The effects of agriculture and forestry on the distribution, movements and survival of wood turtles in an intensively managed landscape

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A report prepared for the Nova Scotia Habitat Conservation Fund

October 2008

INTRODUCTION

The wood turtle (*Glyptemys insculpta*)

The wood turtle is a medium-sized freshwater turtle that inhabits slow-moving streams and rivers. Wood turtles are omnivorous generalists, feeding on invertebrates, amphibians, birds, berries, mushrooms and herbaceous vegetation (Compton et al., 2002). Previous research has shown that wood turtles use a variety of aquatic and terrestrial habitats including wetlands, forests, meadows, clear-cuts and agricultural fields (Compton et al., 2002; Arvisais et al., 2004; Saumere et al., 2007; Greaves, 2007). In temperate regions, wood turtles spend nearly half of the year over-wintering on the bottoms of streams and rivers.

Population declines have been reported throughout the species' range, primarily in response to habitat loss, increased rates of adult mortality and collection for the pet trade (Garber & Burger, 1995; Daigle & Jutras, 2005; Saumere et al., 2007). In Nova Scotia, the wood turtle is found primarily in small, isolated populations, nearly all of which occur in unprotected working landscapes. Recent research has indicated that the Saint Mary's River watershed (SMRW) in eastern Nova Scotia contains an exceptionally large population, perhaps the largest in the species' range.

The SMRW is one of the largest and most disturbed watersheds in the province. This region consisting of landscapes that have been highly fragmented and disturbed by over 200 years of agriculture and forestry. However, to date, the effects of these practices on the distribution, movements and survival of wood turtles have been largely ignored.

The goal of this project was to recommend sustainable management practices that will ensure the viability of wood turtles and other components of riparian and forest biodiversity. Our specific objectives were to:

i) identify wood turtle nesting and overwintering sites.

ii) determine whether agriculture and forestry influence the distribution of wood turtles at multiple spatial and temporal scales.

iii) assess whether current land-use regulations adequately conserve wood turtles.

iv) examine the effects of forestry and agricultural activities on the injury and survival rates of wood turtles.

Figure 1. This research took place in the St. Mary's River watershed, one of the largest and most disturbed watersheds in the province (shown in red).

Objective one: Identify nesting and overwintering sites

Twenty-seven adult wood turtles were caught opportunistically by hand from June 2005-May 2007 and equipped with radio-transmitters. Turtles were visually located one to five times a week from April 18-October 18 2007 and the coordinates of each location were recorded using a Garmin GPS unit (Garmin Ltd., OR, USA) with an accuracy of ~5 m.

Five unique nesting beaches were located via radio-telemetry. All five sites were along the main river channel and were on private property. Voluntary land management plans were therefore developed for all five of these properties. One female traveled almost 4 km from her overwintering site to reach her nesting site, while several other females migrated over 1 km.

Overwintering habitat on the other hand seems to be less critical. Turtles overwintered in a variety of aquatic habitats including rivers, streams and brooks. Several individuals over-wintered in small (~ 1 m wide) streams several kilometers from the main river channel, illustrating that all lotic habitats are critical to the persistence of wood turtle populations.

Objective two: Do agriculture and forestry influence the distribution of wood turtles?

To determine whether agriculture and forestry effect the distribution of wood turtles we compared habitat variables at turtle locations and paired random locations (See the attached article in **Appendix 1**: *Intra-specific niche partitioning obscures the importance of fine-scale habitat data in predictive habitat models* for details). Figures 2-5 illustrate the predictions of these habitat models throughout our study area.

The results of the best model for females indicated that after controlling for the effects of distance to water and aspect, female wood turtles showed a preference for regenerating stands. Indeed, ten out of 15 females tracked in this study used regenerating stands from June to October. Females also frequented agricultural fields, although fields were not selected significantly more often than scrub-shrub habitats.

Male wood turtles rarely used regenerating stands but were commonly seen in agricultural fields. However, after controlling for the effects of distance to water, aspect and elevation, fields were again not selected more often than scrub-shrub habitats.

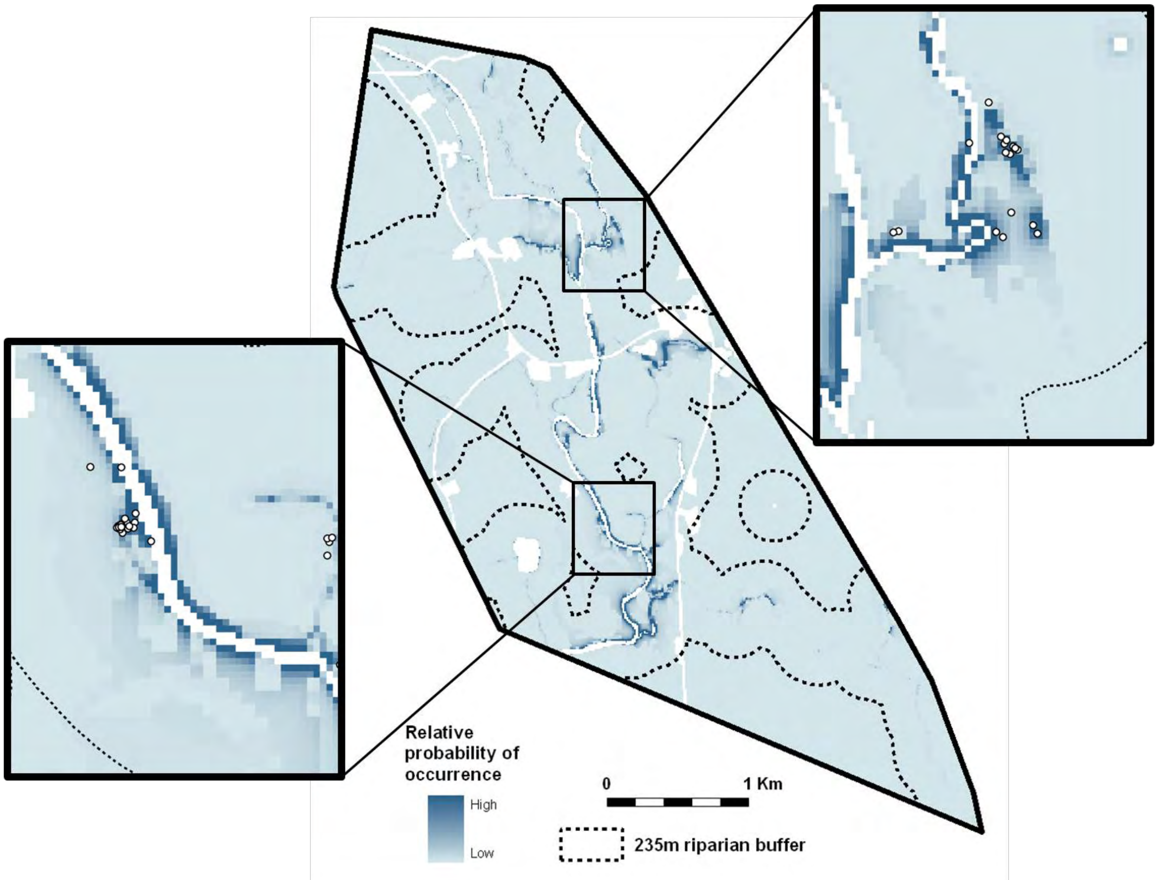

Figure 2. Predicted relative probability of occurrence of female wood turtles during May in the Saint Mary's River watershed, Nova Scotia. White areas represent land-cover types that were outside of the environmental domain of model calibration. White dots shown in pull-out boxes represent sightings of female wood turtles in May, 2006 and 2007. These occurrences were not used in model development.

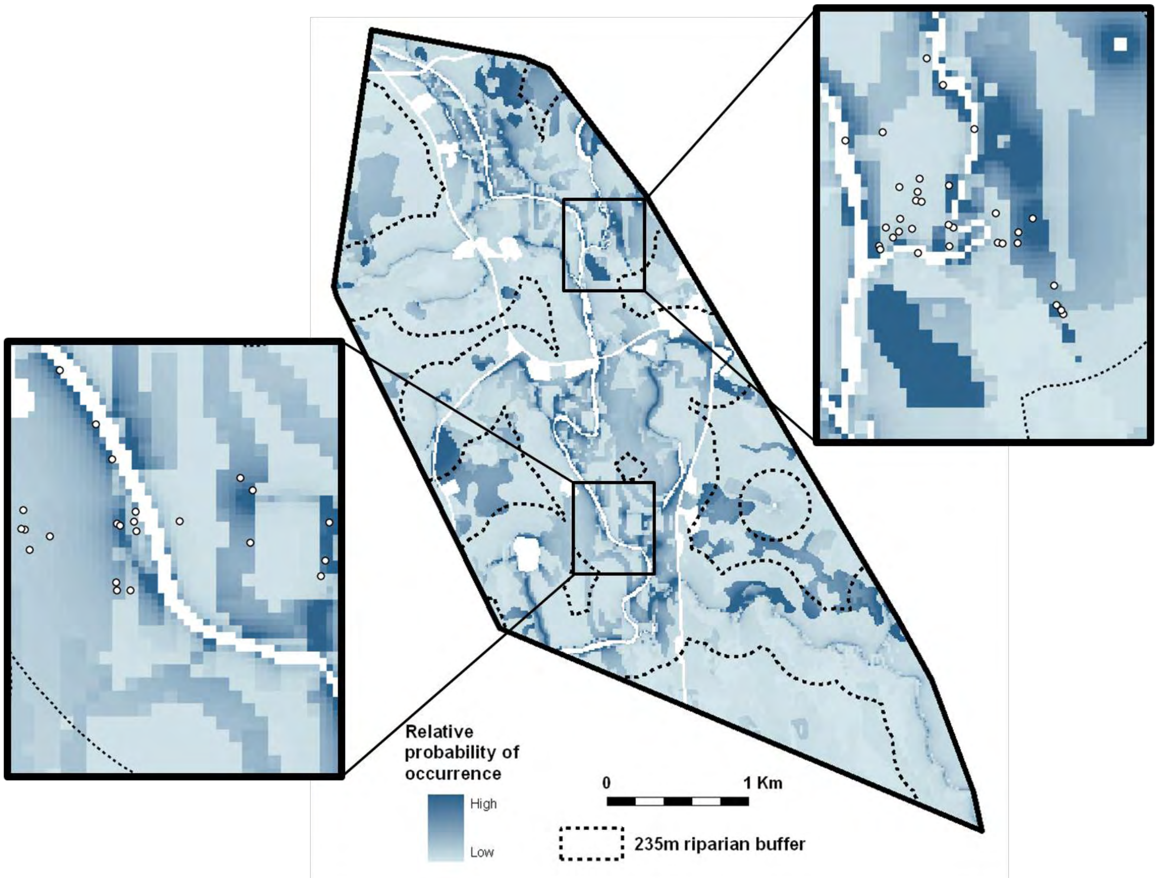

Figure 3. Predicted relative probability of occurrence of female wood turtles during June in the Saint Mary's River watershed, Nova Scotia, Canada. White areas represent land-cover types that were outside of the environmental domain of model calibration. White dots shown in pull-out boxes represent sightings of female wood turtles in June, 2006 and 2007. These occurrences were not used in model development.

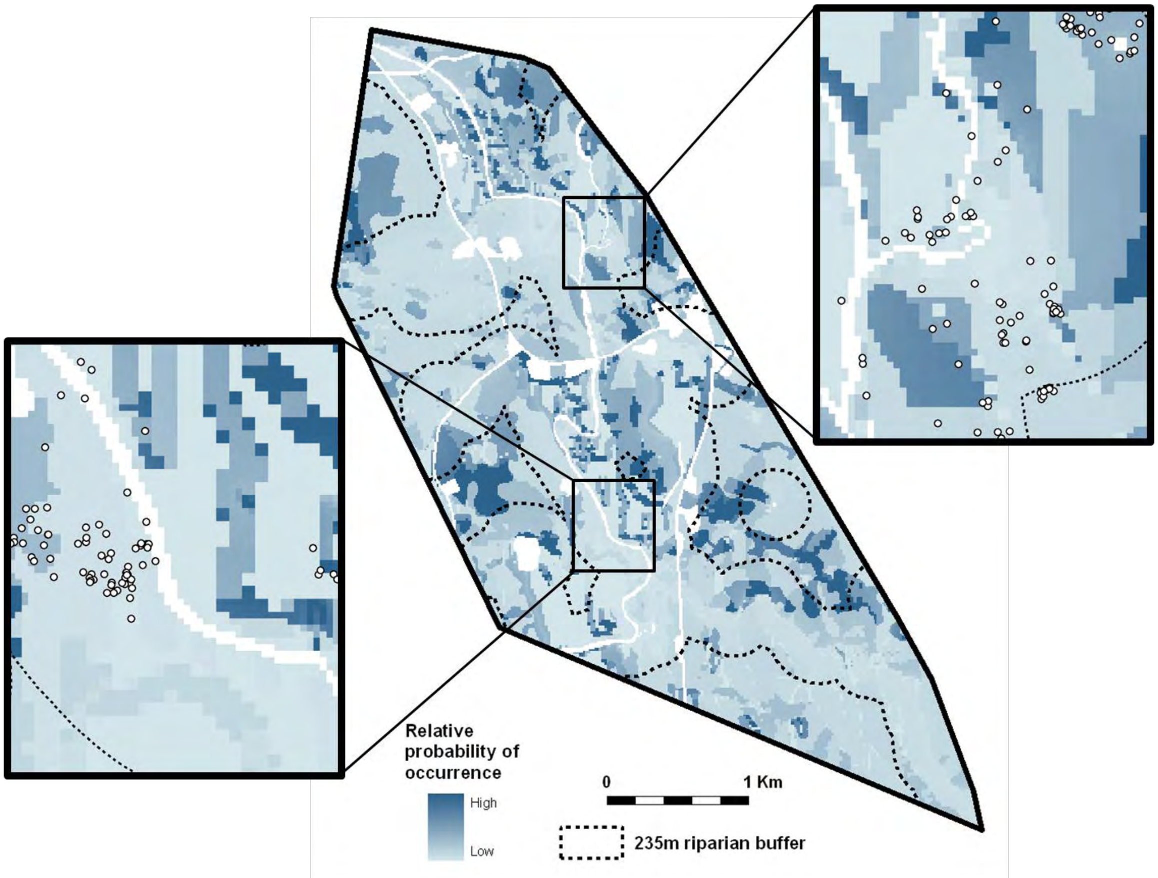

Figure 4. Predicted relative probability of occurrence of female wood turtles from July 1 to September 31 in the Saint Mary's River watershed, Nova Scotia, Canada. White areas represent land-cover types that were outside of the environmental domain of model calibration. White dots shown in pull-out boxes represent sightings of female wood turtles from July 1 to September 31, 2006 and 2007. These occurrences were not used in model development.

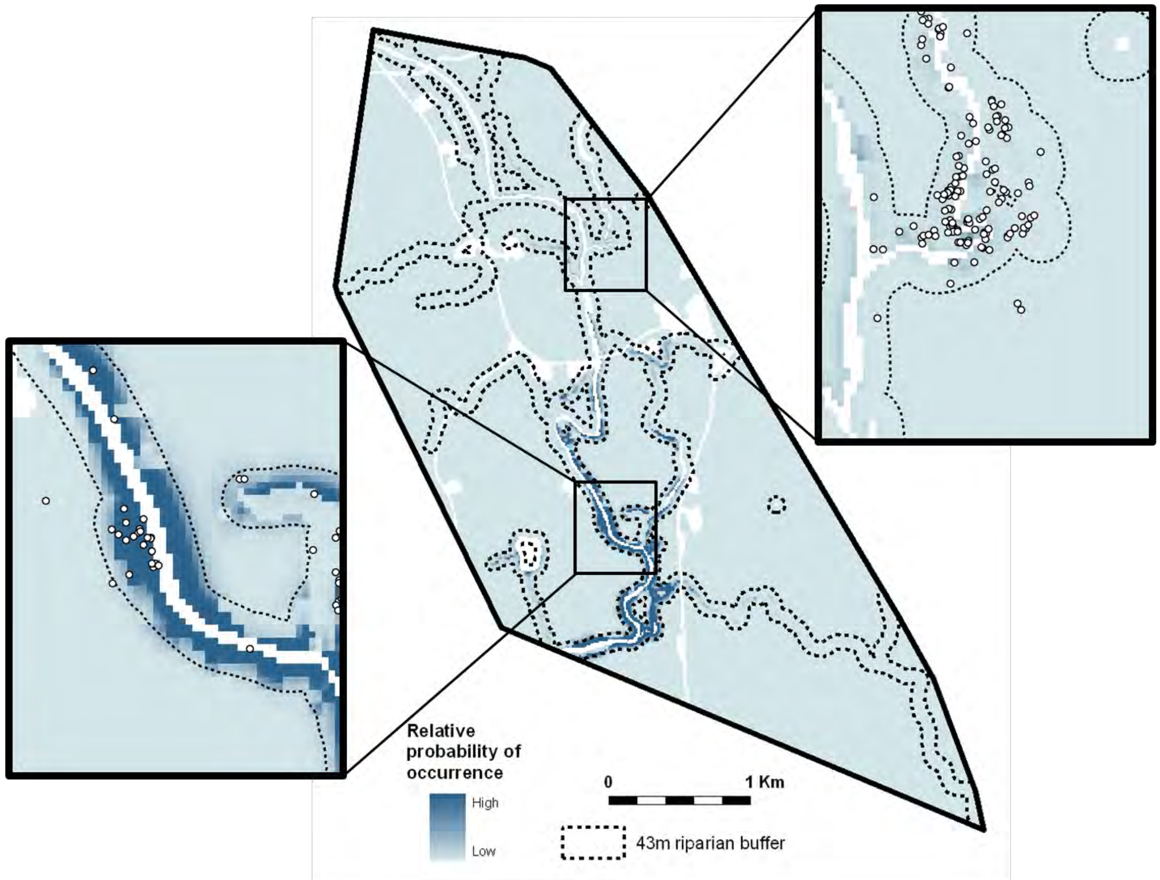

Figure 5. Predicted relative probability of occurrence of male wood turtles in the Saint Mary's River watershed, Nova Scotia, Canada. White areas represent land-cover types that were outside of the environmental domain of model calibration. White dots shown in pull-out boxes represent sightings of male wood turtles in 2006 and 2007. These occurrences were not used in model development.

Objective three: are current regulations adequate?

Because aquatic habitats are critical to the persistence of wood turtle populations, we calculated the proportion of telemetry locations falling within different-sized riparian buffers to determine how far current buffer zones would need to be expanded in order to encompass the majority of wood turtle habitat.

The results of the buffer-based approach indicated that riparian buffer zones of 182 m would accommodate 95% of all wood turtle sightings (Table 1). However, females were much more terrestrial than males. Female wood turtles were observed nearly 400 m from the nearest water body in early and late summer. Riparian buffers would need to be expanded to 235 m to encompass 95% of all female locations. For males, less than 0.01% of observations were further than 100m from water. A buffer zone of 43 m would protect male wood turtles 95% of the time.

Table 1. Distances (m) that wood turtles were observed from the nearest water body in the Saint Mary's River watershed, Nova Scotia, Canada (n=1497).

Decile	Males	Females	Combined
10	0.854	2.08	1.38
20	2.35	4.44	3.24
30	3.76	7.67	4.92
40	4.88	12.2	8.21
50	7.73	20.8	12.7
60	11.8	38.2	19.6

Table 1. Cont'd

70	16.4	67.1	31.6
80	22.2	113	54.4
90	34.9	170	123
95	42.7	235	182
100	142	389	389

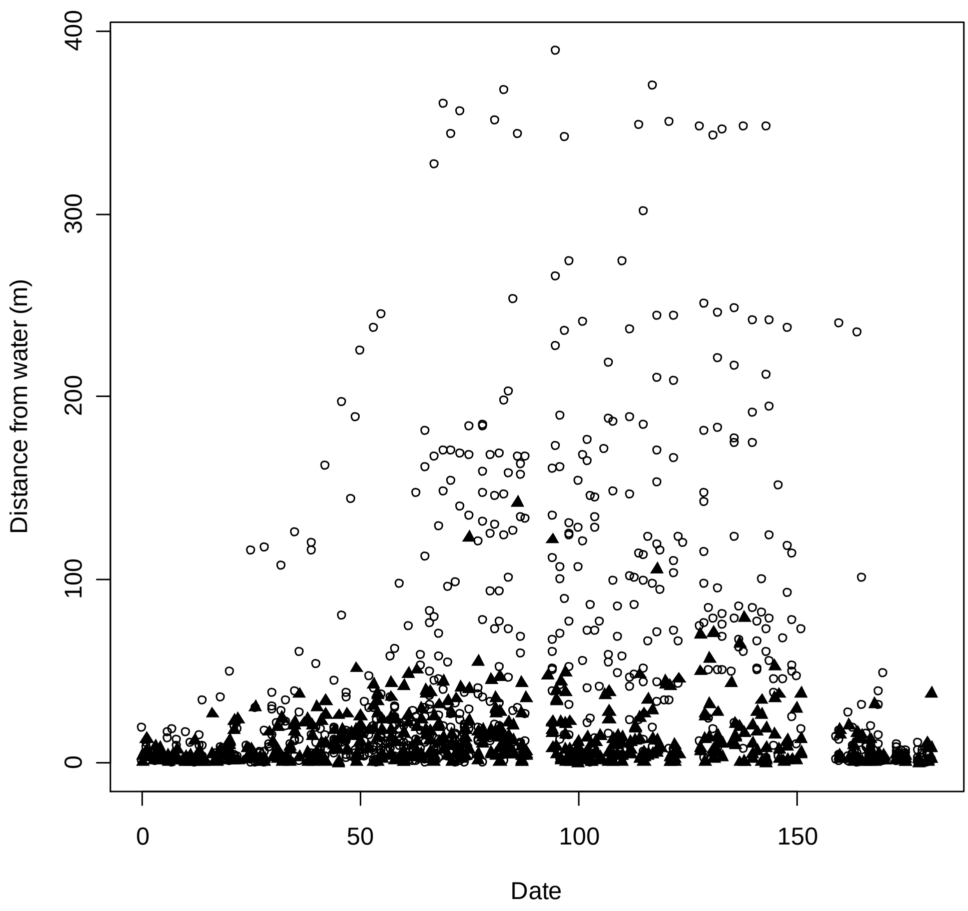

Figure 6. Terrestrial movements made by male (triangles) and female (circles) wood turtles in the Saint Mary's River watershed, Nova Scotia, Canada. Date is shown on the x-axis as the number of days since April 20, 2007.

Objective four: Making sustainable land-management decisions

a. Agricultural activities

Our results suggest that males may be more at risk of agricultural mortality than females. The number of instances in which males were observed in hay fields (n=35) was nearly double that of females (n=20). Furthermore, males use agricultural fields for more than a month longer than females. Indeed, the only recorded mortalities in 2007 were both males hit during the second harvest. We also documented more severe injuries among males, although predation cannot be ruled out as a potential source of these high rates of injury. Furthermore, injury severity was not correlated with the amount of agricultural land present in various sized buffers. However, many fields in the Nova Scotia Department of Natural Resources' (NSDNR) GIS database have long been abandoned and this temporal lag between our data and that contained in the NSDNR database may have weakened the relationship between injury severity and land-use.

Although our buffer-based analysis indicated that expanding riparian buffers to 43 m would protect male wood turtles from agricultural machinery 95 % of the time, such buffers on private agricultural lands are unlikely without financial compensation for farmers (Compton, 1999; Saumere et al., 2007). We therefore suggest farmers raise the blades on their disc mowers to 100 mm. Raising disc mower blades has been shown to increase yields, reduce wear on machinery and decrease soil erosion (Saumere et al., 2007).

Saumere et al. (2007) suggested that the blades on disc mowers could be raised during the first harvest only as most turtles at their study site returned to the river by this time. Clearly this is not recommended in Nova Scotia. Nevertheless, both males and females used agricultural fields most extensively in the spring and early summer and are therefore more likely to be injured or killed during the first harvest. Certainly, two females and one male were hit during the first harvest in 2005.

Sustainable agricultural recommendations

1. Raise blades on disc mowers to a minimum of 100 mm during the first and second harvest.
2. Maintain a mosaic of native riparian shrubs, particularly alders (*Rugus* spp.), and open areas around all streams and rivers occupied or suspected to be occupied by wood turtles.

b. Sustainable forestry recommendations for wood turtles in Nova Scotia

Nova Scotia is one of the most fragmented regions of the Acadian forest region (Ricketts et al., 1999). Furthermore, the area that is clear-cut annually in the province continues to rise (Wilson et al., 2001). Unfortunately, we know very little about the effects of forestry on wood turtle survival. Unlike farmers or motorists, foresters would rarely realize that they had struck a turtle. Females also commonly bury themselves in brush piles, making carcass searches highly ineffective. Although no turtle in this study was killed by forestry machinery, one female was dangerously close to being hit by a logging truck on several occasions. Injury severity was not correlated with the amount of treated or natural forest; however, this is to be expected given that most forestry equipment would result in mortality, not injury.

Despite these concerns, our results suggest that forestry practices may be conducive to female wood turtles if timed properly. Small-scale clearings promote the growth of herbaceous vegetation and berries and provide nesting and basking opportunities (Saumere et al., 2007).

Compton et al. (2002) and Arvisais et al. (2004) both documented the importance of areas with low canopy cover for wood turtles.

However, maintaining a mosaic of forested and managed stands will be critical as forests provide important resources such as mushrooms and cover. Furthermore, the benefits of canopy manipulation may become obsolete if even a small number of wood turtles are killed by machinery. Compton (1999) estimated that the removal of three adult wood turtles annually would lead to the extinction of a hypothetical population of 100 individuals in only 50 years. While forestry activities are unlikely to produce such high rates of mortality due to relatively long rotation times, synergistic relationships between forestry-, road- and agricultural-related mortality could easily extirpate wood turtle populations of this size (Saumere et al., 2007; R. Tingley, personal observation). We therefore suggest that forestry activities take place between mid-October and late-April when turtles are over-wintering.

During the active season, maintaining typical riparian buffer strips will do little to minimize the probability of female encounters with forestry machinery. In Nova Scotia, current forestry regulations stipulate that no vehicles are prohibited within 7 m of any water course > 50 cm wide. Our results suggest that such buffers afford protection to female wood turtles only 28 % of the time. Riparian buffers should be expanded to a minimum of 235 m during the active season if wood turtle encounters with forestry machinery are to be minimized.

Sustainable forestry recommendations

1. Ideally, forestry activities should not take place within 400 m of all water bodies occupied by wood turtles from late-April to early-October. Such a buffer would encompass 100% of all female movements observed in this study.

2. When the above recommendation is not feasible, forestry activities should be restricted within 235 m (the 95% quantile of terrestrial movements) of all water bodies occupied by wood turtles during the active season. Absolutely no forestry machinery should be used within 235 m of all water bodies occupied by wood turtles from late-May to mid-September.

3. Riparian buffers should be visually compared to the predictions of the GIS-based models developed here to identify suitable habitat that lies outside the proposed 235 m buffer zones.

4. Foresters should strictly adhere to the 7 m riparian buffer zone from October – late April to maintain the integrity of waterways and riparian vegetation. Sandy or gravel beaches along streams and rivers should be avoided at all costs as these areas often serve as nesting habitat.

5. Brush piles should be left intact as they are often used for thermoregulation. However, some open areas should be maintained to facilitate the growth of herbaceous vegetation and berries.

6. Temporary bridges should be constructed across all streams and rivers to avoid siltation and direct mortality. Using brush piles as bridges reduces siltation but still poses a threat to turtle survivorship.

Conclusion

Our results suggest that maintaining 235 m riparian buffer zones from late-April to mid-October would greatly decrease the probability of wood turtle mortality caused by forestry machinery. Such buffers would encompass all male movements observed in this study and would afford significant protection to females in most instances. Furthermore, maintaining 235 m riparian buffer zones would likely accommodate the majority of terrestrial movements made by a variety of amphibian and reptile species (Semlitsch & Bodie, 1998; Bodie, 2001). Although these recommendations are unquestionably ambitious, recent research in eastern Nova Scotia has already persuaded a major forestry company (New Page) not to harvest within 300 m of all high priority rivers and streams.

The predictions of the GIS-based habitat models developed here will also allow wood turtles to be more easily accommodated in multi-species conservation initiatives (Compton et al., 2002) and will lead to the development of more sustainable land-use practices. After all, addressing the management needs of a generalist species such as the wood turtle should not only ensure its own well being, but also that of the diverse ecosystems it inhabits.

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Appendix 1: Intra-specific niche partitioning obscures the importance of fine-scale habitat data in predictive habitat models. Article to be submitted to the journal *Landscape Ecology*.

ABSTRACT

Geographic information systems (GIS) allow researchers to make cost-effective, spatially explicit predictions of species' distributions across broad geographic areas. However, there has been little research as to whether fine-scale habitat data collected in the field could produce more robust predictions of species' distributions. Here we used radio-telemetry data on a declining species, the North American wood turtle (*Glyptemys insculpta*), to test whether fine-scale habitat variables were better predictors of occurrence than land-cover and topography variables measured in a GIS. Patterns of male and female occurrence were similar in the spring; however, females used a much wider array of terrestrial habitats from June-October. This spatio-temporal niche partitioning between males and females obscured the importance of fine-scale habitat variables. The occurrence of males was successfully predicted using GIS data, whereas the occurrence of females was best predicted using fine-scale variables. These results demonstrate the importance of taking a more sex-specific and temporally dynamic view of the environmental niche.

INTRODUCTION

Predictive habitat models now form the foundation of conservation programs in many parts of the world. These models provide spatial predictions that can be used to locate undiscovered populations (Guisan et al., 2006), identify potential sites for reintroduction (Mladenoff et al., 1995) or designate areas in need of legal protection (Ferrier, 2002). For species that are susceptible to road- or machinery-related mortality, habitat models can also be used to target areas where mitigation measures may increase survival probabilities (Johnson et al., 2004).

Geographic information systems (GIS) are at the core of predictive habitat modeling. GIS data are an attractive alternative to fine-scale habitat data collected in the field because they provide a way for researchers to make cost-effective, spatially explicit predictions over broad geographic domains (Betts et al., 2006). However, GIS databases rarely contain information on causal limiting factors such as prey abundance or cover and as a result, land-cover and topography variables are often used as distal surrogates (Gibson et al., 2004; Dormann, 2007). The use of environmental variables collected in the field on the other hand allows researchers to develop models based on variables thought to be more causally related to the occurrence of the species in question. The development of such fine-scale habitat models may therefore lead to predictions that are more applicable in both space and time (Guisan & Zimmermann, 2000; Harvey & Whitehead, 2006; Austin, 2007).

Land-cover designations are also subjective and prone to classification error. Whereas aerial photograph interpretation may be adequate for forest management, such data may not provide information that is detailed enough to accurately model species' distributions at local scales (Seoane et al., 2004). Digital elevation models which serve as the foundation for topographic variables are also typically available at a coarse resolution and are based on interpolation algorithms which limit heterogeneity at fine extents. Despite the widespread use of GIS-based habitat models in theoretical and applied research, relatively few studies have tested whether models built using fine-scale resources can outperform models based solely on GIS data (but see Saveraid et al., 2001; Jengathan et al., 2004; Betts et al., 2006; Harvey & Whitehead, 2006). Furthermore, although researchers have long been aware of how sexual (Passinelli, 1999; Pearson et al., 2002; Sunde & Redpath, 2006) or temporal (Schooley, 1994; Arvisais et al., 2004) differences in resource use can influence observed correlations between a species and its environment, there have been no studies on how these factors might affect the need for fine-scale habitat data.

Here we explore the relative utility of GIS- and fine-scale predictors using radio-telemetry data collected on a riparian species at risk, the North American wood turtle (*Glyptemys insculpta*). Female wood turtles make extensive seasonal movements among rivers, riparian zones and upland areas, whereas males generally remain near aquatic habitats throughout most of the year (Arvisais et al., 2002). In this article, we show that this spatio-temporal niche partitioning between males and females not only results in different resource selection patterns, but also obscures the importance of fine-scale habitat data in predictive habitat models.

METHODS

Study area and species

This research was conducted on the eastern mainland of Nova Scotia, Canada (~45° N) in the Saint Mary's River watershed (SMRW). The study area encompasses 11.91 km^2 and follows ~ 8 km of main river channel. Elevation ranges from 16 – 95 m.

The SMRW is heavily forested and has been extensively managed for over 150 years. Although the number of farms in the watershed has declined over the past 40 years (Buckland-Nicks, 1995), agricultural practices related to hay and cattle production continue to persist in the study area. Stands of fir (*Abies balsamea*) and spruce (*Picea* spp.) dominate due to past logging practices. Today, private woodlot management comprises a large proportion of all forestry activity. Riparian shrubs primarily consist of alder (*Alnus spp*.), hawthorn (*Crataegus* spp.) and cherry (*Prunus* spp.). Grasses (*Poacea* spp.) and sedges (*Carex* spp.) are prevalent along many sections of the river and its tributaries. Herbaceous vegetation is stand-dependent but is mainly composed of sensitive fern (*Onoclea sensibilis*), bracken fern (*Pteridium aquilinum*), swamp dewberry (*Rubus hispidus*), wood sorrel (*Oxalis acetosella*), bunchberry (*Cornus canadensis*) and strawberry (*Fragaria virginiana*).

The main river channel is highly dynamic, with water levels fluctuating by as much as four meters within a single year. Despite extensive land-use in the past, the river remains relatively clear and has a pH of 5.4 – 7.0 (Buckland-Nicks, 1995).

Human population density is typically low, although portions of the watershed are extensively used by fishermen and outdoor enthusiasts throughout the summer. See Table 1 for a further description of the study area.

The wood turtle is an omnivorous generalist, feeding on invertebrates, amphibians, birds, berries, mushrooms and herbaceous vegetation (Compton et al., 2002). Previous research has shown that wood turtles use a variety of aquatic and terrestrial habitats including wetlands, forests, meadows, clear-cuts and agricultural fields; however, rivers and streams typically serve as the base of operations for wood turtle populations (Compton et al., 2002; Arvisais et al., 2004;

Saumere et al., 2007; Greaves, 2007). In temperate regions, wood turtles spend nearly half of the year over-wintering on the bottoms of streams and rivers.

Population declines have been reported throughout the species' range, primarily in response to habitat loss, increased rates of adult mortality and collection for the pet trade (Garber & Burger, 1995; Daigle & Jutras, 2005; Saumere et al., 2007). Within the SMRW, vehicle- and machinery-related mortality are considered the greatest threats to population persistence. Recent research has indicated that the SMRW contains an exceptionally large population, perhaps the largest in the species' range (Biggar et al., unpublished manuscript).

Radio-telemetry

Nineteen adult wood turtles (11 females, 8 males) were caught opportunistically by hand from June 2005-May 2007 and equipped with 30-g Model AI-2F Holohil transmitters (Holohil Systems Ltd., ON, CA). Transmitters were attached to the posterior carapace of each turtle with a waterproof epoxy (Protective Coating Co., PA, USA). Transmitters weighed between 1.9 and 3.0 % of turtle body mass and did not inhibit movement or copulation (Saumere et al., 2007; R. Tingley, personal observation).

Turtles were visually located one to five times a week from April 18-October 18 2007 and the coordinates of each location were recorded using a Garmin 76CS or Garmin 76 GPS unit (Garmin Ltd., OR, USA) with an accuracy of ~5 m. Individual turtles accounted for between 3.9 and 6.4 % of all observations used to develop our habitat models.

To reduce the effect of dispersal limitations and seasonal resources on habitat selection patterns, turtle locations were paired with a random location that was assumed to be available to the animal between successive captures (Compton et al., 2002; Fortin et al., 2005). The inter-quartile range of movement rates from data collected on turtles in 2006 (7-36 m/day) was used to select a random movement rate for each day between relocations in 2007 (R. Tingley, unpublished data). Random points were based on a random movement rate and random bearing from the turtle's previous location (Fig. 1).

Field variables

Habitat data were sampled at terrestrial locations only to avoid confounding the influence of variables relating to food and cover (see Table 2 for variable descriptions). From a management perspective, sampling only terrestrial locations does not change our recommendations. Aquatic habitats are used for migration, mating, feeding, thermoregulation and overwintering; these areas must therefore be protected in terrestrial areas with a high probability of wood turtle occurrence. Furthermore, provincial and federal regulations already afford protection to aquatic habitats in Nova Scotia.

Field variables were chosen in part based on personal observations of wood turtle foraging behaviour and in part adopted from Compton et al. (2002). Percent cover of grasses, herbaceous vegetation and litter (deciduous leaves, dead grasses and shrubs) was estimated visually in four 0.3 m x 0.2 m quadrats surrounding each turtle and random location. Percent cover of herbaceous vegetation was recorded from the perspective of a turtle (i.e. all vegetation less than ~ 10 cm tall). Earthworms were sampled by digging a hole (~17 cm deep by ~10 cm square) at the perimeter of each of the four quadrats. We also recorded the presence or absence of mushrooms (a preferred food item) within 3m but did not use this variable in habitat models as mushrooms were ubiquitous in most habitat plots. Berries were only recorded as present in a plot if plants possessed ripe fruit (Compton et al., 2002). The presence of berries was not used in models for males as berries were present at only four percent of all locations. Percent cover of grasses (the field variable with the lowest explanatory power in preliminary analyses) was omitted for females to keep the number of field- and GIS-based variables equal. To reduce observer bias, the same individual (RT) collected all fine-scale habitat data.

GIS variables

Elevation, slope and aspect were derived from a 20-m digital elevation model of Nova Scotia (N. Deagle, personal communication). Land-cover data were provided by the Nova Scotia Department of Natural Resources (NSDNR) as a polygon coverage. The NSDNR database is the result of aerial photograph interpretation conducted in 1998. Updates based on field data and satellite imagery are conducted every one to three years. Despite being nearly ten years old, the NSDNR database is the highest-resolution forest coverage of Nova Scotia. The NSDNR database was updated by walking all small streams, permanent water bodies, recent clear-cuts and scrub-shrub riparian buffers bordering agricultural fields with a hand-held GPS unit.

To reduce the number of variables in the final analysis, the original land-cover classification consisting of over 40 categories was merged into six classes: i) coniferous, deciduous or mixed forest stands, ii) clear-cuts, iii) abandoned agricultural fields and orchards, iv) biannually harvested straw fields, v) wetlands and vi) scrub-shrub habitats (Table 1). Unfortunately, small sample sizes prevented the inclusion of clear-cuts for males (n = 1) and agricultural fields for females (n =10); locations falling within these habitat types were therefore reassigned to forest and field habitats, respectively. Small sample sizes coupled with the low prevalence of certain forest types in the study area also prevented a more fine-grained analysis of forest cover. The fact that Compton et al. (2002) were still able to develop a strong predictive model when different forest types were merged further justifies this decision.

Correlations between predictors

Linear (Grs, Ltr, Hrb) and logistic (Bry, Ald, Wrm) regressions were used to determine how much of the variation in the distribution of each fine-scale habitat variable could be explained by GIS-based predictors (see Table 2). All continuous response variables were square-root transformed prior to analysis. The final model for each fine-scale habitat variable was derived using a manual backward stepwise procedure based on F-tests (linear regression) or chi-square tests (logistic regression). For logistic regressions, model fit was assessed using the pseudo-adjusted-R^2 measure proposed by Weisberg (1980) (Guisan & Zimmermann, 2000).

Habitat selection analyses

Case-control (i.e. conditional or paired) logistic regression was used to determine which factors best differentiated turtle locations from matched control locations. A critical assumption of both ordinary and case-control regression is that observations are independent, an assumption that is typically violated in radio-telemetry studies. Such autocorrelation results in biases in the standard errors of parameter estimates (Fortin et al., 2005). Compton et al. (2002) described an approach to account for autocorrelation in which separate models are fit for each individual and selection is then tested across animals. However, this method may lack statistical power because it requires large sample sizes for each animal. Here we used an alternative approach in which a robust sandwich estimate of the covariance matrix is used to derive standard errors of each parameter estimate. This method requires the specification of clusters of correlated observations. In all analyses we assumed that observations from the same individual were correlated, whereas observations from different individuals were independent (Fortin et al., 2005).

Models were fit for males and females separately because preliminary analyses indicated that habitat selection differed between the sexes. For both sexes, scrub-shrub habitat and an aspect of 0 were used as reference categories in all models. The effects of different land-cover types and aspects are therefore relative to these types of habitats.

Distance to water (Wtr) was entered as a covariate in all candidate models for males because previous studies have shown that male wood turtles remain near rivers and streams throughout much of the year (Compton et al., 2002; Greaves, 2007; R. Tingley, unpublished data). Females typically remain near water in the spring and fall (Fig. 2), but are terrestrial throughout much of the summer; we therefore included an interaction between log(Wtr) and time of year in all models for females. Two-way interaction terms between environmental variables and time of year were included when temporal variation in resource selection patterns was suspected.

Model selection

The primary goal of this study was to determine whether habitat variables measured in the field were better predictors of wood turtle occurrence than variables derived from a GIS. Two types of models were therefore constructed: those containing only field-based variables and those containing only GIS predictors. Akaike's Information Criterion (AIC) was then used to rank models containing all possible combinations of field and GIS variables. We also constructed a model containing land-cover measured in the field to test whether this variable could be used as a catch-all measure for the various field-based variables. Because slope and elevation were highly correlated for males, we did not include both of these predictors in the same model. The size of the candidate set of models therefore differed slightly between males (n=55) and females (n=63).

Because the number of predictors (k) was large relative to the sample size ($n/k < 40$), we used a modified version of AIC (AIC_c) which further penalizes over-fitting. The final evaluation of different models was then carried out in three steps. First, we calculated Δ_i by subtracting the

AIC_c of each model from the model with the lowest AIC_c score (models with smaller AIC values have greater support). Second, we calculated the likelihood of each model ($g_{i,}$) given the data (y):

$$L(g_i | y) = \exp(-1/2\ \Delta i)$$

Third, we standardized likelihoods across all *R* models by dividing the likelihood of model *i* by the sum of all model likelihoods:

$$\omega_i = \frac{\exp(-1/2\ \Delta i)}{\sum_{j=i}^{R} \exp(-1/2\ \Delta i)}$$

These Akaike weights (ω_i) are equal to the probability that a given model provides the best fit to the data among the models considered (Johnson & Omland, 2004). For each sex, we calculated the set of models that comprised >95% of the Akaike weights. The relative importance of each variable was then calculated by summing the ω_i of models that contained a given predictor. Finally, we contrasted pairs of models using evidence ratios (ER). The ER is calculated by dividing the likelihood of the highest ranking model by the likelihood of model *i*. All statistical analyses were implemented in R© 2.6.1 (R Development Core Team, 2007). See Fortin et al. (2005) for an example of how to fit case-control models in R, S-Plus and SAS.

Visualizing model predictions

To visually assess our case-control models, we mapped the predicted relative probability of occurrence for female and male wood turtles throughout the study area at a 10-m resolution. Predictions were restricted to the 100% minimum convex polygon of all turtle locations to avoid extrapolating too far beyond the sampled environmental conditions. Because there were interactions between time of year and a number of GIS variables for females, we present predictions for three distinct activity periods roughly following those proposed by Arvisais et al. (2002; 2004): prenesting: May, nesting: June, post-nesting: July-October 1. By early October all females had returned to their spring ranges close to the river. Habitat suitability surfaces were produced by averaging predictions of occurrence for each day across all days within a given activity period. All spatial processing was done in Arcview 9.2 (ESRI, CA, USA).

RESULTS

Habitat data were sampled at 328 pairs of turtle and random locations (164 F, 119 M). All six field-based variables were significantly correlated with at least two GIS-based predictors. GIS variables explained between ca. 8 - 37 % of the variation in the occurrence and abundance of field-based variables (Table 3). The amount of herbaceous vegetation (Hrb) displayed the weakest relationship with GIS variables.

For females, field-based habitat models significantly outperformed models built using GIS data (Table 4). Comparisons between the top field-based and GIS-based models revealed that the field-based model was more than 70,000 times more likely to be the best model than the highest ranked GIS-based model. The interaction between distance to water and time of year was always highly significant. The best field model indicated that after controlling for the strong effects of distance to water, occurrence of female wood turtles was positively related to the amount of herbaceous vegetation and leaf litter. These two variables also had the highest relative importance values (Fig. 3).

However, the parameter estimates for leaf litter were typically non-significant. Overall, there was a large degree of model selection uncertainty. Models containing all three of the other field-derived variables (Bry, Wrm, Ald) were frequently represented in the 95% candidate set of models (Table 4).

Although land-cover was commonly selected in the 95% candidate set of GIS models for females, parameter estimates for this variable were typically not significant (Table 5). Replacing the GIS-based estimate of land-cover with an interaction between time of year and land-cover measured in the field substantially improved model fit. Parameter estimates for all four field-based land-cover types were significant (Table 6); we therefore used the coefficients of this model in the production of habitat suitability maps. After accounting for the effects of distance to water and aspect, this model indicated that female wood turtles selected scrub-shrub habitats in the spring, but became more terrestrial as the season progressed, selecting forests, fields, wetlands and regenerating stands over scrub-shrub habitats. However, the best field-based model was still 26 times more likely than the best GIS-based model using land-cover measured in the field.

In contrast to the results for females, models based on field data were relatively poor predictors of male occurrence (Table 7). The top ranked GIS model was greater than 70 times more likely to provide the best fit to the data than the highest ranked field-based model. Again, the effect of distance to water was highly significant in all models. Unlike the results for females, there was only moderate uncertainty in the selection of a single best model for males. A model containing distance to water, aspect, land-cover type and elevation was nearly three times more likely to be the best model relative to all other models considered. The latter three variables were also those with the highest relative importance values (Fig. 4).

Replacing the GIS-based definition of land-cover with land-cover measured at each precise location actually reduced model fit for males. The results of the top ranked GIS-based model indicated that males preferred scrub-shrub habitats over wetlands and forests. Males were commonly found in agricultural fields, although fields were not selected significantly more often than scrub-shrub habitats.

Because temporal interactions were forced into GIS-based habitat models for females and not males, we also ran a stepwise selection of predictors using AIC to test whether inclusion of these interactions was warranted. The best models selected by this stepwise procedure were identical to the highest ranking models reported here, lending further support to the observed temporal shifts in female resource selection.

DISCUSSION

From proxy to proximal

At a conceptual level, the causality of different environmental variables can be viewed as a gradient ranging from proximal to distal (Austin, 2007). Although we measured environmental variables thought to be causally related to the occurrence of wood turtles (i.e. proximal variables), there are a number of mechanisms that could explain our observations regarding the effects of field-derived predictors. For example, grass and herbaceous vegetation are both directly consumed by wood turtles, but may also serve as proxies for thermoregulatory needs. Indeed, the occurrence of female wood turtles displayed a curvilinear relationship with the amount of herbaceous vegetation, indicating that this variable had a positive effect on occurrence until a certain threshold was reached. Such a response may reflect a trade-off between resource acquisition and thermoregulation (Compton et al., 2002) or may simply be a result of feeding saturation.

The positive effects of leaf litter were also likely a result of both food and cover requirements. Strang (1983) found that leaf litter depth was positively associated with invertebrate abundance. Female wood turtles also bury themselves under leaf litter on hot summer days (R. Tingley, personal observation).

The effects of the presence of speckled alder are almost certainly indirect. Turtles may simply use alder swales because they typically border streams and rivers (Quinn & Tate, 1991) or because they provide important food items such as slugs, earthworms and herbaceous vegetation (Compton et al., 2002; Arvisais et al., 2004).

These results illustrate that sound inference in the presence of multicollinearity is always problematic. We acknowledge that in some cases the field-based predictors used here were unlikely to be causal drivers of wood turtle occurrence; however, our estimates of food and cover measured in the field were still likely to be more proximal than variables measured in a GIS, at least for females. The fact that we found strong interactions between time of year and several GIS variables for females would certainly suggest that GIS variables were merely serving as distal surrogates for important seasonal food resources. For example, earthworms are typically more abundant in the spring in low-elevation fields, while berries are more likely to be present in regenerating stands in upland areas in late summer.

Male wood turtles rarely occupied areas that contained berries but were often seen eating herbaceous vegetation, grasses and earthworms, suggesting that the effects of these variables were proximal for males as well. However, GIS-based models still considerably outperformed models built using fine-scale habitat data for males. In the following section we discuss this finding with reference to previous research, suggest a potential cause for this contradiction between males and females and explore the possible mechanisms underlying the proposed explanation.

Do we need fine-scale data to predict wood turtle occurrence?

Previous studies that have examined the relative roles of field- and GIS-based variables have mainly focused on the distributions of birds. Jeganathan et al. (2004) found that satellite imagery was a better predictor of the distribution of Jerden's courser (*Rhinoptilus bitorquatus*) than data collected in the field. Mitchell et al. (2001) and Betts et al. (2006) also found that models based on landscape variables performed equally well as models based on microhabitat characteristics and that the integration of both types of data only slightly improved predictive performance.

However, birds may be more likely to sample their environment at broader spatial scales than ectotherms, which rely on local habitat conditions to behaviourally thermoregulate (Harvey & Whitehead, 2006). Indeed, Harvey & Whitehead (2006) showed that habitat selection by massasauga rattle snakes (*Sistrurus c. catenatus*) at the landscape scale was dramatically reduced when macro-habitats were weighted by their availability of suitable micro-habitats. However, in this study, the effects of sex obscured the importance of micro-habitat data on habitat selection patterns.

What then was the cause of this disparity between males and females regarding the importance of fine-scale habitat data? We argue that spatio-temporal niche partitioning between the sexes was the most likely explanation. Females selected a variety of land-cover types and topographic positions in the summer, making it difficult for a static, GIS-based depiction of the landscape to accurately predict the occurrence of females at this time of year. However, within these macro-habitats, females often chose micro-habitats with high amounts of herbaceous vegetation, a variable that was only weakly correlated with GIS predictors (Table 3). Males on the other hand were fairly consistent in their selection of flat, low-elevation, riparian scrub-shrub habitat, and this consistency in turn led to the development of a strong GIS-based model. The need to remain close to water appears to generally restrict male wood turtles to the use of micro-habitats within narrowly defined riparian zones.

There are at least two hypotheses to explain the spatio-temporal niche partitioning between males and females observed here. Clearly reduced intra-specific competition is a potential mechanism. Males may feed mostly on riparian vegetation and aquatic resources, while females may feed primarily on berries, mushrooms and herbaceous vegetation (Foscarini & Brooks, 1997). If males do indeed rely more on aquatic prey, then this may explain why GIS-based variables were superior predictors of male occurrence as our estimates of food availability measured in the field were exclusively based on terrestrial resources.

Alternatively, because mating typically takes place in or near water, females may use upland habitats in the summer to avoid aggressive mating encounters with males (Greaves et al. 2007). Male wood turtles seek copulation throughout the year (R. Tingley, personal observation). Such encounters would reduce the amount of time and energy that females could devote to the acquisition of resources. Because females are aquatic in early spring and fall, avoidance of males in the summer would unlikely reduce reproductive success (female wood turtles are thought to be capable of storing sperm over the winter: Greaves, 2007). Aquatic breeding would also limit mating opportunities in upland areas, restricting males to the use of riparian habitats.

Taken as a whole, these results suggest that researchers may need to more carefully consider effects of sex on habitat selection patterns. Earlier studies of wood turtle habitat selection have failed to find significant differences between males and females (Compton et al., 2002; Greaves, 2007). This is puzzling given that the terrestrial migrations of females observed here are in line with the findings of previous studies that have examined the seasonal movements of wood turtles in other regions of North America (Kaufmann, 1992; Foscarini & Brooks, 1997;

Arvisais et al., 2002; Tuttle & Carroll, 2003; Remsberg et al., 2006). We suggest that the source of this disparity lies in the fact that earlier studies failed to account for both sexual and temporal variation in resource selection patterns. Spatial niche partitioning between males and females only became truly apparent when the effects of time were explicitly considered.

However, accounting for the effects of sexual and temporal variation in resource selection can quickly diminish statistical power. Furthermore, the need to account for these sources of variation is likely to diminish with increasing grain and extent. Nevertheless, our results demonstrate that incorporating both temporal and sexual variation in habitat models can provide further insight into the abiotic drivers of species distributions and potentially lead to more meaningful conservation recommendations at local scales.

From statistics to sustainability

The GIS-based models developed here show promise for identifying suitable male wood turtle habitat in the Saint Mary's River watershed. Our GIS-based models may also be used to identify high priority female habitat during the pre-nesting and nesting seasons; however, a visual examination of the predictions of our GIS-based models indicated the potential for high rates of omission error during the post-nesting period (see insets of Figs. 7 & 8). These errors appear to be in part due to the fact that time was treated as a continuous variable. As a result, interactions involving the effects of time led to the GIS-based model largely over-predicting the terrestrial migrations made by females in late summer. Indeed, predicted habitat suitability during the nesting period (June) was typically a better predictor of female occurrence in late summer and early spring than predicted habitat suitability during the corresponding post-nesting period (July-October; compare insets of Figs. 6 & 7).

Because the land-cover database used here was 10 years old, classification errors also likely reduced the discriminatory power of the GIS-based model. Ground-truthing land-cover data and collecting fine-scale habitat information may reduce rates of omission error, although recalibrating our models to new areas or timeframes is likely to be too expensive and time-consuming to be realistic in practice. The use of high-resolution (e.g. 1-m) land-cover data may be necessary to make robust predictions of female wood turtle occurrence throughout the species' annual activity cycle.

Conclusion

The results of this study suggest that broad generalizations regarding the importance of fine-scale habitat data are likely to be difficult. Even within a single species, we have shown that spatio-temporal niche partitioning between males and females can provide contradictory results. In reality, the utility of GIS-based habitat models is likely to depend on a number of factors including the accuracy of land-cover and topography data, the spatial grain and extent under investigation and the degree to which GIS variables can serve as adequate proxies for more causal limiting factors. Our results also demonstrate that intrinsic factors such as sexual or temporal variation in habitat selection can also influence the utility of GIS-based habitat models in conservation planning. We urge that researchers more carefully consider these caveats when predicting species distributions using GIS data at local scales.

ACKNOWLDEGEMENTS

This research was funded by the Nova Forest Alliance, Stora ENSO, the Elizabeth Wakeman Foundation, the Nova Scotia Habitat Conservation Fund, the Government of Canada Habitat Stewardship Program for Species at Risk, the Saint Mary's River Association, the Nova

Scotia Department of Natural Resources and an Acadia Graduate Award to RT. K. Krumb, L. Sweet and M. Lupek assisted with the field component of this research. B. Starzomski and D. Shutler helped revise an earlier version of this manuscript.

Table 1. Land-cover classes used in habitat models for wood turtles in the Saint Mary's River watershed, Nova Scotia, Canada.

Land-cover type	% of study area	Description
Wetland (Wet)	7.39	Any area that is inundated by surface- or ground-water for at least part of the year. Includes open and treed bogs, fens, marshes and swamps.
Agriculture (Agr)	8.52	Biannually harvested fields of straw or corn.
Field (Fld)	4.55	Abandoned agricultural fields and apple orchards. Typically mosaics of tall shrubs (e.g. *Alnus spp.*), woody herbaceous vegetation and short grasses.
Forest (Frt)	54.9	Coniferous, deciduous or mixed forest stands. Stands generally had high canopy closure and were greater than 10 years old.
Regenerating forest (Rgn)	9.96	Any forested area in the early stages of regeneration (typically < 10 years post-harvest). Includes clear-cuts, young plantations and Christmas tree farms with low total canopy closure.
Scrub-shrub (Reference)	8.53	Composed of non-merchantable tree species, primarily *Alnus*, *Crataegus* and *Prunus spp.*

Table 2. Habitat variables used to predict the distribution of wood turtles in the Saint Mary's River watershed, Nova Scotia, Canada.

Variable	Description
Field variables	
Bry [a]	Presence/absence of berries within 3m
Ald	Presence/absence of speckled alder (*Alnus rugosa*) within 3m
Wrm	Presence/absence of earthworms in four samples
Ltr	% cover of leaf litter in four 0.06 m^2 quadrats
Grs [b]	% cover of grasses in four 0.06 m^2 quadrats
Hrb	% cover of herbaceous vegetation in four 0.06 m^2 quadrats
Wtr [c]	Distance to water (m)
CvrF	Dominant habitat type within 3m
GIS variables	
Slp	Slope (%)
Asp	Aspect (5-level factor; **NULL**: 0˚, **N**: 0-45˚; 315-360˚, **E**: 45-135˚, **S**: 135-225˚, **W**: 225-315˚)
Elv	Elevation (m)
CvrG	Landcover type taken from NSDNR GIS database
WtrG [d]	Distance to water (m)
Sun	Incoming solar radiation from April 1 – November 1, 2007

[a.] Used in models for females only. Includes strawberries (*Fragaria virginiana*), raspberries (*Rubus* spp.) and blueberries (*Vaccinium* spp.).
[b.] Used in models for males only.
[c.] Estimated in the field if less < 10 m, otherwise estimated from GIS.
[d.] Only measured from GIS coverage of streams and open water.

Table 3. Correlations between field- and GIS-based habitat variables used to predict the distribution of wood turtles in the Saint Mary's River watershed, Nova Scotia, Canada. Table columns represent explanatory (GIS-based) variables, while rows represent response (field-based) variables that were used in linear (Ltr, Grs, Hrb) or logistic (Bry, Ald, Wrm) regression models. Parameter estimates for each GIS-based variable are shown as positive (+), negative (-) or quadratic (∩,∪). P-values are represented with asterisks (**** P < 0.001, *** P <0.01, ** P < 0.05, * P < 0.10) and refer to the null hypothesis that parameter estimates are not significantly different from zero.

		Aspect					Land-cover							
	Slp	E	N	S	W	Elv	Agr	Fld	Frt	Rgn	Wet	WtrG	Sun	Adjusted R-squared
Bry	-*	+	-***	+	+	∩**	-	-	+	+*	-	+*		23.1
Ald	+*	-	+	-**	+	∪***	-****	-****	-****	-****	-**		+**	24.7
Wrm	∪**					-***	+***	+**	-****	-***	+			22.5
Ltr	-****						-****	+	-**	-***	-	-***		21.8
Grs		-*	-****	-	+	∩***	+****	+**	-****	-****	+			36.8
Hrb						∩****	-	-	-	+**	-			7.68

Table 4. Number of parameters (k) and Akaike weights (ω_i) of habitat models for female wood turtles in the Saint Mary's River watershed, Nova Scotia, Canada. Because field models comprised > 95% of the Akaike weights, we present the 95% confidence set of models that used GIS predictors only. However, to keep comparisons between ω_i valid, we report the ω_i when both field and GIS models were considered.

Model (w =)	k	ω_i
Field models		
log(Wtr)*Date + log(Hrb) + Ltr	5	0.23
log(Wtr)*Date + log(Hrb) + Ltr + Bry	6	0.17
log(Wtr)*Date + log(Hrb) + Ltr + Ald*Date	7	0.11
log(Wtr)*Date + log(Hrb) + Ltr + Bry + Ald*Date	8	0.099
log(Wtr)*Date + log(Hrb) + Ltr + Wrm*Date	7	0.092
log(Wtr)*Date + log(Hrb) + Ltr + Bry + Wrm*Date	8	0.085
log(Wtr)*Date + log(Hrb)	4	0.039
log(Wtr)*Date + log(Hrb) + Ltr + Bry + Wrm*Date + Ald*Date	10	0.038
log(Wtr)*Date + log(Hrb) + Ltr + Ald*Date + Wrm*Date	9	0.035
log(Wtr)*Date + log(Hrb) + Bry	5	0.025
log(Wtr)*Date + log(Hrb) + Ald*Date	6	0.022
log(Wtr)*Date + log(Hrb) + Bry + Ald*Date	7	0.018
GIS models		
log(WtrG)*Date + Asp*Date + CvrG	15	$3.2*10^{-6}$
log(WtrG)*Date + Asp*Date + CvrG + Elv	16	$1.6*10^{-6}$
log(WtrG)*Date + Asp*Date + CvrG + Slp	16	$1.6*10^{-6}$
log(WtrG)*Date + Asp*Date + CvrG + Sun	16	$1.1*10^{-6}$
log(WtrG)*Date + Asp*Date + CvrG + Elv + Slp	17	$9.1*10^{-7}$
log(WtrG)*Date + Asp*Date + CvrG + Slp + Sun	17	$6.0*10^{-7}$
log(WtrG)*Date + Asp*Date + CvrG + Elv + Sun	17	$5.7*10^{-7}$
log(WtrG)*Date + Asp*Date + CvrG + Elv + Slp + Sun	18	$3.0*10^{-7}$
log(WtrG)*Date + CvrG	7	$1.8*10^{-7}$
log(WtrG)*Date + CvrG + Sun	8	$1.6*10^{-7}$
log(WtrG)*Date + Asp*Date	11	$1.0*10^{-7}$
log(WtrG)*Date + Asp*Date + Elv	12	$1.0*10^{-7}$

Table 5. Parameter estimates, standard errors and P-values for the highest ranking GIS-based model of female wood turtle occurrence in the Saint Mary's River watershed, Nova Scotia, Canada. Estimates of land-cover in this model were taken from the Nova Scotia Department of Natural Resources GIS database. The effect of date was not estimated as it was a matching variable that was used in interactions only.

Variable	Coefficient	SE (Coefficient)	P
log(Wtr)	-521	145	0.000330
East	-2120	924	0.0220
North	-2740	117	0.0190
South	-2810	923	0.00240
West	-1780	925	0.0540
Field	-0.543	0.521	0.300
Forest	-0.996	0.639	0.120
Regenerating	1.69	1.16	0.140
Wetland	-0.556	1.01	0.580
Time*log(Wtr)	0.0132	0.00370	0.000340
Time*East	0.0540	0.0235	0.0220
Time*North	0.0699	0.0299	0.0190
Time*South	0.0715	0.0235	0.00240
Time*West	0.0454	0.0236	0.0540

Table 6. Parameter estimates, standard errors and P-values for the highest ranking GIS-based model for female wood turtle occurrence in the Saint Mary's River watershed, Nova Scotia, Canada. Estimates of land-cover in this model were taken from data recorded in the field. Also note that this model contains interactions between time of year and each land-cover type, while the model presented in Table 5 does not. The effect of date was not estimated as it was a matching variable that was used in interactions only.

Variable	Coefficient	SE (Coefficient)	P
log(Wtr)	-808	265	0.00230
East	-3930	1830	0.0320
North	-5080	2240	0.0230
South	-5050	1890	0.00770
West	-3630	1730	0.0360
Field	-3080	612	$4.60*10^{7}$
Forest	-2970	704	$2.40*10^{5}$
Regenerating	-2140	1080	0.0480
Wetland	-3480	1080	0.00130
Time*log(Wtr)	0.0260	0.00675	0.00230
Time*East	0.100	0.0466	0.0320
Time*North	0.129	0.0571	0.0230
Time*South	0.129	0.0483	0.00770
Time*West	0.0926	0.0442	0.0360
Time*Field	0.0786	0.0156	$4.6*10^{-7}$
Time*Forest	0.0757	0.0179	$2.40*10^{5}$
Time*Regenerating	0.0546	0.0275	0.0480
Time*Wetland	0.0886	0.0276	0.00130

Table 7. Number of parameters (k) and Akaike weights (ω_i) of habitat models for male wood turtles in the Saint Mary's River watershed, Nova Scotia, Canada. Because GIS models comprised > 95% of the Akaike weights, we present the 95% confidence set of models that used field predictors only. However, to keep comparisons between ω_i valid, we report the ω_i when both field and GIS models were considered.

Model (w =)	k	ω_i
Field models		
Wtr + Hrb + Grs + Ltr + Wrm	5	$9.2*10^{-3}$
Wtr + Hrb + Grs + Ltr	4	$5.7*10^{-3}$
Wtr + Hrb + Grs + Ltr + Wrm + Ald	6	$3.3*10^{-3}$
Wtr + Hrb + Grs + Ltr + Ald	5	$2.0*10^{-3}$
Wtr + Hrb + Grs + Wrm	4	$3.3*10^{-4}$
Wtr + Wrm	2	$2.6*10^{-4}$
Wtr + Hrb + Wrm	3	$2.0*10^{-4}$
Wtr + Grs + Wrm	3	$1.8*10^{-4}$
Wtr +Ltr +Grs + Wrm	4	$1.7*10^{-4}$
GIS models		
WtrG + Asp + CvrG + Elv	9	0.65
WtrG + Asp + CvrG + Elv + Sun	10	0.23
WtrG + Asp + CvrG + Slp	9	0.027
WtrG + CvrG + Elv +Sun	6	0.022
WtrG + Asp + CvrG	8	0.020

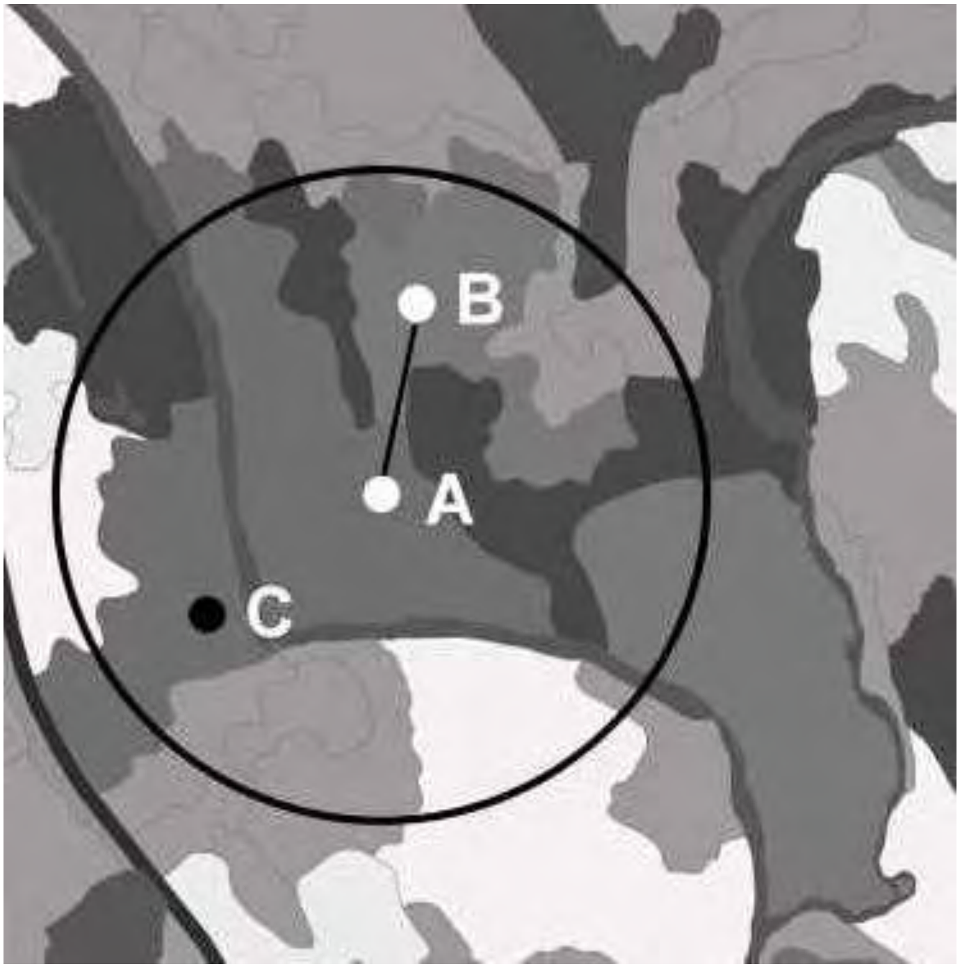

Figure 1. Hypothetical example of the method used to sample available wood turtle habitat in the Saint Mary’s River watershed, Nova Scotia, Canada. All points within a certain radius of the animal’s previous location (point A) are assumed to be available before the animal selects point B. The habitat at point B is then compared to that which is available at point C (see METHODS for a description of how radius size was chosen).

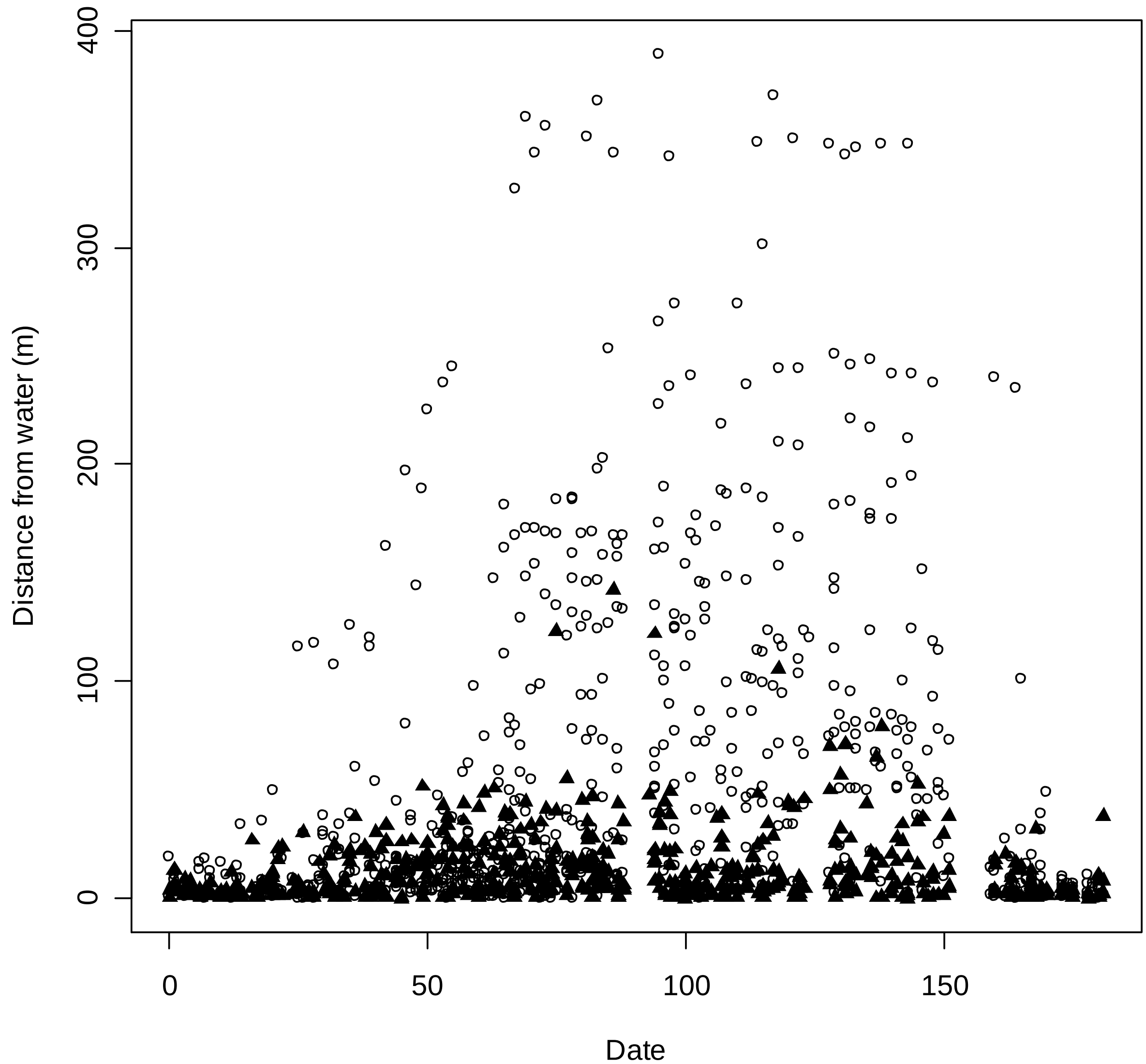

Figure 2. Terrestrial movements made by male (triangles) and female (circles) wood turtles in the Saint Mary's River watershed, Nova Scotia, Canada. Date

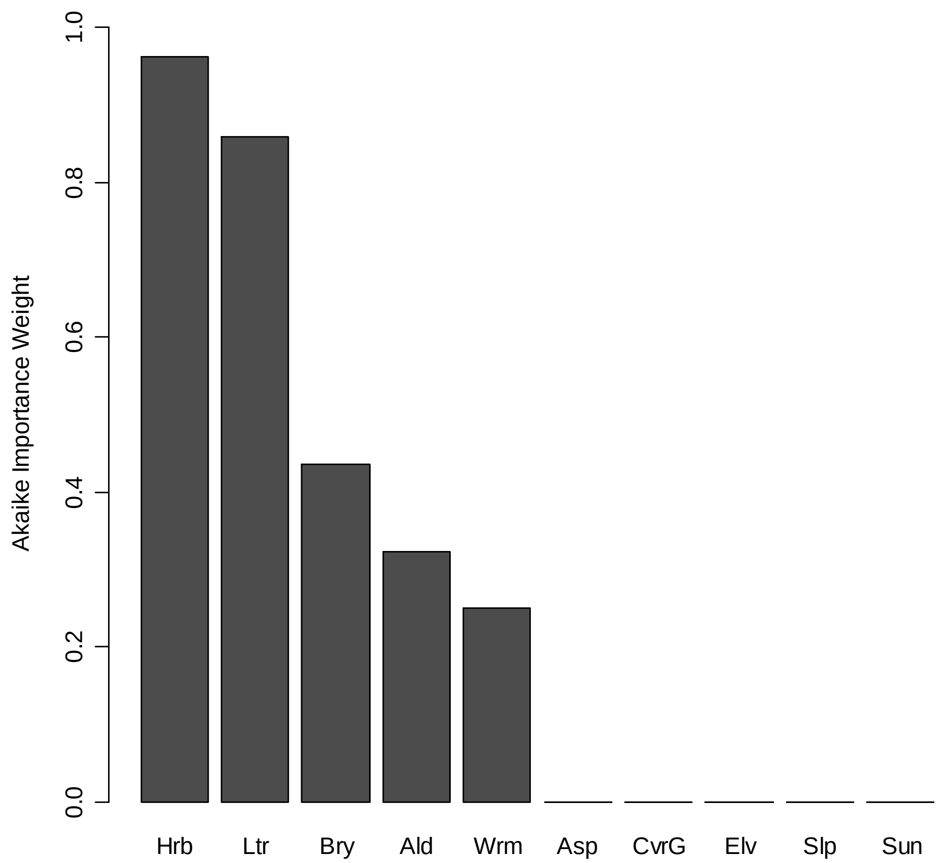

Figure 3. Akaike importance weights for the ten variables used in the construction of habitat models for female wood turtles in the Saint Mary's River watershed, Nova Scotia, Canada.

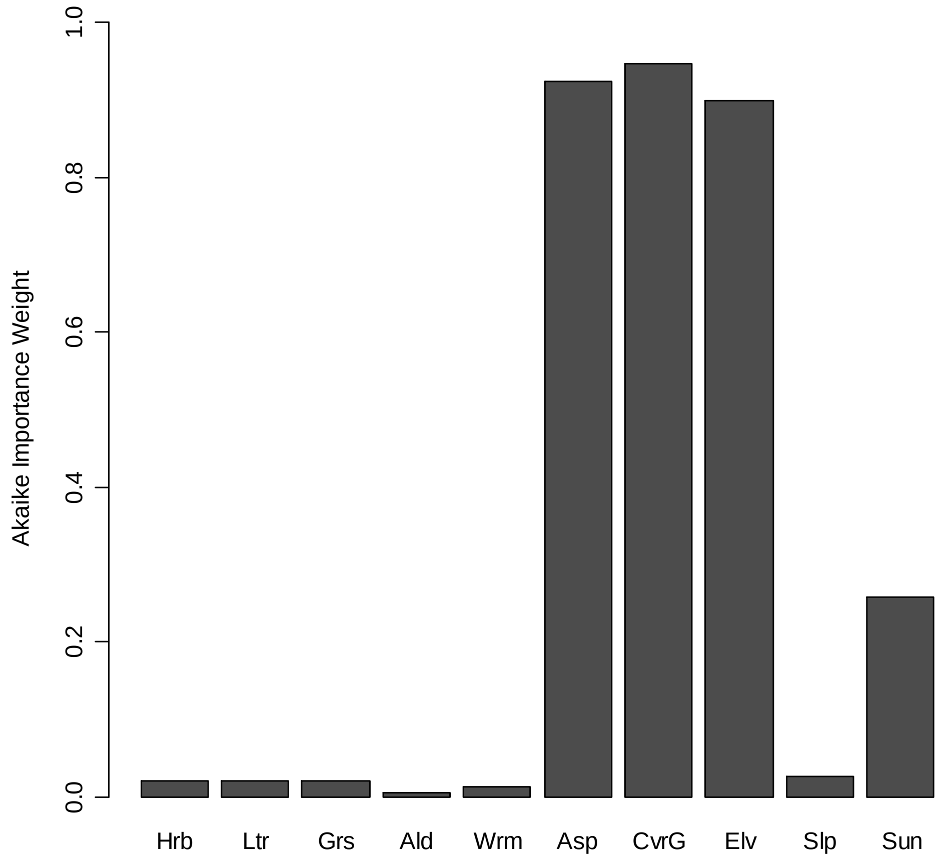

Figure 4. Akaike importance weights for the ten variables used in the construction of habitat models for male wood turtles in the Saint Mary's River watershed, Nova Scotia, Canada.

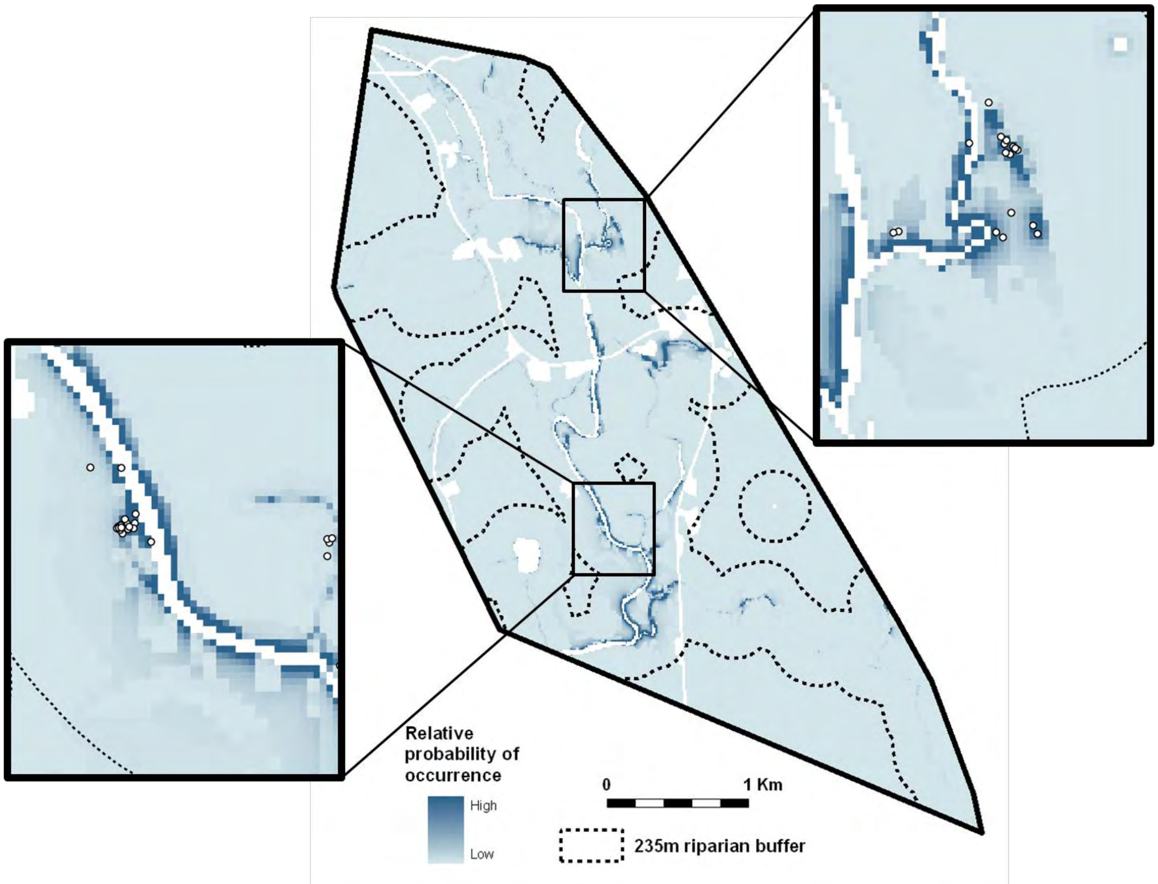

Figure 5. Predicted relative probability of occurrence of female wood turtles during May in the Saint Mary's River watershed, Nova Scotia. White areas represent land-cover types that were outside of the environmental domain of model calibration. White dots shown in pull-out boxes represent sightings of female wood turtles in May, 2006 and 2007. These occurrences were not used in model development.

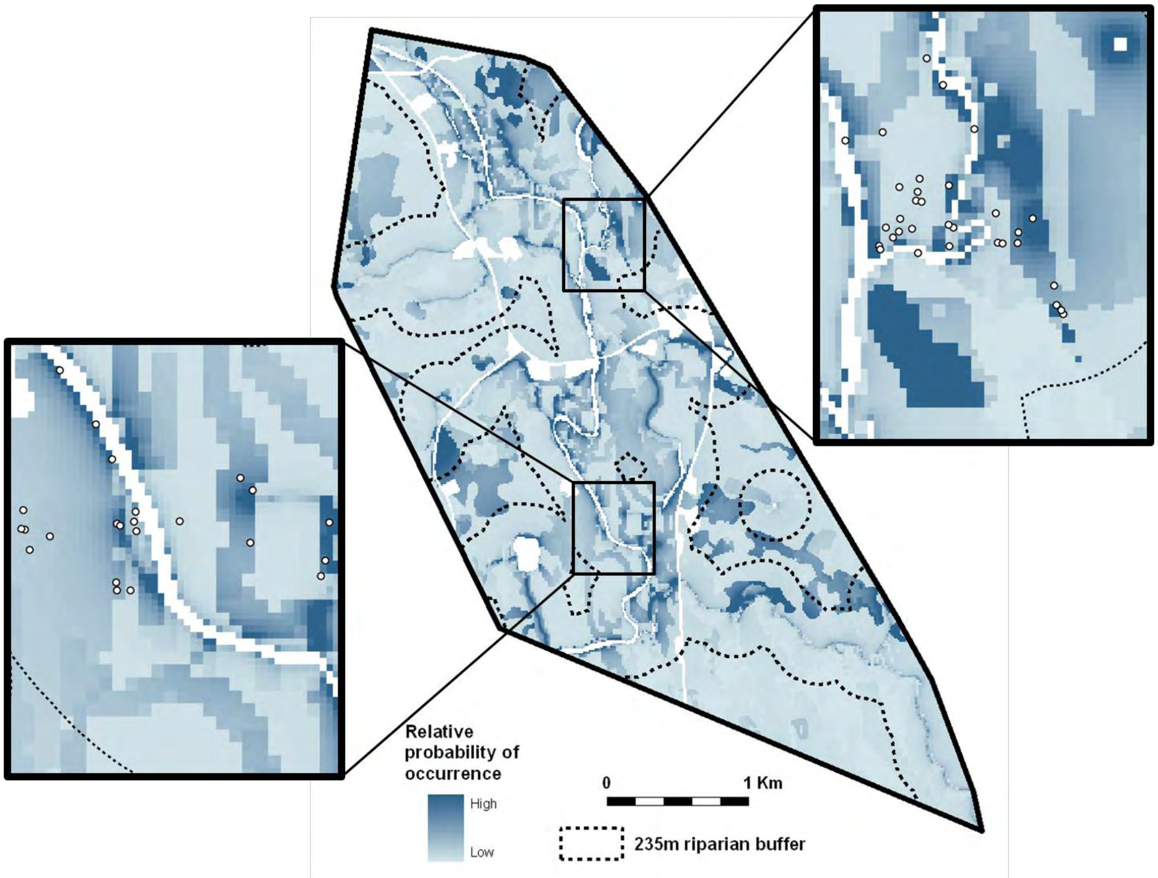

Figure 6. Predicted relative probability of occurrence of female wood turtles during June in the Saint Mary's River watershed, Nova Scotia, Canada. White areas represent land-cover types that were outside of the environmental domain of model calibration. White dots shown in pull-out boxes represent sightings of female wood turtles in June, 2006 and 2007. These occurrences were not used in model development.

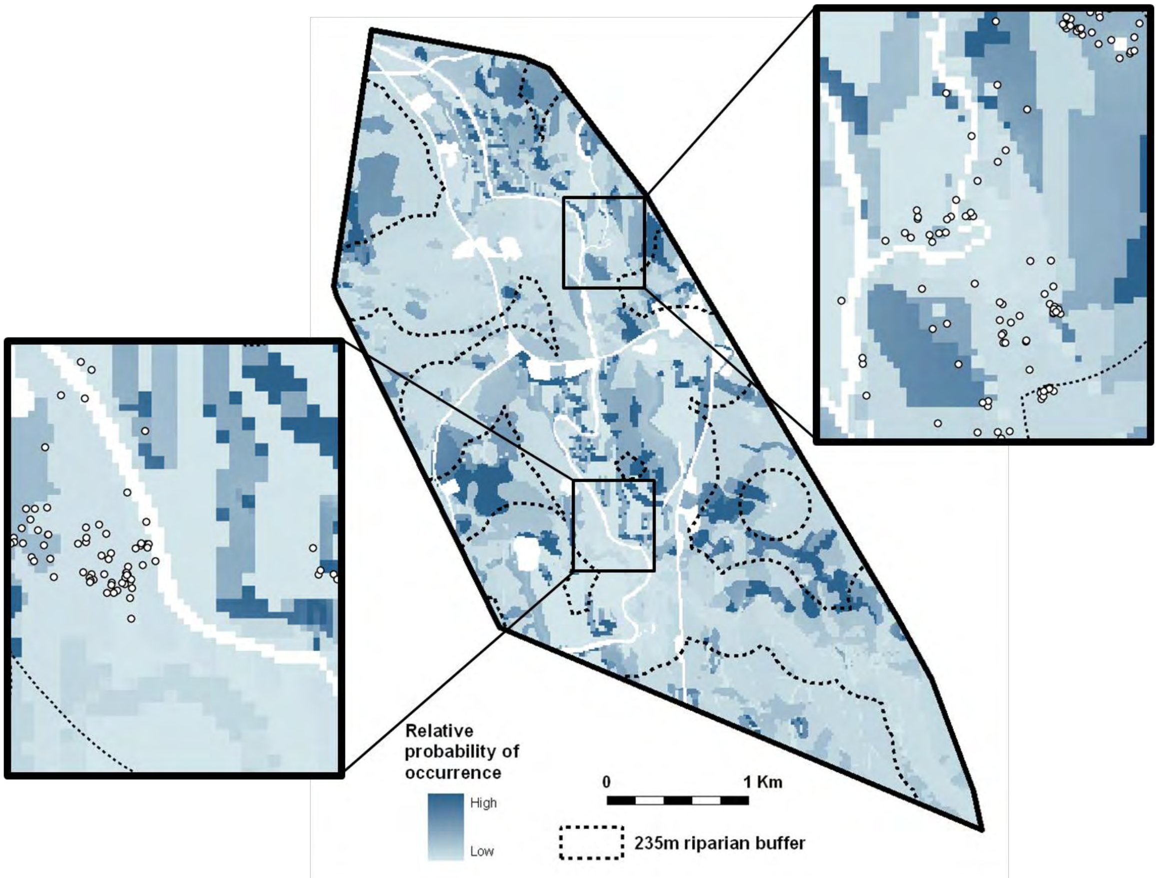

Figure 7. Predicted relative probability of occurrence of female wood turtles from July 1 to September 31 in the Saint Mary's River watershed, Nova Scotia, Canada. White areas represent land-cover types that were outside of the environmental domain of model calibration. White dots shown in pull-out boxes represent sightings of female wood turtles from July 1 to September 31, 2006 and 2007. These occurrences were not used in model development.

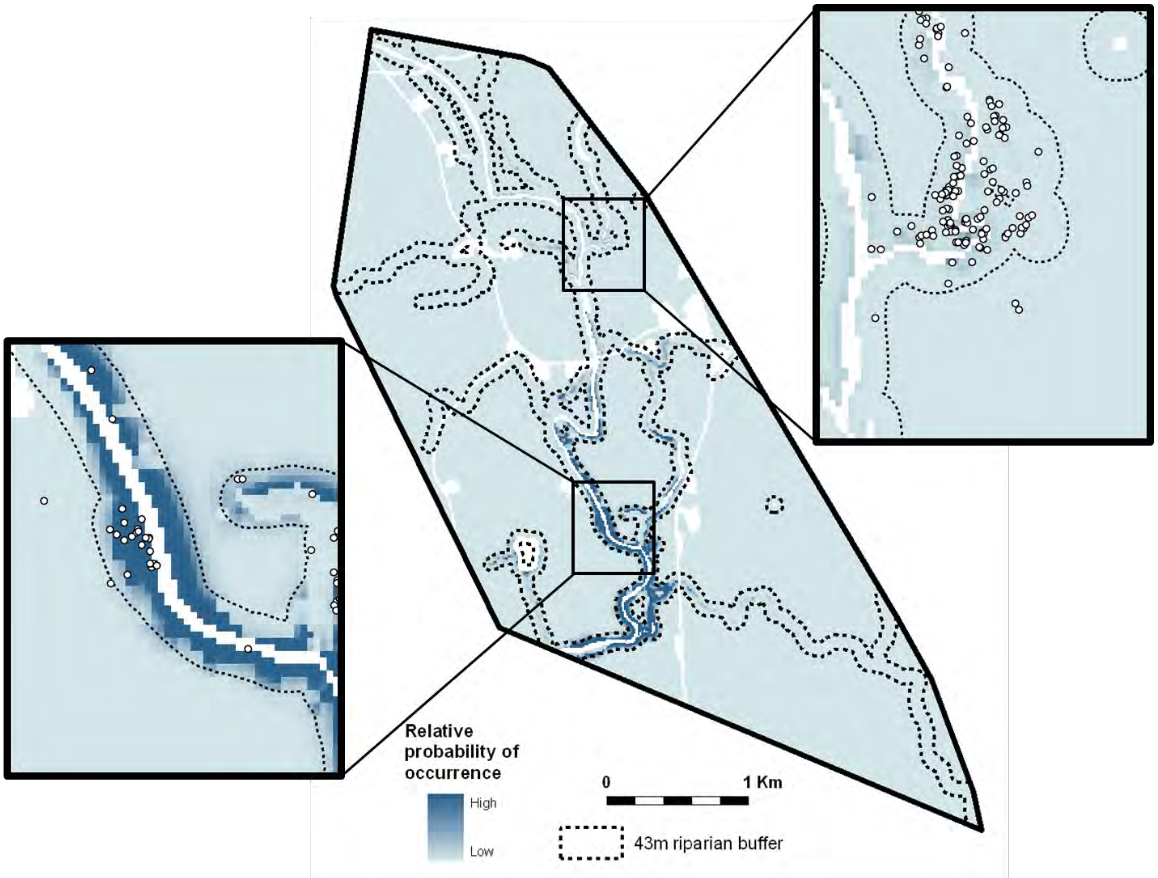

Figure 8. Predicted relative probability of occurrence of male wood turtles in the Saint Mary's River watershed, Nova Scotia, Canada. White areas represent land-cover types that were outside of the environmental domain of model calibration. White dots shown in pull-out boxes represent sightings of male wood turtles in 2006 and 2007. These occurrences were not used in model development.

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