



Effects of habitat loss, habitat configuration and matrix composition on declining wetland species



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ABSTRACT

Worldwide declines in wetland birds and turtles are attributed to landscape-scale habitat loss, habitat fragmentation and anthropogenic land use. However, due to multi-collinearity, the relative importance of these factors is largely unknown. We evaluated the relative effects of wetland amount, wetland configuration (measured as the number of wetland patches), and matrix composition (measured as the amount of forest, cropland and road density) on the occurrence of eight declining wetland bird species and two threatened freshwater turtles across 66–70 landscapes. We selected landscapes to minimize correlations among the landscape-scale predictors and to represent the range of variation in each predictor available in the study region. For wetland birds, we found that the amount of wetland at a landscape-scale was more important than the other landscape variables, whereas surprisingly for turtles, the amount of forest in the surrounding landscape was more important than the other landscape variables. Wetland configuration independent of wetland amount was not an important predictor of any species. This is the first study to assess the relative, independent effects of the landscape-scale factors thought to contribute to wetland bird and turtle declines. Our results confirm that wetland loss is the primary landscape-scale factor of wetland bird declines, but suggest that forest loss may play a greater role in freshwater turtle declines than previously realized; minimizing forest loss will have the most positive outcome for freshwater turtle conservation. Therefore, effective conservation planning requires a multi-taxa approach to meet landscape-scale requirements of all declining wetland fauna.

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1. Introduction

Worldwide declines of wetland birds and turtles are attributed to wetland loss and fragmentation at a landscape-scale, with anthropogenic land-uses such as roads and development also implicated (Millennium Ecosystem Assessment, 2005). However, the relative contributions of these landscape-scale predictors remain unclear. Wetland birds and turtles have received considerably less attention than other taxa (e.g., amphibians) in landscape ecology, and the effects of landscape structure on their abundance and distribution are less well understood (Attum et al., 2008; Joyal et al., 2001; Tozer et al., 2010; Semlitsch and Bodie, 2003).

Habitat loss generally has strong negative effects on species distribution and abundance relative to weaker and variable effects of habitat fragmentation (Fahrig, 2003). In wetland ecosystems, the loss of wetland habitat has strong negative effects (e.g., Naugle et al., 2001; Tozer et al., 2010). Strong negative effects of wetland isolation (e.g.: Joyal et al., 2001; Smith and Chow-Fraser, 2010; At-

tum et al., 2008; Shriver et al., 2004) are also reported for wetland birds and turtles, and these are often reported as fragmentation effects. However, estimating the separate effects of wetland loss and wetland fragmentation is difficult because they are typically strongly correlated (Fahrig, 2003). Therefore, the current understanding of the relative importance of habitat loss and fragmentation for wetland birds and turtles is limited.

In addition to the loss and fragmentation of habitat, the composition of the intervening space between habitat (or matrix composition) can also influence species abundance and distribution (Fahrig, 2001; Prugh et al., 2008). The amount of forest cover, agriculture and roads surrounding wetlands have all been suggested to affect wetland birds and turtles. Forest cover is generally expected to be a positive matrix element (Alsfeld et al., 2010). For turtles, upland forest surrounding wetland is important for movement and refugia (i.e.: short-term inactivity; Buhlmann and Gibbons, 2001). Farmland is generally expected to have negative impacts due to increased dispersal mortality (Saumure et al., 2007), reduced wetland quality from nutrient and pollutant runoff (Sterrett et al., 2011), and wetland infilling from sedimentation (Naugle et al., 2001). Lastly, roads generally have negative effects on wildlife populations (Rytwinski and Fahrig, 2012),

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either due to mortality or road avoidance behavior. However, these matrix composition variables can also be correlated with wetland loss and/or fragmentation (e.g.: landscapes with high agriculture often have high wetland loss) or with each other (e.g.: landscapes with low forest cover often have low road density).

Correlations among landscape predictors (multi-collinearity) may confound inferences about the effects of wetland loss, wetland fragmentation and/or matrix composition. For example, Findlay and Houlahan (1997) were not able to determine whether forest cover or road density was the main driver of landscape effects on wetland biota, due to the high correlation between these two variables. High multi-collinearity reduces statistical power and causes the estimation of regression coefficients to be highly error-prone, leading to variability in the estimated direction and magnitude of effects (Eigenbrod et al., 2011). A possible example is the wide range of reported effects of forest cover on wetland birds (e.g., positive, Alsfeld et al., 2010; negative, Budd and Krementz, 2010; no effect, Findlay and Houlahan, 1997).

It may not be possible to avoid multi-collinearity altogether in landscape ecology studies because the underlying processes causing landscape patterns are often linked. However, a comparative mensurative experimental approach which requires a priori selection of landscapes can minimize these correlations, allowing the estimation of separate effects (Fahrig, 2003). We hypothesize that multi-collinearity among landscape-scale variables has not yet been adequately addressed in previous investigations of the effects of landscape structure on wetland birds and turtles. Therefore the relative importance of the major landscape variables causing declines in these species is largely unknown.

While the literature to date suggests that any or all of wetland loss, fragmentation and matrix composition could explain declines in wetland birds and turtles, in a management context it is important to know their relative effects. Landscape-scale variables represent competing landscape-scale management options that could be applied independently of one another. Therefore, estimating their relative effects would help prioritize future conservation management action. For example, if wetland biota respond negatively to wetland fragmentation (independent of wetland loss) then wetland policies should focus specifically on conserving and restoring large wetlands. Because multi-collinearity can confound inferences about species responses to landscape structure and misguide management recommendations, studies with landscape planning or species recovery applications must disentangle the estimated effects of landscape-scale predictors.

Our objective was to determine the relative effects of wetland loss (measured as wetland amount, i.e.: the proportion of wetland area within a landscape), wetland configuration (measured as the number of wetland patches in the landscape) and matrix composition (measured as the amounts of each of forest, agriculture and road density in the landscape) on the occurrence of declining wetland birds and turtles. To do this we used a comparative mensurative experimental approach, wherein we sampled a set of landscapes specifically selected for low multi-collinearity among these landscape variables and to represent the range of variation in each variable in the study area. Previous studies typically refer to fragmentation as both the loss and breaking apart of habitat. In this study, we assessed habitat fragmentation per se (Fahrig, 2003), i.e. an aspect of the spatial configuration of wetlands independent of wetland loss. To avoid confusion over this distinction, we use the term “wetland configuration” rather than fragmentation. We estimated species presence of declining wetland birds and turtles in 66–70 landscapes (depending on the species group), varying in wetland amount and configuration, and in matrix composition.

2. Methods

2.1. Study area

The study was conducted in the Thousand Islands ecosystem in southeastern Ontario, Canada, which is a ~2000 km² watershed that drains into the St. Lawrence River (Fig. 1). The rural study area is characterized by 33% forest cover, 20% cropland, 14% pasture and field, 10% wetlands, 22% open water and 1% urban development. This landscape composition is typical of rural northeastern North America (e.g.: Saumure et al., 2007); however there is less cropland in our study area, possibly due to localized reforestation. Forest is deciduous and mixed, and cropland is primarily corn, hay and soy. There are 5 wetland types (Ecological Land Vegetation classification for southern Ontario, OMNR, 2009): (1) shallow open aquatic (water depth <2 m), dominated by floating aquatic vegetation (lily pads; *Nymphaea odorata* and *Nuphar variegata*), and submerged macrophytes (e.g., *Potamogeton* spp.), (2) emergent marsh, dominated by cattail (*Typha* spp.), (3) shrub thicket swamp, primarily willow (*Salix* spp.) and alder (*Alnus* spp.), (4) deciduous swamp, dominated by maple (*Acer* spp.) and ash (*Fraxinus* spp.), and (5) mixed swamp, consisting of maple and white cedar (*Thuja occidentalis*).

2.2. Species groups and specific wetland habitats

We identified habitat for each species group, from the five wetland types in our study area (Sub section 2.1), based on known habitat associations of the species; wetland types were used for habitat identification only.

2.2.1. Wetland birds

We selected 8 wetland bird species that are declining in our region (Crewe et al., 2005): red-winged blackbird (*Agelaius phoeniceus*), swamp sparrow (*Melospiza georgiana*), marsh wren (*Cistothorus palustris*), American coot (*Fulica americana*), common Moorhen (*Gallinula galeata*), sora (*Porzana carolina*), virginia rail (*Rallus limicola*) and least bittern (*Ixobrychus exilis*). Least bittern is designated threatened in Canada and is considered at-risk in 36 US states (NatureServe, 2012). Wetland types identified as habitat for wetland birds were emergent marsh or shrub thicket swamp (i.e., wetland types 2 or 3; Sub section 2.1) (Bannor and Kiviat, 2002; Eddleman et al., 1988; Gibbs et al., 2009; Mowbray, 1997). We excluded wetland patches <0.4 ha (Gibbs et al., 2009).

2.2.2. Turtles

We selected two declining freshwater turtle species. Blanding's turtle (*Emydoidea blandingii*) is designated as threatened in Canada and considered at-risk in 14 of the 15 states in the US within its range (NatureServe, 2012). Eastern musk turtle (*Sternotherus odoratus*; hereafter ‘musk turtle’) is designated as threatened in Canada and considered at-risk in three US states (NatureServe, 2012). Wetland types identified as wetland habitat for Blanding's turtle were shallow open aquatic wetland adjacent to any other wetland type (i.e., wetland types 1 and 2 or 3 or 4 or 5, Sub section 2.1) (Joyal et al., 2001; Sajwaj and Lang, 2000). For musk turtle, shallow open aquatic wetland (i.e., wetland type 1, Sub section 2.1) located on a lake or river network (Edmonds and Brooks, 1996; Picard et al., 2011) was identified as wetland habitat.

2.3. Study design and landscape selection

Here we define “landscape” as the spatial area within which the landscape variables were calculated (i.e.: spatial scale). We based landscape size on movement distances and home range estimates

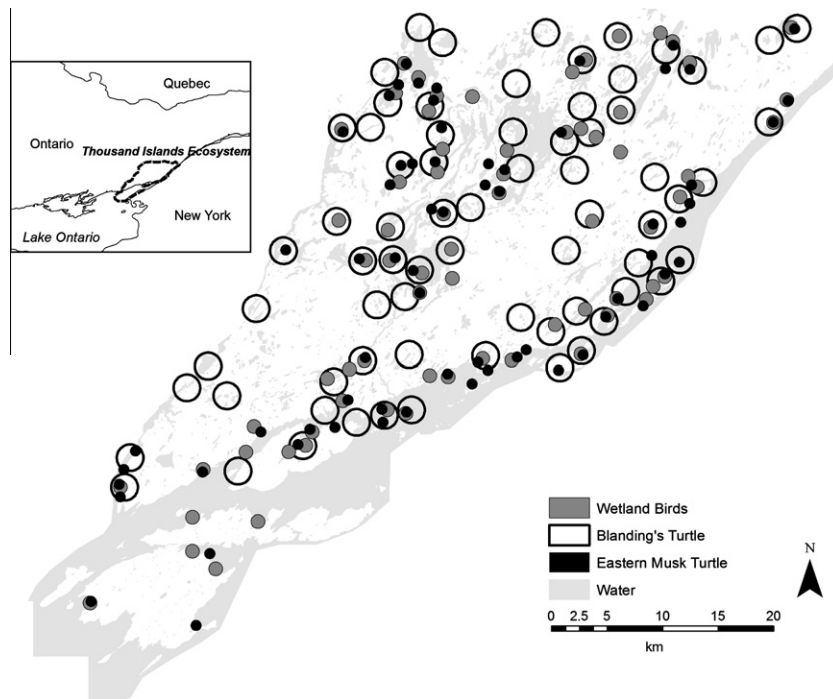


Fig. 1. Distribution of landscapes sampled across the Thousand Islands ecosystem ($\sim 2000 \text{ km}^2$) study area in southeastern Ontario, Canada. Landscapes were defined as the area within a 625 m radius for wetland birds ($n = 70$ landscapes), a 1.2 km radius for Blanding's turtle (*Emydoidea blandingii*) ($n = 70$ landscapes), and a 500 m radius for eastern musk turtle (*Sternotherus odoratus*) ($n = 66$ landscapes).

from radio-telemetry studies for each species group (Jackson and Fahrig, 2012; Table A1). Landscapes were circles having a 625 m, 1.2 km and 500 m -radius for wetland birds, Blanding's turtle and musk turtle, respectively.

We characterized the landscape structure of the study area to assess collinearity among landscape variables prior to landscape selection. Twelve candidate landscape variables were selected to represent: (1) wetland amount, (2) wetland configuration (total wetland edge, mean wetland nearest neighbor distance, number of wetland patches, wetland perimeter-area ratio, mean wetland patch size) and (3) matrix composition (agriculture, pasture and field, forest, open water, and road density). All landscape variables were quantified from the Ontario Land Cover dataset (OMNR, 2003), except wetlands (OMNR, 2009; Sub section 2.1), and analyzed in Fragstats 3.3 and ArcGIS 9.3. We used a moving window analysis across the study area to measure each candidate variable such that the size of the window matched the landscape size selected for each species group (625 m, 1.2 km and 500 m; above). We then performed principal components analyses (varimax rotation) on a random subset of 1000 landscapes for each species group. The first 5 principal components explained 81–85% of the total variation in landscape structure in the study area. We selected one landscape variable from each orthogonal principle component based on the strongest factor loadings and ecological rationale for wetland species: (1) wetland amount (area (ha) of wetland habitat as identified for each species group within a landscape; Sub sections 2.2.1 and 2.2.2), (2) number of patches (the number of wetland habitat patches within a landscape) as a measure of wetland configuration, and three variables to measure matrix composition, (3) forest amount (area (ha) of forest cover in a landscape), (4) agriculture amount (area (ha) of cropland cover in a landscape), (5) road density (total length of all road types divided by the total area of the landscape (km/km^2)). Using only one variable for wetland amount and wetland configuration, versus three

variables for matrix composition might imply that our study was biased in favor of finding matrix effects. However, we suggest the inclusion of three matrix variables was justified because the summed variation in landscape structure explained by the three matrix variables was similar to the proportions of the variation explained by each of the other two variables (Table A2).

We used a randomized stratified sampling design to select 100 non-overlapping landscapes for each species group and to minimize multi-collinearity among the five landscape variables. For landscape selection, we defined three strata for each variable, based on the proportion of area or density of that variable within a landscape (e.g., wetland amount: 0–30% “low”, 31–70% “medium” and 71–100% “high”). To the extent possible, an equal number of landscapes were selected per stratum. To avoid a correlation between wetland amount and configuration, we ensured that all possible combinations of the two variables were sampled; this required searching specifically for landscapes with unusual combinations, e.g., high wetland amount with high number of patches, or low wetland amount with low number of patches. We then conducted site visits of each candidate landscape to verify wetland type (Sub section 2.2) and obtain landowner permission for wetland access. This resulted in a final set of 70 landscapes for wetland birds, 70 landscapes for Blanding's turtle and 66 landscapes for musk turtle. In each final set of landscapes, we sampled the full range in variation of each landscape variable, with the exception of the high stratum for agriculture amount (i.e.: 71–100% cropland area in a landscape). The number of wetland patches ranged from 1 to 9 patches in landscapes for wetland birds and 1 to 8 patches in landscapes for both turtle species. Road densities in landscapes ranged from 0 to 9 km/km^2 for wetland birds, 0 to 5.7 km/km^2 for Blanding's turtle, and 0 to 8.7 km/km^2 for musk turtle. For all species groups, all pair-wise correlations between landscape variables in selected landscapes were $r < 0.46$ and variance inflation factors (VIF) < 3.2 (Tables A3 and A4).

2.4. Field surveys

The aim of the field surveys was to determine whether a landscape was occupied by a focal wetland species. We surveyed wetland within in each landscape, beginning at the center of the landscape, to determine presence/non-detection, given that we expected low abundance for rare species. For all species groups, we used time-limited surveys to standardized effort across landscapes; travel time between wetlands was excluded from search effort. We were not able to search the entire wetland area of each landscape, or to conduct repeat visits due to logistical constraints. A common challenge of landscape ecology studies is to obtain a sufficient sample of the landscape-scale predictors of interest, across the range of each predictor, while sampling at large spatial scales. To obtain sufficient statistical power to detect independent effects of several landscape variables, we needed to sample a large number of landscapes, here 66–70 landscapes. To achieve this, we spread the sampling over 2 years, 2009 and 2010, with approximately half of the landscapes surveyed in each year; each landscape for each species group was surveyed once.

A potential limitation of this sampling approach is that we are unable to estimate and statistically control for detection probability of each species. However, we designed our field methods to maximize detection probability and minimize potential sources of bias in detectability to the extent possible (Sub sections 2.4.1 and 2.4.2). For wetland birds, we used call-broadcast surveys which are demonstrated to significantly increase detection probabilities of secretive wetland birds; we selected call-broadcast frequencies tailored to each species. For Blanding's turtle, we used visual surveys when basking turtles are highly detectable, and for musk turtles, we used active short-range searches. These methods are the most effective, given that we could not conduct trapping, which would have required multiple visits to multiple wetlands in each landscape, a logistical impossibility. In fact, preliminary tests of baited traps were completely unsuccessful for musk turtle. We also minimized variation in detectability across landscapes by restricting sampling to correspond with reported activity periods (e.g.: breeding, spring basking) for each species group in our study region to limit seasonal variability. Overall, in the trade-off between the number of visits vs. the number of landscapes, we chose to maximize the number of landscapes surveyed, but we used survey protocols tailored to maximize detection probabilities of each species group.

To avoid spatio-temporal correlations in our results, we sampled landscapes following a randomized block design wherein the study region was divided into four spatial blocks (north, west, east, south), containing equal numbers of study landscapes. The sequence of landscape sampling was then determined by rotating through the four blocks and, within each, randomly selecting a landscape for sampling.

2.4.1. Wetland bird surveys

We sampled wetland birds using time-limited (1.5 h) auditory surveys with call-broadcasts. Call-broadcasts significantly increases detection rates for most rails (e.g.: by 65% for virginia rail; Conway and Gibbs, 2005) and five call-broadcasts improves detection of least bittern (by 80%; Bogner and Baldassarre, 2002). Our sampling protocol was a modified combination of the Marsh Monitoring Program (MMP, 2009) and the National Least Bittern Survey (Jobin et al., 2009) protocols. In each landscape, we established 1–5 sample points in wetland habitat at least 50 m from the landscape edge and at least 250 m apart. The number of sample points increased with the amount of wetland in the landscape. Five sample points (totaling 1.5 h) was the maximum number logistically possible during the sampling time from sunrise and 10 h00. At each sample point, we conducted the following 18 min survey: (1)

1 min pre-survey silence, (2) 5 min unlimited-radius auditory survey, (3) 5 min least bittern call-broadcast (30 s on/30 s off), (4) 3 min unlimited-radius auditory survey, and (5) 4 min call-broadcast sequence of American coot, sora, common moorhen and virginia rail, where each species call was broadcasted once (30 s on/30 s off). We conducted most surveys from a canoe, with the exception of wetlands that were only accessible by foot. We conducted all surveys from late May to early July by the same observer under conditions of no precipitation, temperature >13 °C and wind speed <20 km/h.

2.4.2. Turtle surveys

We sampled Blanding's turtles using time-limited (maximum 4 h; Marchand and Litvaitis, 2004) visual surveys (Attum et al., 2008) during mid-April and May, when typically >90% of individuals aerially bask (Sajwaj and Lang, 2000) and visibility is maximized as seasonal vegetation growth has not yet begun. We used high-power binoculars from multiple vantage points that maximized visibility of the wetland shoreline and other potential basking sites (e.g., emergent rocks, logs, muskrat lodges, vegetation clumps and mats; Rowe and Moll, 1991). Once we thoroughly searched the wetland in the center of the landscape, we moved to the nearest wetland, when there was >1 wetland patch in a landscape. Surveys concluded when a Blanding's turtle was detected or the time limit was reached. All surveys were conducted by the same observers between 8 h00 and 17 h30 when the air temperature was >15 °C (Rowe and Moll, 1991) and there was no precipitation.

We sampled musk turtles by time-limited (maximum 8 h over two survey days; Marchand and Litvaitis, 2004) active searches. Musk turtles typically bask at the surface of water under floating aquatic vegetation (Edmonds and Brooks, 1996). Therefore, we manually searched under floating aquatic vegetation (primarily lily pads) and submerged macrophytes at the water surface within a 1 m × 1 m area directly in front of the observer, wearing polarized sunglasses to increase visibility. We searched by wading through the water within 5 m of the shoreline, where water depth was <1 m; search parameters were based on musk turtle activity patterns reported in Carrière (2007). This type of manual search yields higher detection rates relative to other methods (baited traps, dip nets and snorkel; Carrière, 2007; Edmonds and Brooks, 1996; Quesnelle et al., unpublished data). In addition, it minimizes non-detection error because, if a turtle was within 1 m of an observer, she was almost certain to detect it. Once we thoroughly searched the wetland in the center of the landscape, we moved to the nearest wetland, when there was >1 wetland patch in a landscape. Surveys concluded when a musk turtle was detected or the 8-h time limit was reached. All surveys were conducted by the same observers between 8 h00 and 16 h00 and from mid-July to mid-August (Carrière, 2007) when there was no precipitation.

2.5. Statistical analyses

All landscape variables were standardized to a mean of 0 and a standard deviation of 1. We modeled species that were recorded at 10–90% of landscapes. We used generalized linear models with a logit link function (logistic regression) within a discrete Bayesian model averaging (BMA) framework (Wintle et al., 2003) to determine the effects of landscape structure on wetland species occurrence. The BMA method calculates model-averaged regression coefficients based on Bayesian information criterion (BIC) values to weight models and produces the posterior probability of a non-zero coefficient [$\text{Pr}(i)$] for each predictor (Wintle et al., 2003). We used the “bic.glm” function in the package ‘BMA’ (Raferty et al., 2012) in R (R Development Core Team, 2012).

We compared regression coefficients from BMA to assess the relative importance of landscape variables in predicting the probability of wetland species occurrence, as other methods for assessing relative importance (e.g., variance partitioning, summed Akaike weights) have been shown to be biased (Smith et al., 2009).

3. Results

Species were detected in the following proportion of landscapes: red-winged blackbird (1.0), swamp sparrow (0.9), marsh wren (0.5), virginia rail (0.5), least bittern (0.3), common moorhen (0.1), sora (0.1), and American coot (0.0), musk turtle (0.6), and Blanding's turtle (0.4). Marsh wren, virginia rail, least bittern, Blanding's turtle and musk turtle were suitable for analysis (Sub section 2.5).

3.1. Relative importance of landscape predictors

3.1.1. Wetland Birds

Wetland amount in a landscape was consistently more important than other landscape predictors for all wetland birds analyzed. For two of the three species, wetland amount was more important by an order of magnitude, based on model-averaged regression coefficients (Fig. 2). There was strong evidence that increased wetland cover at the landscape-scale increased the probability of wetland bird occurrence (Fig. 3). Wetland amount had the highest posterior probability of inclusion in models for wetland birds, where $\text{Pr}(i) > 0.68$ (Table A5). There was no substantial evidence of effects of wetland configuration, forest cover, agriculture cover, or road density (all $\text{Pr}(i) < 0.58$) on occurrence of wetland birds (Table A5).

3.2. Turtles

For both Blanding's turtle and musk turtle the amount of forest in a landscape (a measure of matrix composition) was more important by an order of magnitude than any other predictor variable, based on model-averaged regression coefficients (Fig. 2). There was strong evidence that forest cover at the landscape-scale increased the probability of turtle occurrence (Fig. 3) and the posterior probability of a non-zero coefficient [$\text{Pr}(i)$] was 1.0 and 0.90 for Blanding's and musk turtle, respectively (Table A5). There was no substantial evidence of effects of wetland amount, wetland configuration, agriculture cover, or road density (all $\text{Pr}(i) < 0.20$) on turtle occurrence (Fig. 2; Table A5).

4. Discussion

This is the first study to evaluate the independent, relative effects of habitat amount, habitat configuration, and matrix composition on wetland birds and turtles. Our results support our a priori expectation that the amount of wetland in a landscape (i.e., wetland loss) is more important than other landscape predictors of wetland bird distribution. A positive effect of wetland amount at a landscape-scale has been detected in previous studies for several wetland bird species and across several spatial scales (500–4000 m). This positive effect is most likely due to higher food and nesting site availability in landscapes with more wetland (Tozer et al., 2010).

We found that wetland configuration, when unconfounded with wetland amount (i.e. habitat fragmentation per se), did not have an important effect on any wetland species (bird or turtle). We therefore suggest that the negative effects of wetland isolation found in previous studies actually represent a strong positive effect

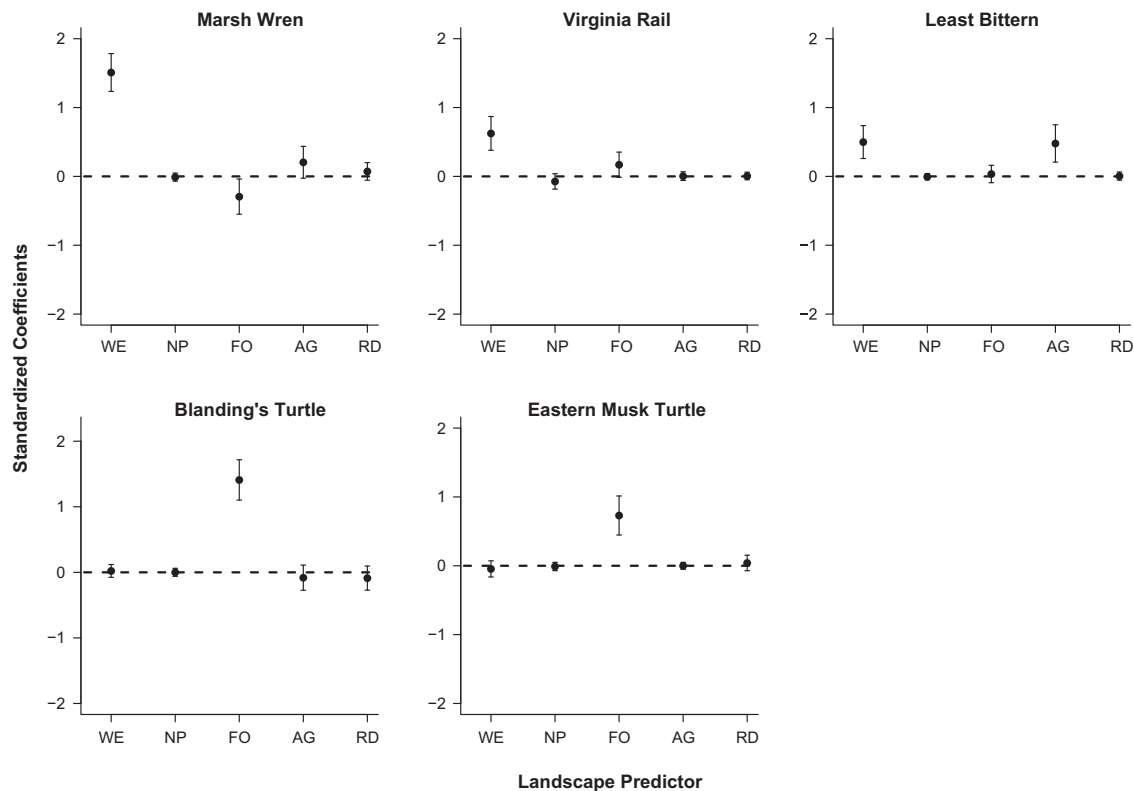


Fig. 2. Bayesian model averaged coefficients from generalized linear models (logistic regression) of wetland species occurrence on landscape predictors: amount of wetland (WE), number of wetland patches (NP), amount of forest (FO), amount of agriculture (AG), and road density (RD), within sampled landscapes. Predictors were standardized (mean 0, SD 1) before analysis.

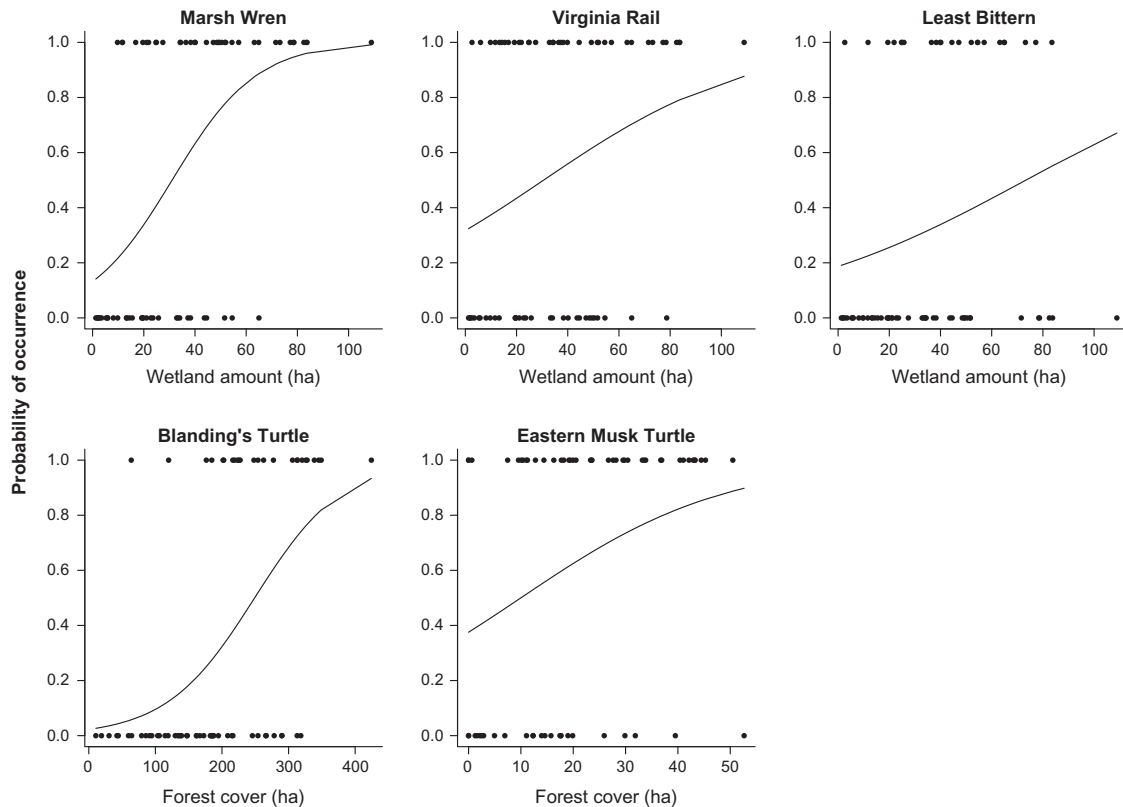


Fig. 3. Logistic regression models of the landscape predictor with the strongest effect on the probability of occurrence for each wetland species determined by Bayesian model averaging (see Fig. 2; Table A5). Points are raw response data (presence/non-detection). Predictions were made holding other landscape variables at a constant mean value.

of wetland amount at the landscape scale. In fact, wetland isolation should not be used as an index of wetland fragmentation since, in general, distances between habitat patches *decrease* with increasing fragmentation, when total habitat amount is held constant (Fahrig, 2003).

We found that forest and agriculture cover were less important predictors of wetland bird distribution than was wetland amount; a similar result was found by Smith and Chow-Fraser (2010). Previous studies showing an effect of forest cover on wetland birds (e.g., Budd and Kremenetz, 2010) did not control for the correlation between forest amount and wetland amount in the landscape, so these results may have been due to wetland amount rather than forest amount. On the other hand, forest amount in these studies could have affected wetland birds through its negative correlation with agriculture; landscapes with >50% cropland are thought to have a negative effect on wetland birds due to high nutrient loading and sedimentation (Naugle et al., 2001). Since landscapes with very high agriculture cover (>55%) were not available in our area, we may have underestimated the potential effect of cropland. On the other hand, the signs of the coefficients relating agriculture to wetland birds were positive (Fig. 2), suggesting that cropland, at least at lower levels in the landscape (<55%), may provide supplementary resources (Johnson and Dinsmore, 1985).

We found essentially no effect of road density on wetland birds and turtles. This does not appear to be due to the ranges in road density values in our study, since our ranges in values (birds, 0–9 km/km²; turtles 0–5.7 km/km² and 0–8.7 km/km²) were comparable to those in studies that found significant effects of road density on wetland bird communities (e.g.: 0–2.52 km/km², Whited et al., 2000; 0–8.8 km/km², Shriver et al., 2004) and turtle population structure and sex-ratios (e.g.: 0.5–11.1 km/km², Marchand and Litvaitis, 2004; 0.1–7.7 km/km², Steen and Gibbs, 2004). It is

possible that roads are affecting population abundances in our study but we did not detect these effects because we sampled for presence/absence, not abundance. If our presence/absence sampling was biased to detecting larger, older individuals, and if these individuals are less likely to be killed by roads than younger individuals in the population, then our occurrence data would be a poor indicator of the effects of roads on abundance. On the other hand, it should be noted that a significant negative effect of roads on turtle abundance (as opposed to population structure) has not yet been demonstrated in the literature, so it is possible that our results are actually consistent with previous findings, at least for turtles. It is also likely that occurrence of at least some of the wetland species would be negatively affected by higher road densities than those in our study, such as those in urban areas (e.g.: Smith and Chow-Fraser, 2010).

Our results did not support our a priori expectation that the amount of wetland in a landscape should be more important than other landscape-scale predictors of turtle distributions; instead, forest amount was the most important predictor. A positive effect of forest amount on turtles at a landscape scale has been detected in previous studies (Attum et al., 2008; Findlay and Houlahan, 1997). For Blanding's turtles we hypothesize that landscapes with more forest provide better access to complementary resources thus indirectly supporting greater abundance (i.e. landscape complementation; Dunning et al., 1992). Blanding's turtles are semi-aquatic; individuals can spend up to 38% of the active season in upland forest (Joyal et al., 2001). Forests are used by Blanding's turtles for short-term basking prior to leaf emergence (Beaudry et al., 2009), nesting sites in exposed rocky outcrops or canopy breaks, and refugia for short-term inactivity (Joyal et al., 2001). Vernal pools (small ephemeral wetlands) in forests provide Blanding's turtles with seasonally abundant food resources and rehydration,

mating sites and pre-nesting staging areas (Beaudry et al., 2009; Grgurovic and Sievert, 2005). Vernal pools are typically not represented in landcover data because the forest overstorey obscures their detection by remote sensing devices. Therefore, vernal pools could explain the relationship with forest cover we found. Finally, Blanding's turtles can migrate large distances (up to 2050 m) to different habitat types required for their life cycles, and they typically use multiple wetlands throughout a season (Joyal et al., 2001). Semi-aquatic turtles including Blanding's may preferentially use upland forests for movement relative to open habitats, possibly due to reduced thermal stress (Bowne, 2008). Since turtle demography relies on high adult survivorship, factors that reduce adult mortality during movement (i.e.: forest cover) could have a strong effect on the distribution of semi-aquatic turtles. Overall, our results suggest that the availability of forest in the landscape represents a more limiting factor than wetland availability on the distribution of Blanding's turtles. If true, it is possible that the apparent sensitivity of Blanding's turtle to aquatic habitat loss and fragmentation found by Grgurovic and Sievert (2005) may actually reflect sensitivity to declining forest amount, which is usually correlated with wetland loss and fragmentation.

In contrast to Blanding's turtles, musk turtles are highly aquatic and seldom leave the water, although gravid females will move overland to nest (mean 851 m), with nests located within 50 m from water (Steen et al. 2012). We suggest that the positive effect of forest cover on musk turtles may result from increasing accessibility to nesting habitats. Musk turtles exhibit relatively high evaporative water-loss (Ernst, 1968), resulting in dispersal mortality (Buhlmann and Gibbons, 2001); therefore, if accessibility to nesting sites is a limiting factor for this species, this could result in a strong effect of forest cover even though the species is primarily aquatic. Alternatively, since musk turtles are relatively sedentary, local wetland conditions, affected by forest cover (e.g.: water quality, hydroperiod), may limit this species. Forest cover may buffer wetlands from fertilizer inputs and sedimentation; DeCatanzaro and Chow-Fraser (2010) observed that musk turtles were not found in wetlands of low water quality. On the other hand, we did not find an effect of agriculture on musk turtle. This is not say that such an effect would not occur at cropland covers higher than those in our study (>55%); however it does imply that the positive effect of forest cover we observed is not an indirect negative effect of agricultural inputs. A related explanation is that more forested landscapes could maintain wetland hydrology and drainage patterns within a landscape (Richardson and McCarthy, 1994), to support the occurrence of musk turtles. However, the negative correlation between wetland amount and forest amount at the landscape scale (Table A4) indicates this alternate explanation is unlikely. Therefore, we suggest that the most likely explanation for the positive effect of forest cover on musk turtle occurrence is the higher accessibility of nesting sites, which is presumably a limiting factor for their distribution.

We also considered that the relatively strong positive effect of forest cover on both turtle species could be due to a negative correlation between forest cover in the landscape and wetland riparian disturbance. Forested riparian loss can affect the abundance of turtles (Sterrett et al., 2011) by influencing wetland microclimate (water temperature), resource availability (food), and microhabitat (large woody debris). We calculated proportion forested riparian in each sampled landscape as the total length of wetland edge immediately adjacent to forest, divided by the total wetland edge length. We conducted post hoc analyses of the effect of proportion forested riparian on turtle occurrence by including it as a predictor in models with the landscape variables. Proportion forested riparian did not improve model fit for either turtle species (Table A6), which suggests that forest cover beyond the wetland riparian zone

likely explains the occurrence of both turtle species, as argued above.

It is surprising that wetland amount in the landscape had essentially no effect on the occurrence of the two turtle species. However, unlike wetland birds where feeding and breeding occur solely in wetlands, turtles require different habitats in their life cycle, which necessitates overland movement, increasing the importance of matrix composition (e.g., forest cover). Indeed, local extirpation and shifting population structure of freshwater turtles has occurred despite protection of aquatic habitat in an area of intense anthropogenic development (Browne and Hecnar, 2007), highlighting the importance of matrix composition. In fact, reptiles in general have relatively weak responses to patch area effects (Prugh et al., 2008).

We were unable to estimate the probability of detection of the wetland species surveyed because the study design necessitated a large sample size and logistical constraints prevented repeated visits. However, we suggest that our sampling methods maximized detectability of each species (Sub section 2.4) such that additional visits would only marginally increase the probability of detecting occupancy in a landscape. We also note that occurrence rates of marsh wren, virginia rail and least bittern in this study were within the range of detection reported in other landscape-scale studies using call-broadcast with multiple visits (Rehm and Baldassarre, 2007; Tozer et al., 2010). Also, the occurrence rate of Blanding's (0.36) was similar to or higher than occurrence rates from trapping with repeated visual surveys (0.26; Joyal et al., 2001) or repeated visual surveys alone (0.10; Attum et al., 2008). Similarly for musk turtle, the sampling method selected (active surveys) yielded higher detection rates relative to baited traps and we maximized detectability by conducting searches over 2 days, if necessary.

Although our detection rates are high, it is possible that detectability covaried with landscape predictors, such that there were higher detection probabilities of wetland birds in landscapes with more wetland cover or of turtles in landscapes with more forest cover, which could cause spurious results. We evaluated this possibility by testing, post hoc, for correlations between factors that could affect detectability and landscape predictors. These factors included Julian day, air temperature, cloud cover, and length of wetland shoreline. All of these were weakly correlated ($r < 0.2$) with landscape variables, indicating our results for wetland cover and forest cover are likely not spurious effects of detectability bias caused by these factors (Table A7). Alternatively, perhaps an unknown local variable covaried with detectability and the landscape predictors, thus introducing a detection bias for which we are unable to test (Gu and Swihart, 2004). While this is possible, such a bias would have to be quite strong to produce the large magnitude of effects of wetland amount and forest cover (Fig. 2) we observed.

5. Conclusions

Given that wetland birds and turtles are undergoing some of the steepest wildlife population declines worldwide (Millennium Ecosystem Assessment, 2005), this study has important implications for wetland conservation and landscape planning. Our results confirm that wetland loss is the primary landscape-scale factor of wetland bird declines and suggest that forest loss plays a greater role in freshwater turtle declines than previously realized. Firstly, this suggests that minimizing wetland loss, irrespective of configuration, will be of most benefit for wetland bird conservation. Secondly, given the protection of core wetland habitat (Semlitsch and Bodie, 2003), minimizing forest loss surrounding protected core wetlands will be of most benefit for freshwater turtle conservation. The large effect of forest cover on turtles provides the first

(unconfounded) support for arguments that wetland buffers are insufficient and protected forest in wetland policy is imperative to conserve turtles, both as habitat (Buhlmann and Gibbons, 2001) and travel corridors (Roe and Georges, 2007). It also suggests that increases in landscape complementation (i.e. access to multiple resources) should take priority over reductions in wetland isolation (i.e. wetland amount) in landscape planning for turtle conservation. Moreover, our results suggest that wetland creation alone would have little impact on declining freshwater turtles; restoration of the matrix (i.e. reforestation) surrounding protected core wetlands would be more effective. For all declining wetland species, wetland policies and restoration plans based on wetland configuration (e.g., mean wetland size, nearest-neighbor distance) would have low returns unless they simultaneously increased total wetland amount or forest amount; alterations to configuration alone cannot offset the effects of overall loss of wetland or forest on birds and turtles, respectively. Therefore, our results demonstrate that understanding the relative importance of landscape-scale effects can inform priorities for habitat conservation and restoration in the context of multi-species conservation.

Despite that the birds and turtles we studied are all 'wetland-dependent fauna', the two taxa responded to different landscape factors. This is consistent with the general observation that there are low correlations between taxa in their responses to environmental change (Wolters et al., 2006). Our results suggest that these low correlations could be due to differences in landscape-scale requirements. Wetland-nesting obligates that depend on specific wetland vegetation communities (e.g., least bittern, marsh wren) were more sensitive to landscape structure than were wetland-nesting generalists (e.g., red-winged blackbird), and species with life-cycles requiring more than one habitat type (turtles) were more strongly affected by landscape complementation, than wetland loss. Given these differences in responses to landscape structure, the practice of using one taxon (often birds) as a biodiversity model for landscape planning is likely to fail for other groups. Even for a group of species identified by their primary habitat use (here 'wetland-dependent fauna'), a multi-taxa approach should be a mandatory component of landscape conservation planning.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2013.01.020>.

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