostered by low-intensity agriculture, and may benefit from associated increases in habitat heterogeneity (Kaufmann, 1992). However, the widespread increase of highly mechanized agricultural practices (e.g., rotary mowers) in recent decades (Saumure et al., 2007), suggests this pattern could represent an ecological trap leading to population declines even with low levels of agriculture. Alternatively, agricultural practices most common at low levels on the landscape may also be lower intensity (e.g., irregular mowing), and thus pose a reduced (but still present) threat. Future research should examine population-level effects of low-intensity agriculture on turtles.

Roads are frequently cited as a primary threat to North American freshwater turtles (Steen et al., 2012), but while their effects on population structure are documented (Marchand and Litvaitis, 2004a; Gibbs and Steen, 2005), the effect of roads on population abundance has remained elusive (Quesnelle et al., 2013; Dorland et al., 2014; Jones and Willey, 2015). We present evidence that wood turtle abundance is negatively associated with roads, particularly traffic, across a large portion of the species range. This pattern is not surprising given that wood turtles are highly terrestrial and thus likely to encounter roads during their annual activity cycle (Gibbs and Shriver, 2002). However, it is also possible that this relationship was driven by a separate correlated factor that we did not take into account.

Male-skewed sex ratios were associated with higher proportions of mature forest within 90 m, lower levels of undeveloped land within 300 m, and higher road density within 5500 m. Greater forest cover near streams may limit optimal nesting conditions (i.e., high solar exposure and open sandy soils) causing females to emigrate, or seek distant nesting areas, which may disproportionately increase their exposure to sources of anthropogenic mortality (Quesnelle et al., 2015). Marchand and Litvaitis (2004a) proposed the same explanation for a similar pattern observed in painted turtles (*Chrysemys picta*). The observed negative relationship with undeveloped land within 300 m further supports this theory in that females searching for nest sites in less developed landscapes are less likely to encounter vehicles, mesocarnivores, humans, and other threats. The positive relationship between male-skewed sex ratios and road density supports a growing body of literature suggesting that roads are possibly shifting the demographics of turtle populations throughout the United States (e.g. Steen and Gibbs, 2004; Gibbs and Steen, 2005; Steen et al., 2006).

The sharp decline in juvenile proportion in landscapes comprising 0–25% imperviousness indicates that even low levels of impervious surface within 300 m are not conducive to juvenile recruitment. This negative relationship may reflect the increased abundance of mesocarnivores such as raccoons (*Procyon lotor*) in human dominated areas, which are well documented nest and juvenile predators (Harding and Bloomer, 1979; Rutherford et al., 2016). Higher levels of stream stabilization and hardening associated with imperviousness can also eliminate nesting beaches, reduce sand deposition, and increase the intensity of floods that displace turtles (Sweeten, 2008; Jones and Sievert, 2009), and cause nest failure (Spradling et al., 2010; Lapin et al., 2019).

These findings should be interpreted within the context of the limitations of the data. Although a large portion of surveys (37%) yielded zero wood turtle detections, sites were nonetheless biased toward known populations. State-specific survey effort may have also introduced bias into our analyses. We conducted surveys throughout the study area, but the majority took place in Massachusetts, Maine, New Hampshire, New Jersey, Pennsylvania, and Virginia. Fortunately, we believe these states encompass the majority of ecological variation relevant to wood turtles in the northeastern U.S.

We highlight 3 general aspects of our approach to this study that may have helped to foster and sustain large-scale collaboration. First, commitment among primary partners (state agencies) to a core set of shared objectives functioned as a foundation and framework for sustained progress. This was particularly important in accomplishing key steps that often represent critical barriers to collaboration such as the development of a standardized population monitoring protocol. We believe that a firm commitment among partners to the fundamental mission and goals of our study provided assurance to prospective partners that adjusting or shifting away from their existing protocols would be a valuable endeavor. Second, we emphasized regular communication and feedback throughout funded periods via monthly conference calls. This helped to provide structure and maintain engagement among partners that likely would not have existed otherwise. Last, we found that annual in-person meetings and fieldwork outings throughout the study area were critical for enhancing levels of communication, maintaining momentum around overarching goals, and sustaining personal connection among partners.

The dearth of detailed information about the factors affecting turtle populations — despite immense and long-standing concern about the fate of the taxa globally (Gibbons et al., 2000; Lovich et al., 2018; Stanford et al., 2020) — is an indication that there are currently substantial barriers to answering critical questions related to their conservation. There is a need for larger, more geographically representative datasets that can help to discern the complex assortment of factors influencing population viability, and also serve as a baseline for detecting long-term population trends. A shift in the approach to conservation-oriented research of cryptic species that emphasizes collaboration — without sacrificing the security of spatially-explicit data for sensitive species — has the potential to achieve this goal and improve the understanding of the ecology and conservation of turtles, as well as other cryptic and imperiled taxa.

5. Conclusion

This study highlights the valuable role that collaboration can play in the conservation of secretive taxa. Through sustained large-scale collaboration, we provide a detailed assessment of the nature, relative importance, and relevant spatial scale of factors affecting multiple demographic parameters of wood turtle populations across much of the species range. Without collaboration among local experts and across numerous institutions and jurisdictions, it is very unlikely that the same geographic scope and intensity of sampling could have been achieved for this rare and cryptic species. Our findings indicate that landscape-level land protection aimed at restricting road construction and intensive land conversion around populations that still occupy relatively unaltered landscapes, is

likely the most effective conservation action for the wood turtle throughout its range. Although land protection buffer guidelines for freshwater turtles (Semlitsch and Bodie, 2003), and wood turtles specifically (Jones and Willey, 2015; Jones et al., 2018), encompass the vast majority of typical wood turtle movements, the broader landscape context should be considered when making land protection and other conservation decisions for this imperiled species. Effective conservation efforts aimed at supporting demographically robust populations will require that managers consider multiple spatial scales, with management actions tailored to the specific needs of each target population.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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