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Report No. 4-12

Population Viability and Sensitivity Analysis for Marsh Wren, Ovenbird, Red-Shouldered Hawk, and Bobolink in the Quebec Pilot Study Area in Support of NAESI Habitat-Based Biodiversity Standards

Technical Series 2008

Photos:
Bottom Left- clockwise

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POPULATION VIABILITY AND SENSITIVITY ANALYSIS FOR MARSH WREN, OVENBIRD, RED-SHOULDERED HAWK, AND BOBOLINK IN THE QUEBEC PILOT STUDY AREA IN SUPPORT OF NAESI HABITAT-BASED BIODIVERSITY STANDARDS

REPORT NO. 4-12

NOTE TO READERS

The National Agri-Environmental Standards Initiative (NAESI) is a four-year (2004-2008) project between Environment Canada (EC) and Agriculture and Agri-Food Canada (AAFC) and is one of many initiatives under AAFC's Agriculture Policy Framework (APF). The goals of the National Agri-Environmental Standards Initiative include:

- Establishing non-regulatory national environmental performance standards (with regional application) that support common EC and AAFC goals for the environment
- Evaluating standards attainable by environmentally-beneficial agricultural production and management practices; and
- Increasing understanding of relationships between agriculture and the environment.

Under NAESI, agri-environmental performance standards (i.e., outcome-based standards) will be established that identify both desired levels of environmental condition and levels considered achievable based on available technology and practice. These standards will be integrated by AAFC into beneficial agricultural management systems and practices to help reduce environmental risks. Additionally, these will provide benefits to the health and supply of water, health of soils, health of air and the atmosphere; and ensure compatibility between biodiversity and agriculture. Standards are being developed in four thematic areas: Air, Biodiversity, Pesticides, and Water. Outcomes from NAESI will contribute to the APF goals of improved stewardship by agricultural producers of land, water, air and biodiversity and increased Canadian and international confidence that food from the Canadian agriculture and food sector is being produced in a safe and environmentally sound manner.

The development of agri-environmental performance standards involves science-based assessments of relative risk and the determination of desired environmental quality. As such, the National Agri-Environmental Standards Initiative (NAESI) Technical Series is dedicated to the consolidation and dissemination of the scientific knowledge, information, and tools produced through this program that will be used by Environment Canada as the scientific basis for the development and delivery of environmental performance standards. Reports in the Technical Series are available in the language (English or French) in which they were originally prepared and represent theme-specific deliverables. As the intention of this series is to provide an easily navigable and consolidated means of reporting on NAESI's yearly activities and progress, the detailed findings summarized in this series may, in fact, be published elsewhere, for example, as scientific papers in peer-reviewed journals.

This report provides scientific information to partially fulfill deliverables under the Biodiversity Theme of NAESI. This report was written by J. Tews of Noreca Consulting. The report was edited and formatted by Denise Davy to meet the criteria of the NAESI Technical Series. The information in this document is current as of when the document was originally prepared. For additional information regarding this publication, please contact:

Environment Canada
National Agri-Environmental Standards
Initiative Secretariat
351 St. Joseph Blvd. 8th floor
Gatineau, QC
K1A 0H3
Phone: (819) 997-1029
Fax: (819) 953-0461

NOTE À L'INTENTION DES LECTEURS

L'Initiative nationale d'élaboration de normes agroenvironnementales (INENA) est un projet de quatre ans (2004-2008) mené conjointement par Environnement Canada (EC) et Agriculture et Agroalimentaire Canada (AAC) et l'une des nombreuses initiatives qui s'inscrit dans le Cadre stratégique pour l'agriculture (CSA) d'AAC. Elle a notamment comme objectifs :

- d'établir des normes nationales de rendement environnemental non réglementaires (applicables dans les régions) qui soutiennent les objectifs communs d'EC et d'AAC en ce qui concerne l'environnement;
- d'évaluer des normes qui sont réalisables par des pratiques de production et de gestion agricoles avantageuses pour l'environnement;
- de faire mieux comprendre les liens entre l'agriculture et l'environnement.

Dans le cadre de l'INENA, des normes de rendement agroenvironnementales (c.-à-d. des normes axées sur les résultats) seront établies pour déterminer les niveaux de qualité environnementale souhaités et les niveaux considérés comme réalisables au moyen des meilleures technologies et pratiques disponibles. AAC intégrera ces normes dans des systèmes et pratiques de gestion bénéfiques en agriculture afin d'aider à réduire les risques pour l'environnement. De plus, elles amélioreront l'approvisionnement en eau et la qualité de celle-ci, la qualité des sols et celle de l'air et de l'atmosphère, et assureront la compatibilité entre la biodiversité et l'agriculture. Des normes sont en voie d'être élaborées dans quatre domaines thématiques : l'air, la biodiversité, les pesticides et l'eau. Les résultats de l'INENA contribueront aux objectifs du CSA, soit d'améliorer la gérance des terres, de l'eau, de l'air et de la biodiversité par les producteurs agricoles et d'accroître la confiance du Canada et d'autres pays dans le fait que les aliments produits par les agriculteurs et le secteur de l'alimentation du Canada le sont d'une manière sécuritaire et soucieuse de l'environnement.

L'élaboration de normes de rendement agroenvironnementales comporte des évaluations scientifiques des risques relatifs et la détermination de la qualité environnementale souhaitée. Comme telle, la Série technique de l'INENA vise à regrouper et diffuser les connaissances, les informations et les outils scientifiques qui sont produits grâce à ce programme et dont Environnement Canada se servira comme fondement scientifique afin d'élaborer et de transmettre des normes de rendement environnemental. Les rapports compris dans la Série technique sont disponibles dans la langue (français ou anglais) dans laquelle ils ont été rédigés au départ et constituent des réalisations attendues propres à un thème en particulier. Comme cette série a pour objectif de fournir un moyen intégré et facile à consulter de faire rapport sur les activités et les progrès réalisés durant l'année dans le cadre de l'INENA, les conclusions détaillées qui sont résumées dans la série peuvent, en fait, être publiées ailleurs comme sous forme d'articles scientifiques de journaux soumis à l'évaluation par les pairs.

Le présent rapport fournit des données scientifiques afin de produire en partie les réalisations attendues pour le thème de la biodiversité dans le cadre de l'INENA. Ce rapport a été rédigé par J. Tews de Noreca Consulting. De plus, il a été révisé et formaté par Denise Davy selon les critères établis pour la Série technique de l'INENA. L'information contenue dans ce document était à jour au moment de sa rédaction. Pour plus de renseignements sur cette publication, veuillez communiquer avec l'organisme suivant :

Secrétariat de l'Initiative nationale d'élaboration de normes agroenvironnementales
Environnement Canada
351, boul. St-Joseph, 8eétage
Gatineau (Québec) K1A 0H3
Téléphone : (819) 997-1029
Télécopieur : (819) 953-0461

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EXECUTIVE SUMMARY

To develop habitat-based biodiversity performance standards under the ‘Biodiversity Theme’ of the National Agri-Environmental Standards Initiative (NAESI) we completed in-depth population and sensitivity analyses for four selected surrogate species of the Québec pilot study area. Each population analysis includes two main components: a sensitivity analysis of demographic model parameters based on randomized parameter sets and a detailed re-assessment of species-specific, habitat-based performance standards. For the spatial model input we employed a ‘moving window’ analysis by sampling series of smaller landscape subsets from the NAESI Québec pilot study area. Performance standards (i.e., thresholds) of minimum habitat amount and associated average patch sizes were then assessed by running and modifying the landscape subset scenarios until the following performance targets were achieved: (i) viability (<5% extinction risk over 50 years), (ii) stability (<10% population decline over 50 years), and (iii) functionality (<5% risk of decline to 50% of the initial abundance over a simulation trajectory of 50 years).

All habitat-based standards are based on species-specific model assumptions, a simulation trajectory of 50 years and a 95% confidence for 1000 simulation replicates. The recommended standards are intended as broad management guidelines to ensure a minimum supply of habitat for viable, stable and functional metapopulations and so that ecological functions and processes of these surrogate species are maintained at appropriate spatial and temporal scales. Based on empirical knowledge, demographic analyses and spatial population viability analysis (PVA) we suggest the following set of habitat-based standards.

Marsh Wren: (i) a minimum patch size of 10 ha to reduce possible population sink dynamics, (ii) a minimum patch size of ~65 ha of suitable habitat (based on an average population density of 0.25 ha per male) to support a single, viable population over 50 years, (iii) a maximum inter-

patch distance of ~2 km to facilitate sufficient natal and breeding dispersal, (iv) a minimum amount of ~1% (~100 ha) suitable habitat and an average patch size of more than 20 ha to support a viable metapopulation on a spatial scale of 100 km^2, (v) a minimum amount of 15% (~15 km^2) suitable habitat and an average patch size of more than 50 ha to support a stable metapopulation on a spatial scale of 100 km^2.

Ovenbird: (i) a minimum patch size of ~200 ha to facilitate population source dynamics, (ii) a minimum patch size of ~850 ha of suitable habitat (based on an average population density of 0.24 individuals per ha) to support a single, viable population over 50 years, (iii) a minimum amount of ~10% (~2500 ha) suitable habitat and an average patch size of more than 60 ha to support a viable metapopulation on a spatial scale of 250 km^2, (iv) a minimum amount of 17.5% (~4375 ha) suitable habitat and an average patch size of more than 200 ha to support a stable metapopulation on a spatial scale of 250 km^2, (v) a minimum amount of 40% (~100 km^2) suitable habitat and an average patch size larger than the minimum viable patch size (i.e., 850 ha) to support a functional metapopulation on a spatial of 250 km^2; for lower standard deviations in vital rates thresholds for stability and functionality may be significantly smaller.

Bobolink: (i) a minimum patch size of ~20 ha for patch occupancy, (ii) a minimum patch size of ~135 ha of suitable habitat (based on an average population density of 1.5 individuals per ha) to support a single, viable population over 50 years, (iii) a maximum inter-patch distance of 15 km to facilitate sufficient natal and breeding dispersal, (iv) no hayfield harvesting prior to the first week in July, (v) a minimum amount of ~6.5% (~650 ha) suitable habitat and an average patch size of more than 50 ha to support a viable metapopulation on a spatial scale of 100 km^2, (vi) a minimum amount of 23% (~2300 ha) suitable habitat and an average patch size of more than 125 ha to support a stable metapopulation on a spatial scale of 100 km^2, (vii) a minimum amount of

30% (~3,000 ha) suitable habitat and an average patch size larger than 150 ha to support a functional metapopulation on a spatial of 100 km^2

Red-shouldered Hawk: (i) a minimum patch size of ~26 km^2 of suitable habitat (based on an average population density of 1.7 individuals per km^2) to support a single, viable population over 50 years, (ii) a minimum amount of ~0.8% (~39 km^2) suitable habitat to support a viable metapopulation on a spatial scale of 4869 km^2, (iii) a minimum amount of ~1.6% (~78 km^2) suitable habitat to support a stable metapopulation on a spatial scale of 4869 km^2, (iv) a minimum amount of ~4% (~195 km^2) suitable habitat to support a functional metapopulation on a spatial scale of 4869 km^2 when standard deviations in fecundity rates are reduced to ~30% of the mean.

1 INTRODUCTION

As part of the ‘Biodiversity Theme’ of the ‘National Agri-Environmental Standards Initiative’ (NAESI) several pilot projects have been established across agricultural regions in Canada to develop and test a decision support process for the development of habitat-based biodiversity performance standards. One of the goals of this process is to determine the quantity (and quality) of habitat required to meet the habitat requirements for a set of selected surrogate species that represent a desired level of biodiversity. For this purpose a series of demographic and spatial population viability models were developed and applied for the Eastern Ontario and Québec pilot study areas (Noreca Consulting and Elutis Modeling and Consulting Inc., 2007; Akçakaya et al. 2007; Pearce et al., 2007).

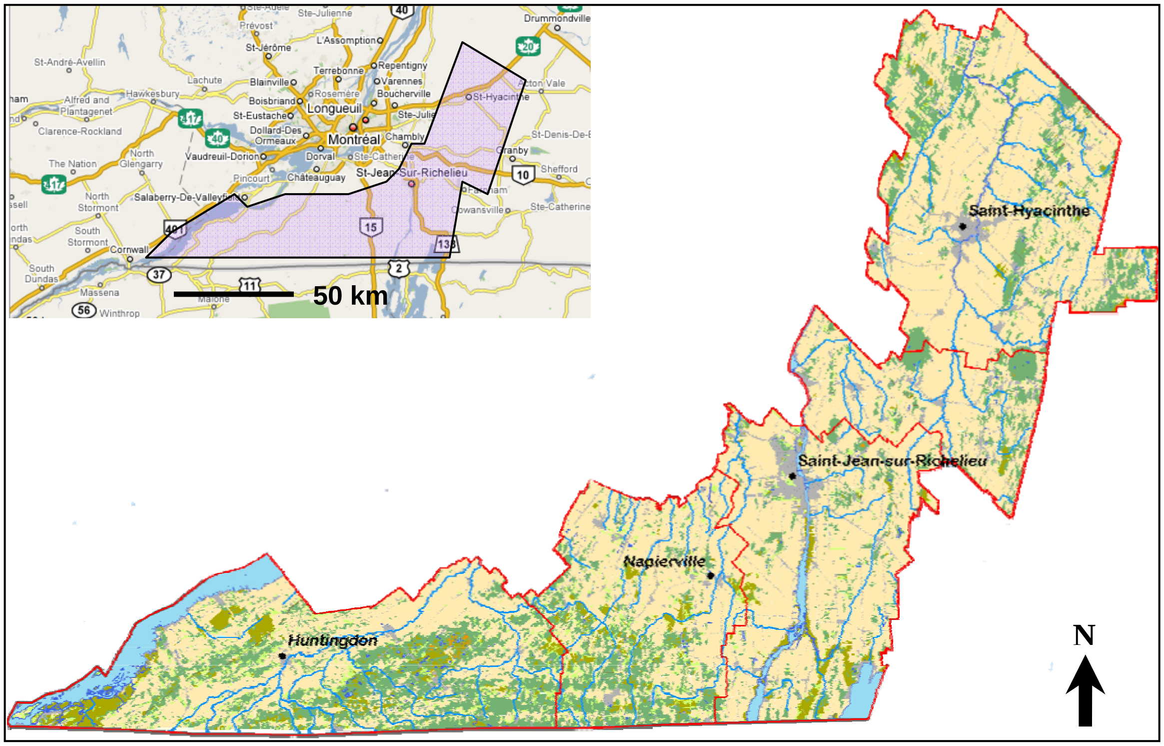
Population Viability Analysis (PVA) is a widely used management and conservation tool to evaluate the threats of extinction or decline for species of concern. Due to their stochastic nature population viability models produce estimates of the probability of extinction and expected population sizes based on species’ life histories, vital rates and dispersal characteristics. Such analyses can be non-spatial, spatial-implicit or spatial-explicit. Ramas©GIS (Akçakaya and Root, 2005) is a software tool that allows spatial-implicit analysis linking habitat data with demography and will be used for population analyses conducted for this report.

In a previous study standardized population analyses were conducted for 10 surrogate species of the Québec pilot study area in order to develop sets of species-specific habitat-based standards (Tews, 2008) (for a map of the Québec pilot study area see Figure 1). For the standardized NAESI PVA approach three performance measures and their targets were defined (Tews, 2008). A population is considered (i) ‘viable’ if the extinction risk over a time frame of 50 years is less than 5%, (ii) ‘stable’ if the population abundance in the final (i.e., 50th) year is more than or equal to 90% of the initial population size, and (iii) ‘functional’ if the risk of decline to 50% of the initial population size in any year is less than 5% (over the course of 50 years). The goal of a population analysis is to find the amount of habitat required (and other habitat-based pre-requisites) to achieve each performance target.

Based on the findings and recommendations from this study we were contracted to complete in-depth population analyses for a sub-set of surrogate species (i.e., Marsh Wren, Ovenbird, Red-shouldered Hawk, and Bobolink). For each species the additional analyses comprise the following two components.

The first component in each species’ report section consists of a detailed sensitivity analysis (SA) of demographic model parameters. In a sensitivity analysis parameters are changed systematically (or randomly) and variations in model outputs are used to assess the sensitivity of the model toward changes in each parameter. As we show in this report a sensitivity analysis is able to reveal important information and can be of high value for the assessment of habitat-based standards. The method we propose utilizes an R script named GRIP (Curtis and Naukokaitis, 2008) which allows exploring the effects of randomized sets of parameter combinations on model output variations. This methodological approach extends the standard SA tool provided with the Ramas©GIS software package.

Figure 1: Location of the NAESI Québec pilot study area south of Montreal, Québec, Canada. The study area is approximately 4869 km^2 in size.



Secondly, we conduct a 'moving window' analysis for three surrogate species with smaller home ranges and operational scales (i.e., Marsh Wren, Ovenbird, Bobolink). For this type of analysis a 'moving' spatial grid (100 km^2 and 250 km^2, respectively) is dynamically placed across the entire habitat suitability map in the Québec pilot study area and subsequently used as the input for the spatial PVA. This type of analysis allows to use a wide range of landscape scenarios as model inputs and to more thoroughly assess standards (i.e., thresholds) of habitat amount for each performance measure (i.e., viability, stability, and functionality). Given a sufficient amount and overlap of landscape subsets across the study region it may also allow to merge all landscape 'samples' into a single habitat map for each species indicating average degrees of viability, stability and functionality for each habitat patch across the entire study area. However, due to software limitations and methodological constraints the latter 'visual' product could not be completed for this part of the project (see discussion in section 2.2).

2 METHODS

2.1 Sensitivity Analysis

In general, three sensitivity analysis (SA) methodologies are most often applied: (i) conventional SA, (ii) relative SA, and (iii) logistic regression SA (Cross and Beissinger, 2001). Conventional and relative SA are used to determine the change in the likelihood of extinction related to a change in a model parameter by a certain percentage. These two approaches only allow for a subset of possible parameter combinations since only one model parameter is varied at a time (i.e., opposite to combinations where two or more parameters are varied simultaneously). Thus, such analyses do not consider interaction effects among parameters and their relative importance for the simulated response variable. For the third approach (logistic regression) all parameter values are varied independently in a random fashion and model runs with different parameter sets are replicated until a sufficiently large range of variation has been simulated for each parameter. Then a statistical analysis is used to assess how variations in the model output can be explained by changes in each parameter.

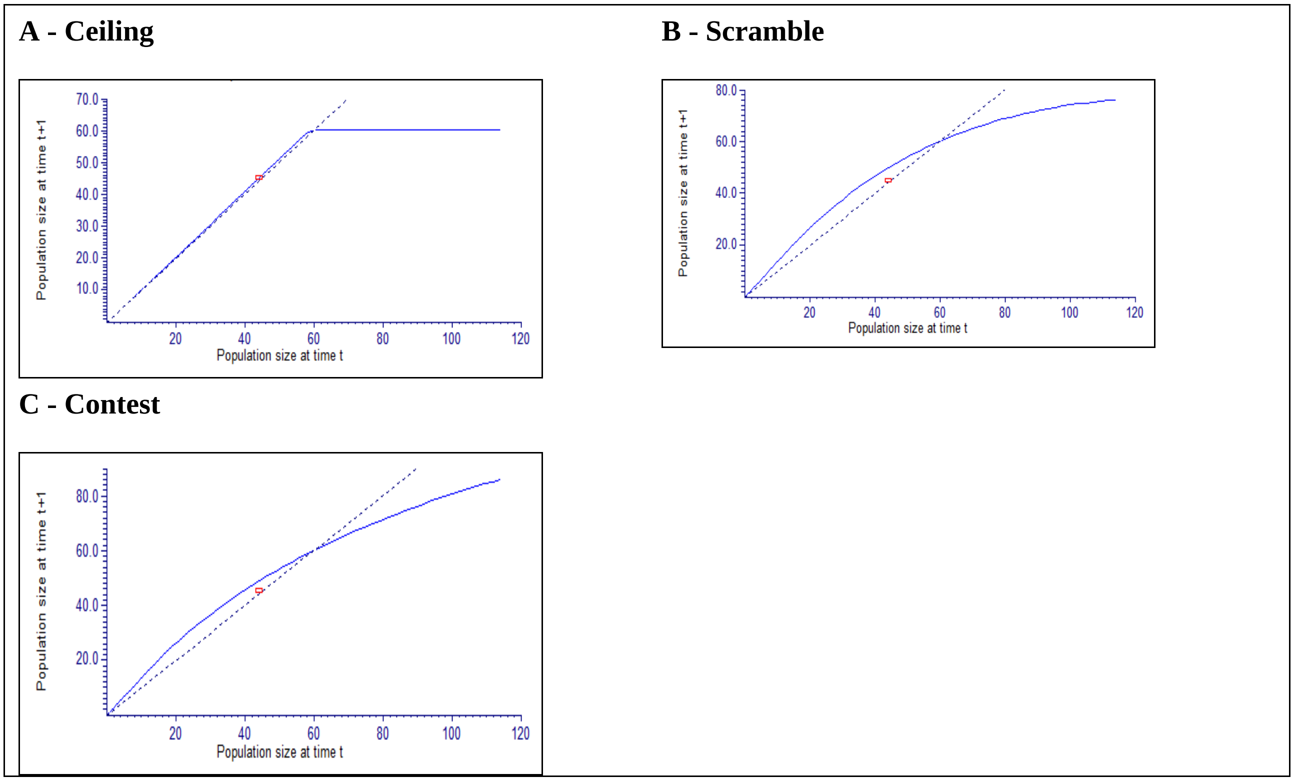
However, generating random sets of input parameters is a labor-intensive step if completed manually or semi-manually. We therefore used a program called GRIP (Generation of Random Input Parameters) (Curtis and Naujokaitis-Lewis, in press). GRIP has been developed using the freely available programming language R 2.3.1 and was further modified for the purpose of this project. GRIP varies model parameters randomly and automatically executes Ramas©Metapop (a sub-program of Ramas©GIS) for each randomized parameter combination. Thus, it provides an automated sensitivity analysis based on randomized parameter variations of the initial population model. For each SA we implemented a variation of 20% by drawing random numbers from normal distributions with the base parameterization in each study as the average value. We ran a set of 1000 randomized parameter combinations for each demographic model and then replicated each Ramas©Metapop parameter scenario 50 times to compute model output (i.e., extinction risk and final abundance).

We used GRIP to conduct a sensitivity analysis for each demographic model parameter for all four species. Demographic model parameters include all vital rates in the stage matrix (4 parameters for 2-stage matrices, 8 parameters for 4-stage matrices and polygynous mating systems) as well as initial abundances and carrying capacities, i.e., a total of 6 to 10 demographic parameters, depending upon the model specifications. Note, that Ramas©Metapop requires the use of standard deviations (SD) for stochastic variations of the vital rates and not the coefficient of variation (CV) (the latter would be better suited). That is, under parameter randomizations, lower vital rates (sampled and simulated during the SA) will receive proportionally higher variations as the SD remains constant (a CV would change the variation relative to the average). As a rule of thumb increase in stochastic variation usually increases extinction risk. Thus, extinction risk most likely increases disproportional with lower vital rates. However, as this effect applies to all vital rates equally relative difference in parameter sensitivity remains the same. On the other hand, neglecting stochastic variations in the vital rates (over the course of a simulation trajectory) would result in near-deterministic simulations that would only account for demographic stochasticity and unrealistically increase the relative importance of the carrying capacity.

The relative importance of the carrying capacity depends on the type of density dependence (DD) implemented in each PVA model. As we can see in Figure 2 the three different DD types result in different patterns of replacement or recruitment curves. Under the ceiling DD type a population grows until it reaches the ceiling (i.e., carrying capacity), and then remains at that level. A population that reaches the carrying capacity remains at that level until a population decline (e.g., a random fluctuation or an emigration) takes it below the ceiling. It is important to denote that ceiling type DD does not assume that the population would recover from low densities; this only depends on the vital rates in the stage matrix. As shown in Figure 2 under ceiling DD no further population growth is tolerated when the population reaches the carrying capacity K, as opposed to scramble and contest competition. Thus, if K is varied during the SA it will show a higher relative impact on the output variable (e.g., extinction risk) as under scramble or contest DD types. Choosing contest competition as the DD function in a population model will show the lowest relative importance of the carrying capacity in a SA (compared to the vital rates) as it allows population growth above the carrying capacity. Thus, the interpretation of the importance of the carrying capacity in each SA needs to take into account the type of density dependence that is chosen for that species.

To assess the relative importance of each demographic parameter in the SA we plotted the sampled parameter ranges (e.g., 1000 parameter values for adult fecundity) against the independent variable (e.g., extinction risk or final abundance) and then evaluated the R-squared of a linear regression. Statistically, the R-squared of the regression is the fraction of the variation in the dependent variable that is accounted for (or predicted by) the independent variable. Thus, comparing the different R-squared values for each parameter allows the ranking of parameters with respect to their relative importance for the model output.

Figure 2: Replacement curves for three different types of density dependence in Ramas©MetaPop: A = ceiling type, B = scramble competition (Logistic Ricker equation), and C = contest competition.

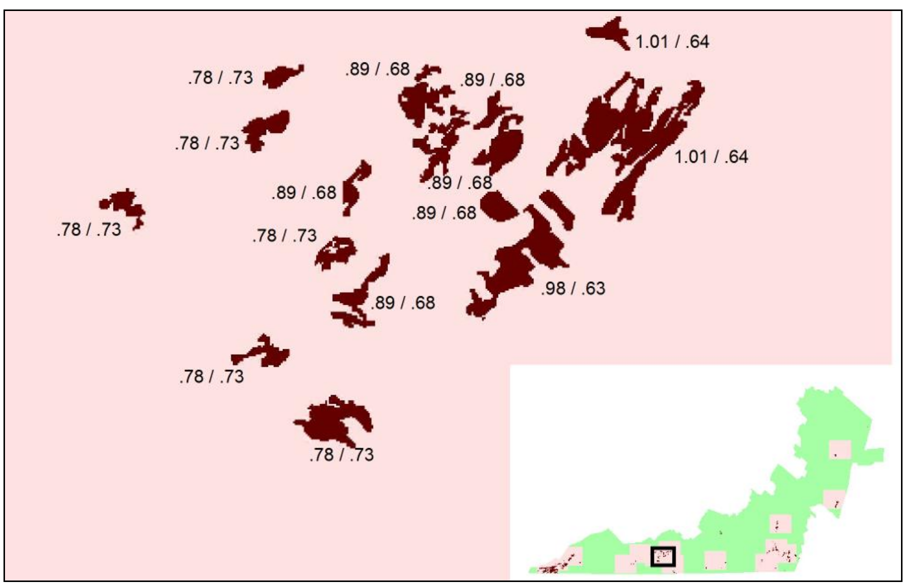


2.2 Moving window analysis

As the second component in each population analyses we conducted a spatial 'moving window' analysis of landscape subsets in the Québec pilot study area. We were able to apply this method for three species with smaller home ranges and dispersal distances: Marsh Wren, Ovenbird, and Bobolink. The reason for this approach was three-fold. Firstly, it can be assumed that for these species the actual spatial scale of metapopulation dynamics is smaller than the entire Québec pilot study area scale. Secondly, by sampling a wide array of overlapping landscape subsets and averaging model output values (e.g., 50-year population trend) across the entire study area it is possible to plot average performance measures for each habitat patch in a map format. This would result in a quasi-scale-free map product based on a specifically chosen operational species scale (see map example in Figure 3). Thirdly, and most importantly, by sampling a wide set of landscape subsets this approach provides a database of different 'landscape scenarios' with differing habitat amounts and patch sizes which then allows to derive habitat-based standards.

The map in Figure 3 gives an example that shows the distribution of average performance measure values based on the results of the Marsh Wren PVA. In this case average values for 'stability' and 'functionality' are based on three overlapping landscape subsets. For example, based on the PVA results from three landscape subsets, the patch next to the insert (.98 / .63) (red circle) supports (on average) a near stable 50-year population trend (i.e., 2% decline in abundance over 50 years) whereas the risk of 50% decline is 63%. Initially, we intended to develop such habitat patch maps for three of the four surrogate species. Due to unforeseen data format and technical issues we were not able to do so.

Figure 3: Results from the spatial-explicit Marsh Wren PVA from an area with three overlapping landscape subsets merged into a single habitat patch map (insert shows location of sample area within Québec pilot study area). The area is approximately 10*10 km in size. The first numerical value represents the average value for 'stability' (i.e., 50 year population trend), the second represents average 'functionality' measured as risk of decline to 50% of the initial population abundance.



The above example is based on a manual calculation based on the outcomes of three spatial population analyses. However, due to the large area involved this process requires an automated routine which we were not able to develop within the designated time frame. We were able to develop a routine which cuts landscape subsets out of the Québec pilot study area habitat map and exports these as ASCII files for population analysis in Ramas©MetaPop. However, the technical problem appears once a spatial PVA has been completed. Prior to that a subprogram called Ramas©HabDyn calculates the patch structure, based on the imported habitat suitability map, the neighborhood distance (which determines how suitable cells are 'glued' together to form a patch) and the habitat suitability threshold value (which determines whether or not a cell is considered as suitable or unsuitable). In a second step, the patch map created by Ramas©HabDyn is then imported into Ramas©MetaPop where the actual population analysis is executed. Once the desired model output variables have been computed (e.g., extinction risk) these values need to be re-assigned for each suitable habitat cell within each sampled landscape subset (in the Arc©GIS environment) and then averaged across the NAESI study region. Due to compatibility issues the latter step could not be completed within the designated time frame. Shifting the main focus to develop this external routine would have been detrimental for other important study outcomes, namely the re-assessment of habitat-based standards. It is also important to note that such a mapping product would not improve our knowledge with respect to the development of habitat-based standards; it is rather a visual summary of averaged results from all landscape subsets presented in a map format.

3 MARSH WREN

The Marsh wren (*Cistothorus palustris*) is a small songbird of the wren family and inhabits fresh to brackish fens, seasonal, semi-permanent, or permanent wetlands with dense, mixed, or monotypic stands of emergent aquatic vegetation (Zimmerman et al., 2002). The Marsh wren was chosen as a surrogate species as it is a frequent inhabitant of cattail marshes in the St. Laurence Lowlands Ecoregion (see Noreca Consulting and Elutis Modeling and Consulting Inc., 2007). A summary of demographic and spatial model parameters used in this population analysis is given in Table 1. Literature references for parameters in the Marsh Wren model are given in Noreca Consulting and Elutis Modeling and Consulting Inc. (2007) and Tews (2008).

A population analysis conducted for the Québec pilot study area (Tews, 2008) suggested the following habitat-based standards: i) a minimum patch size of 2 - 10 ha to avoid patches being a strong population sink (depending on habitat quality), (ii) a minimum patch size of 65 ha of suitable habitat (based on an average population density of 0.25 ha per male) to support a single, viable population, (iii) a maximum inter-patch distance of 2 km to allow sufficient natal and breeding dispersal, and (iv) a minimum amount of 0.9% suitable marsh habitat to support a viable, and stable metapopulation. With this in-depth population analysis we will conduct a detailed sensitivity analysis and re-assess the above habitat-based standards.

In Section 3.1 we will discuss the results of the sensitivity analysis. In the following section we will then outline the results from the 'moving window' procedure (Section 3.2). The larger number of subsets compiled through this spatial landscape sampling (compared to the previous study, see Tews, 2008) will facilitate a more thorough assessment of standard #4. That is, we ask, based on the assumptions of the population model, under which specific habitat conditions 'viability', 'stability' and 'functionality' can be achieved. If one of the latter standards can not be achieved by changes in habitat amount alone we will provide recommendations for additional requirements. For the moving window analysis we chose a spatial scale of 10*10 km (10,000 ha). We believe that this scale is appropriate since a landscape unit of this size is able to capture a habitat amount several orders of magnitude larger than the minimum viable patch size. On the other hand, enlarging the spatial scale of investigation may increase the degree of 'noise' for model interpretation as the 'regional' metapopulation may then be comprised of subsets (or compartments) of 'local' metapopulations. This is due to the fact that during the patch formation calculation in Ramas©GIS smaller home ranges will most likely decrease the degree of patch aggregation and smaller dispersal distances may result in lower rates of connectivity.

Table 1: Summary of demographic and spatial model parameters used in the Marsh Wren PVA.

Parameter	**Value / Comment**
Replications	1000
Duration	50 years
Stage 1	Female juveniles
Stage 2	Female adults
Stage 3	Male juveniles
Stage 4	Male adults
Vital rate 1	0.6033 (juvenile fecundity, female offspring per juvenile female)
Vital rate 2	0.6033 (adult fecundity, female offspring per adult female)
Vital rate 3	0.3 (juvenile survival, females)
Vital rate 4	0.68 (adult survival, females)
Vital rate 5	0.3946 (juvenile fecundity, male offspring per juvenile female)
Vital rate 6	0.3946 (adult fecundity, male offspring per adult female)
Vital rate 7	0.3 (juvenile survival, males)
Vital rate 8	0.68 (adult survival, males)
SD of vital rates	25% coefficient of variation (CV)
SD of vital rate 1	0.1508
SD of vital rate 2	0.1508
SD of vital rate 3	0.075
SD of vital rate 4	0.17
SD of vital rate 5	0.0986
SD of vital rate 6	0.0986
SD of vital rate 7	0.075
SD of vital rate 8	0.17
Stage-specific dispersal rates	50% (adults), 100% (juveniles)
Density Dependence type	Ceiling (affects all stages)

Table 1: Summary of demographic and spatial model parameters used in the Marsh Wren PVA.

Parameter	Value / Comment
Sex ratio	0.3952 (males) : 0.6048 (females)
Mating system	Polygynous: each male can mate with up to 3 females
Carrying capacity K	10 individuals per ha of highly suitable marsh habitat
SD of K	10% CV due to annual variations in water levels
Initial abundance	50% of K
HSI threshold	0.5
Neighborhood distance	60 m
Demographic stochasticity	Included
Environmental stochasticity	Lognormal distribution
Within population correlation	All vital rates correlated
Correlation distance function	Increases linearly from 75% to 100% from maximum (edge to edge) to minimum (adjacent cells) distance within landscape subset (a=1.0; b=30.0; c=1.0)
Dispersal distance function	a = 0.25; b = 1.0; c = 1.4; Dmax = 3.0;
Size of landscape subsets	100 km^2

3.1 Sensitivity analysis

We generated a set of 1000 parameter combinations by randomly varying 10 demographic parameters of the Marsh Wren model. The parameters include all vital rates of the stage matrix (vital rate 1-8) as well as the carrying capacity and the initial abundance.

The most important parameter was adult female survival (R^2 = 0.4172 for abundance and R^2 = 0.482 for extinction probability after 50 years). That is, changes in adult female survival explained most of the variation of the randomized parameter set. When abundance after 50 years was used as the model output variable the second most important parameter was the carrying capacity, followed by juvenile female survival (vital rate 3) (Figure 4). This was the opposite when extinction probability was used as the output variable (Figure 5; Table 2).

The Marsh Wren has a polygynous mating system where each male can mate with up to 3 females. According to this one would expect that male survival (as opposed to female survival) is limiting and should therefore show a higher effect if it is changed. However, looking at the assumed sex ratio explains why this is not the case. About 40% of all offspring produced are male (Table 1). Thus, all females are able to reproduce even if male survival is significantly reduced (i.e., a lower male survival rate is sampled during the randomized SA). Since each male can mate with up to 3 females, even under low male abundance full reproduction can occur and population growth therefore strongly depends on the actual number of females in a population. This is evidenced by the high importance of female survival.

To further prove this hypothesis, we ran another full sensitivity analysis where each male is able to mate with only a maximum of 1.3 females (lowest observed empirical rates). We hypothesized that this modification should lower the importance of female survival rates. In fact, reducing maximum polygyny to 1.3 females per male while keeping the female-biased sex ratio at the default value of 0.3952 (males) to 0.6048 (females) strongly reduced the importance of female vital rates (Figures 6 and 7). Using abundance and extinction risk as the model output variable R-squared values indicate that adult female survival is still the most important parameter (0.1874 and 0.2955, respectively). However, adult male survival (R^2 = 0.2697) was nearly as important as adult female survival if extinction risk was considered for parameter comparison (Table 3).

The results from the sensitivity analysis indicate that among all demographic parameters changes in female survival rates (and male survival for lower rates of polygyny) may have the highest impact on habitat-based standards (e.g., minimum habitat amount). In other words, if female survival rates are different from the ones assumed in the model (e.g., change over time or differ among sites) it is most likely that the recommended habitat-based standards need to be adjusted. This might be less so for other demographic parameters including the carrying capacity (i.e., the maximum observed population density). Surprisingly, the carrying capacity had an intermediate importance, although the assumed type of density dependence is ceiling and ceiling type has (among the three density dependence forms) the strongest suppressing effect on population growth.

Figure 4: Average abundances (50 stochastic replicates) after 50 years as a function of ten different demographic parameters included in the Marsh Wren sensitivity analysis (1000 random parameter combinations) (mating system: polygynous with 3.0 females per male). Vital rate 1 = juvenile fecundity (female offspring per juvenile female); vital rate 2 = adult fecundity (female offspring per adult female); vital rate 3 = juvenile survival (females); vital rate 4 = adult survival (females); vital rate 5 = (juvenile fecundity (male offspring per juvenile female); vital rate 6 = adult fecundity (male offspring per adult female); vital rate 7 = juvenile survival (males); vital rate 8 = adult survival (males).

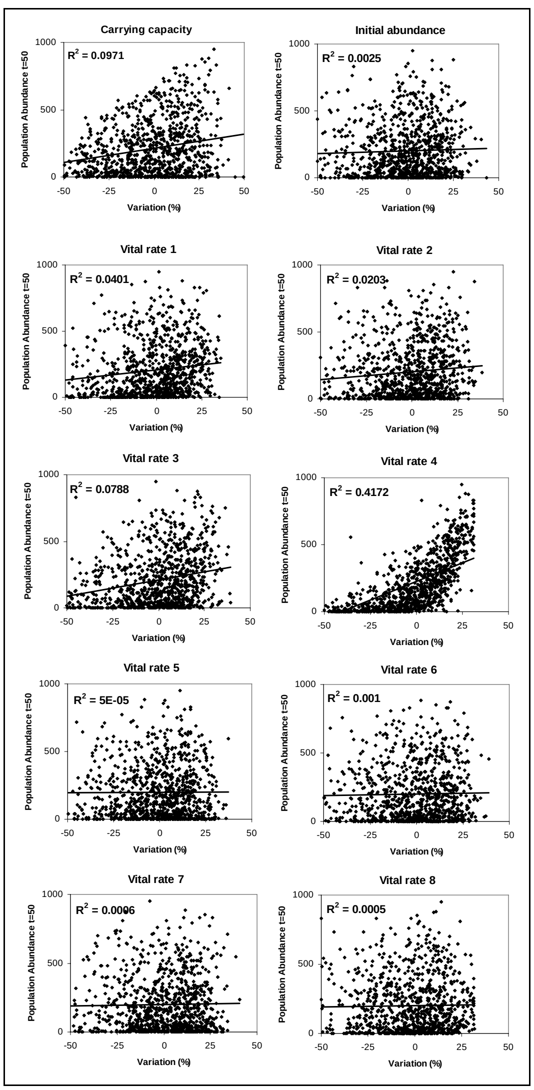


Figure 5: Average extinction probability (50 stochastic replicates) after 50 years as a function of ten different demographic parameters included in the Marsh Wren sensitivity analysis (1000 random parameter combinations) (mating system: polygynous with 3.0 females per male). Vital rate 1 = juvenile fecundity (female offspring per juvenile female); vital rate 2 = adult fecundity (female offspring per adult female); vital rate 3 = juvenile survival (females); vital rate 4 = adult survival (females); vital rate 5 = (juvenile fecundity (male offspring per juvenile female); vital rate 6 = adult fecundity (male offspring per adult female); vital rate 7 = juvenile survival (males); vital rate 8 = adult survival (males).

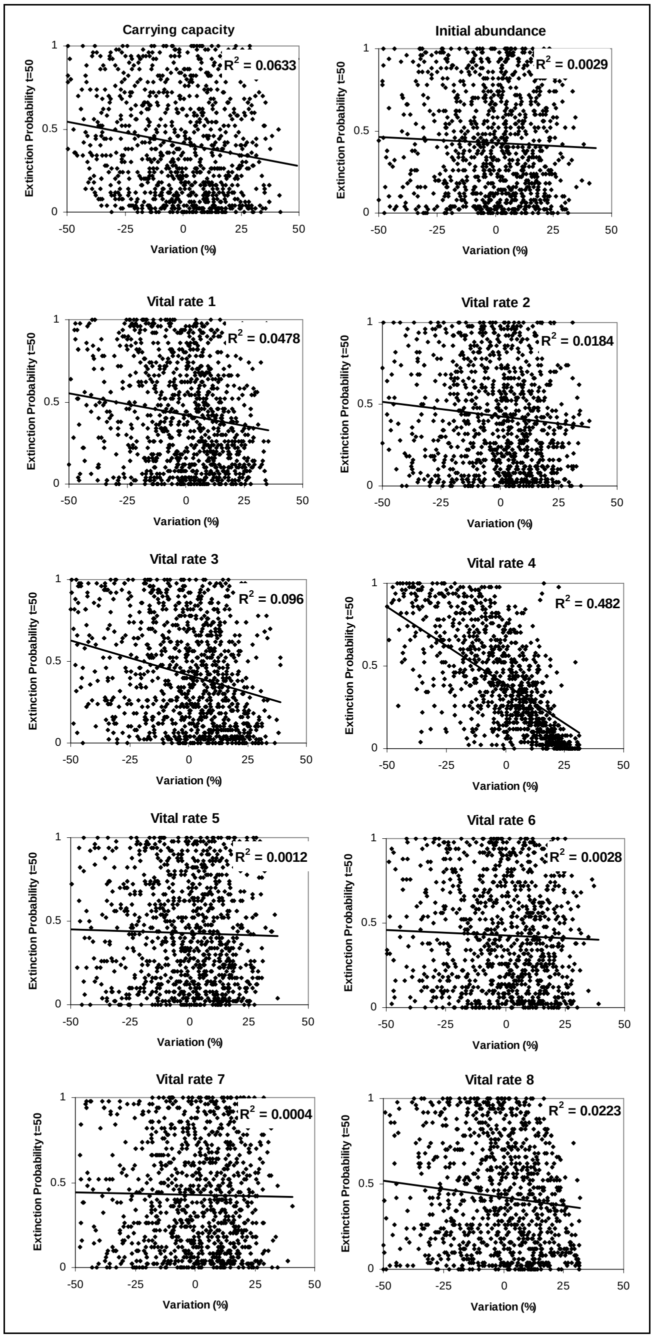


Table 2: Results from the sensitivity analysis (randomized parameter set) with R squared values for each demographic model parameter. The R-squared of the regression is the fraction of the variation in abundance or extinction predicted by each independent variable (i.e., demographic parameter). All model scenarios were based on a polygynous mating system where each male can mate with up to 3 females. The number of stars indicates ranking of the third most important parameters, respectively (* highest effect). Vital rates are represented by the following parameters: vital rate 1 = juvenile fecundity (female offspring per juvenile female); vital rate 2 = adult fecundity (female offspring per adult female); vital rate 3 = juvenile survival (females); vital rate 4 = adult survival (females); vital rate 5 = (juvenile fecundity (male offspring per juvenile female); vital rate 6 = adult fecundity (male offspring per adult female); vital rate 7 = juvenile survival (males); vital rate 8 = adult survival (males).**

	Default value	**R^2 (Abundance 50 yrs)**	**R^2 (Ext. prob.50 yrs)**
Carrying capacity	698	0.0971**	0.0633*
Initial abundance	698	0.0025	0.0029
Vital rate 1	0.6033	0.0401	0.0478
Vital rate 2	0.6033	0.0203	0.0184
Vital rate 3	0.3	0.0788*	0.0960**
Vital rate 4	0.68	0.4172***	0.4820***
Vital rate 5	0.3946	0.0001	0.0012
Vital rate 6	0.3946	0.0010	0.0028
Vital rate 7	0.3	0.0006	0.0004
Vital rate 8	0.68	0.0005	0.0223

Figure 6: Average abundances (50 stochastic replicates) after 50 years as a function of ten different demographic parameters included in the Marsh Wren sensitivity analysis (1000 random parameter combinations) (mating system: polygynous with 1.3 females per male). Vital rate 1 = juvenile fecundity (female offspring per juvenile female); vital rate 2 = adult fecundity (female offspring per adult female); vital rate 3 = juvenile survival (females); vital rate 4 = adult survival (females); vital rate 5 = (juvenile fecundity (male offspring per juvenile female); vital rate 6 = adult fecundity (male offspring per adult female); vital rate 7 = juvenile survival (males); vital rate 8 = adult survival (males).

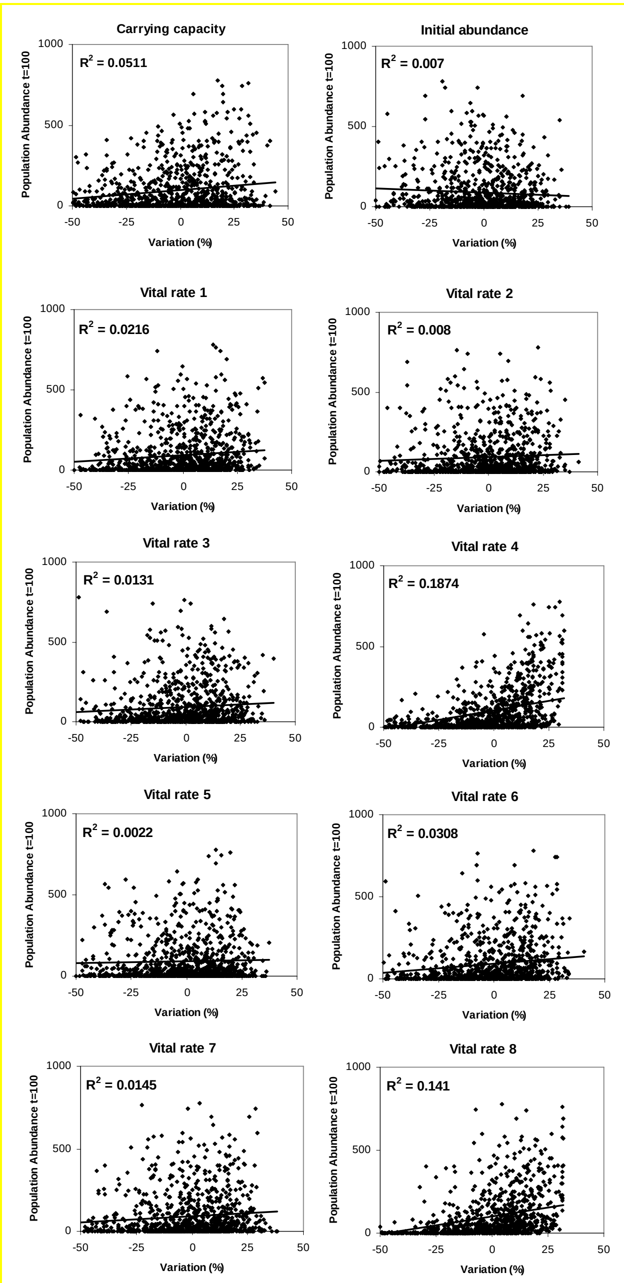


Figure 7: Average extinction probability (50 stochastic replicates) after 50 years as a function of ten different demographic parameters included in the Marsh Wren sensitivity analysis (1000 random parameter combinations) (mating system: polygynous with 1.3 females per male). Vital rate 1 = juvenile fecundity (female offspring per juvenile female); vital rate 2 = adult fecundity (female offspring per adult female); vital rate 3 = juvenile survival (females); vital rate 4 = adult survival (females); vital rate 5 = (juvenile fecundity (male offspring per juvenile female); vital rate 6 = adult fecundity (male offspring per adult female); vital rate 7 = juvenile survival (males); vital rate 8 = adult survival (males).

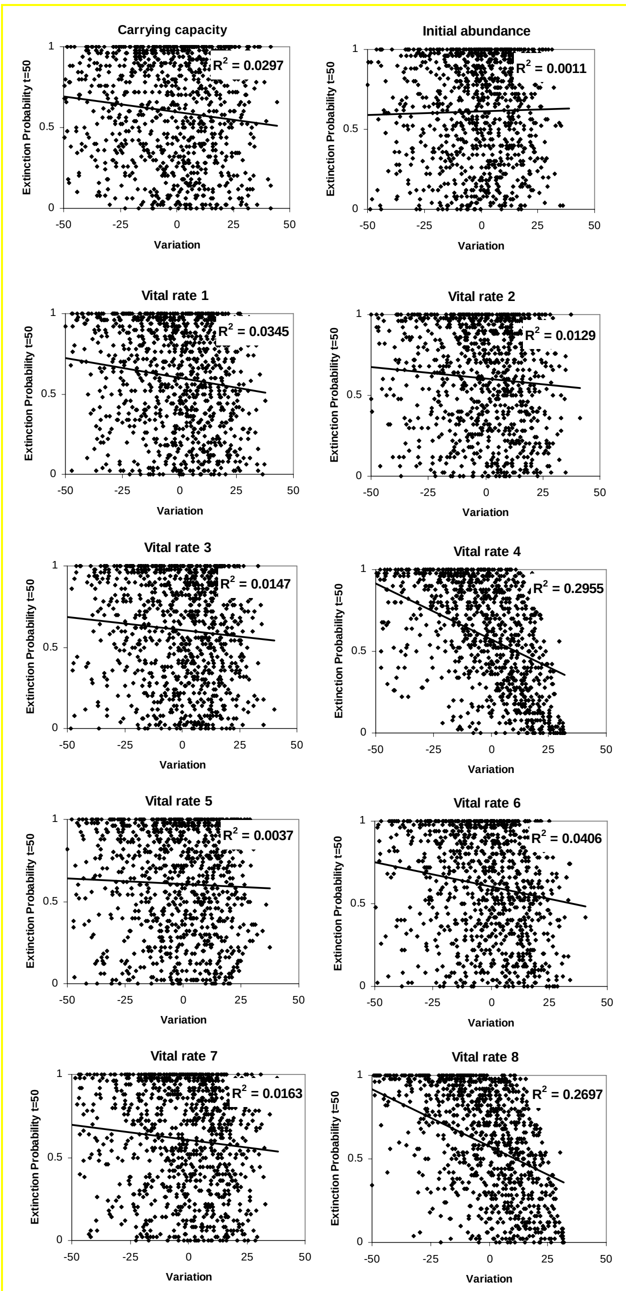


Table 3: Results from the sensitivity analysis (randomized parameter set) with R squared values for each demographic model parameter. The R-squared of the regression is the fraction of the variation in abundance or extinction predicted by each independent variable (i.e., demographic parameter). All model scenarios were based on a polygynous mating system where each male can mate with up to 1.3 females. The number of stars indicates ranking of the third most important parameters, respectively (* highest effect). Vital rates are represented by the following parameters: vital rate 1 = juvenile fecundity (female offspring per juvenile female); vital rate 2 = adult fecundity (female offspring per adult female); vital rate 3 = juvenile survival (females); vital rate 4 = adult survival (females); vital rate 5 = (juvenile fecundity (male offspring per juvenile female); vital rate 6 = adult fecundity (male offspring per adult female); vital rate 7 = juvenile survival (males); vital rate 8 = adult survival (males).**

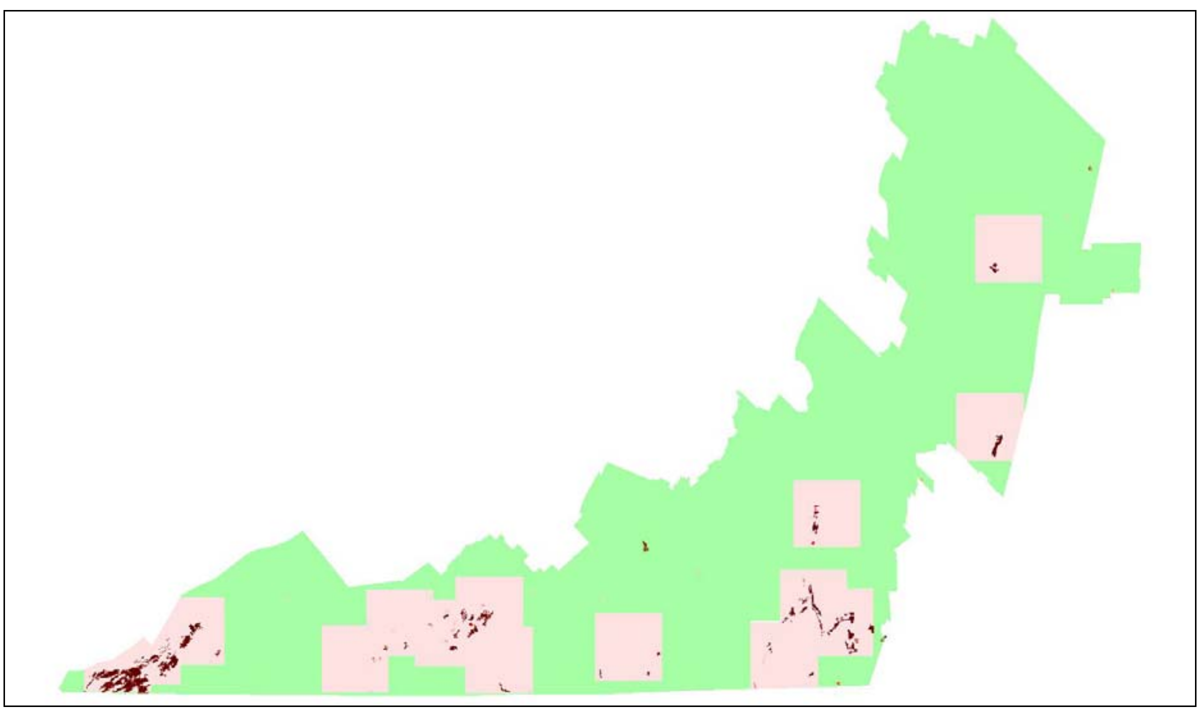
	Default value	**R^2 (Abundance 50 yrs)**	**R^2 (Ext. prob.50 yrs)**
Carrying capacity	698	0.0511*	0.0297
Initial abundance	698	0.0070	0.0011
Vital rate 1	0.6033	0.0216	0.0345
Vital rate 2	0.6033	0.0080	0.0129
Vital rate 3	0.3	0.0131	0.0147
Vital rate 4	0.68	0.1874***	0.2955***
Vital rate 5	0.3946	0.0022	0.0037
Vital rate 6	0.3946	0.0308	0.0406*
Vital rate 7	0.3	0.0145	0.0163
Vital rate 8	0.68	0.1410**	0.2697**

3.2 Moving window analysis

For the Marsh Wren population analysis we conducted a 'moving window' analysis where a 'moving' spatial grid (100 km^2) was dynamically placed across the habitat suitability map in the Québec pilot study area. Subsequently these landscape subsets were used as spatial input for the Marsh Wren population analysis.

Figure 8 shows the placement of 14 landscape subsets across the study region. Note that the placement was selective as suitable Marsh Wren habitat patches were restricted to specific areas. The habitat suitability model was based on the model of Maheu-Giroux (2007) (see also Tews, 2008) where index values range from 0.0 (unsuitable) to 1.0 (highest suitability). For creating the patch maps we assumed a habitat suitability threshold of 0.5 and a neighborhood distance of 2 cells (= 60 m, at a resolution of 30*30m per cell) (see also Table 1). The habitat suitability index (HSI) threshold defines the numerical boundary above which habitat cells are considered suitable. The neighborhood distance was based on average home ranges of adult male Marsh Wren (see Tews, 2008) and can be seen as a virtual 'glue' that aggregates suitable habitat cells into a single habitat patch. That is, if suitable cells are within 60 m of each other they will be considered as a continuous patch. The total habitat suitability of a patch then defines the carrying capacity of that patch. For example, for a patch with 4 cells with HSI = 0.8 and 4 cells with HSI = 1.0, i.e., a total of 8 cells (average HSI = 0.9, total area = 0.72 ha), the carrying capacity of that patch would be K = 6.48 (based on a carrying capacity of 10 males per ha for HSI=1.0; see Table 1).

Figure 8: Habitat suitability map for the Marsh Wren in the Québec pilot study area based on the HS model of Maheu-Giroux (2007). HSI values range from 0.0 (no suitability) to 1.0 (highest suitability). Landscape subsets (100 km^2) were selectively placed over all suitable habitat patches (HS threshold>0.5) and used for further spatial population analysis.



The Marsh Wren patch analysis for all 14 landscape subsets showed habitat amounts varying between 0.19% to 18.71% on a 100 km^2 scale (i.e., 19 ha to 18.71 km^2) (Table 4). Average distance to the nearest patch varied between 60 m to 8.26 km, while average patch size varied between 6.8 ha to 170.4 ha. Total carrying capacity varied between a maximum of 15,189 individuals for landscape subset #1 and 134 for # 5 (Table 4). Besides habitat amount (which co-determines total carrying capacity, in concert with the frequency distribution of habitat suitability classes), average patch size and average inter-patch distance among nearest neighbors are two important measures. Average patch size is an indicator for the degree of self-sustainability of a patch: if a patch is equal or larger than the minimum viable patch size of 65 ha, it is self-sustainable (<5% extinction risk over 50 years), and thus, does not require immigration. If patches are smaller than 65 ha, they require immigration over the course of 50 years in order to have an extinction risk of less than 5%. However, population exchange is only possible if two neighboring patches are closer to each other than the maximum dispersal distance (3 km assumed for Marsh Wren model, see Tews, 2008). Hence, average distance to the nearest patch is an indicator for the possibility of immigration/emigration between neighboring patches. Based on the computed average distances among neighboring patches (Table 4) (only one landscape has an average distance > 3 km) we can see that dispersal does not seem to be a limiting factor in this population analysis.

In the following step we then used all 14 landscape subsets as a spatial input for the Marsh Wren population analysis. Plotting habitat amount (%) versus viability (extinction probability) (Figure 9A) shows that most of the landscapes were viable over the course of 50 years. For habitat amounts of less than 15% a significant proportion of landscape subsets were unstable, i.e., >10% population decline (Figure 9B). All landscape samples also showed risks of 50% decline of larger than 50% (Figure 9C). A similar measure is relative expected minimum abundance (EMA) (Figure 9D). Relative expected minimum abundance is the ratio between expected minimum abundance (EMA = lowest average metapopulation abundance over 50 years) and initial abundance. In other words, a relative EMA of 0.25 would indicate that (on average) the lowest metapopulation abundance (over 50 years, averaged over 1000 replicate runs) was 25% of the initial abundance (i.e., higher values indicate better population performance). Relative EMA was below 50% for all habitat scenarios (Figure 9D). Viability and stability also declined with decrease in average patch size (Figures 10B and C).

Landscape subsets with an average patch size larger than 20 ha and a habitat amount of more than 1% showed an extinction risk of less than 5% over 50 years. For stability, i.e., less then 10% population decline over 50 years, (minimum) average patch size was 50 ha (Figure 10). Variations in average nearest-patch distance did not show any significant impacts as metapopulations were not dispersal limited in the large majority of landscape subsets (Figure 10A).

Figure 9: Simulation results of the spatial-explicit Marsh Wren PVA based on 14 case study areas (10*10 km in size) in the Québec pilot study area. Figures A to D show extinction probability (A), trend in abundance from initial to final year 50 (B), functionality measured as risk of decline to 50% of the initial abundance (C), and relative expected minimum abundance (EMA) (i.e., lowest abundance over the course of a simulation trajectory averaged over all simulation replicates relative to the initial population size) (D). Figure panels A to D are plotted against percent habitat amount for each 100 km² landscape subset.

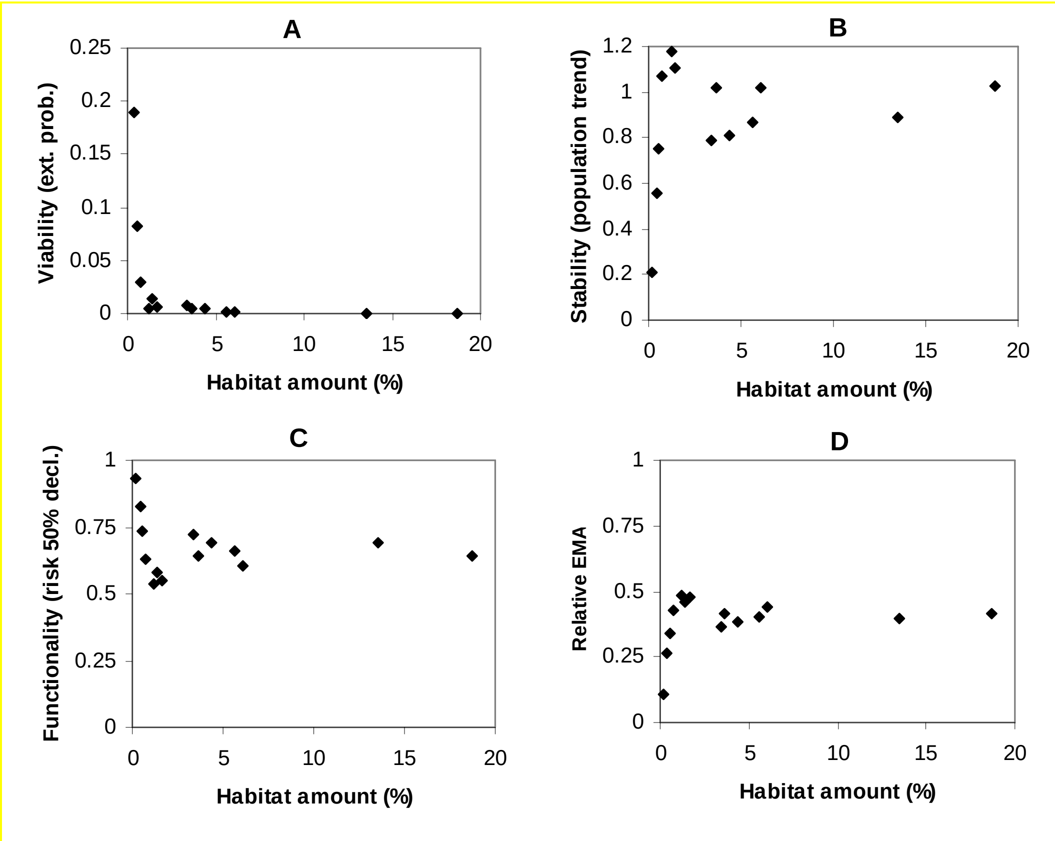


Figure 10: Simulation results of the spatial-explicit Marsh Wren PVA based on 14 case study areas (10*10 km in size) in the Québec pilot study area. Figure A shows extinction probability plotted against average nearest-patch distance (km) (i.e., average distance among all pairs of nearest neighbor patches), B shows viability plotted versus average patch size, and C stability (i.e., 50-year population trend) as a function of average patch size.

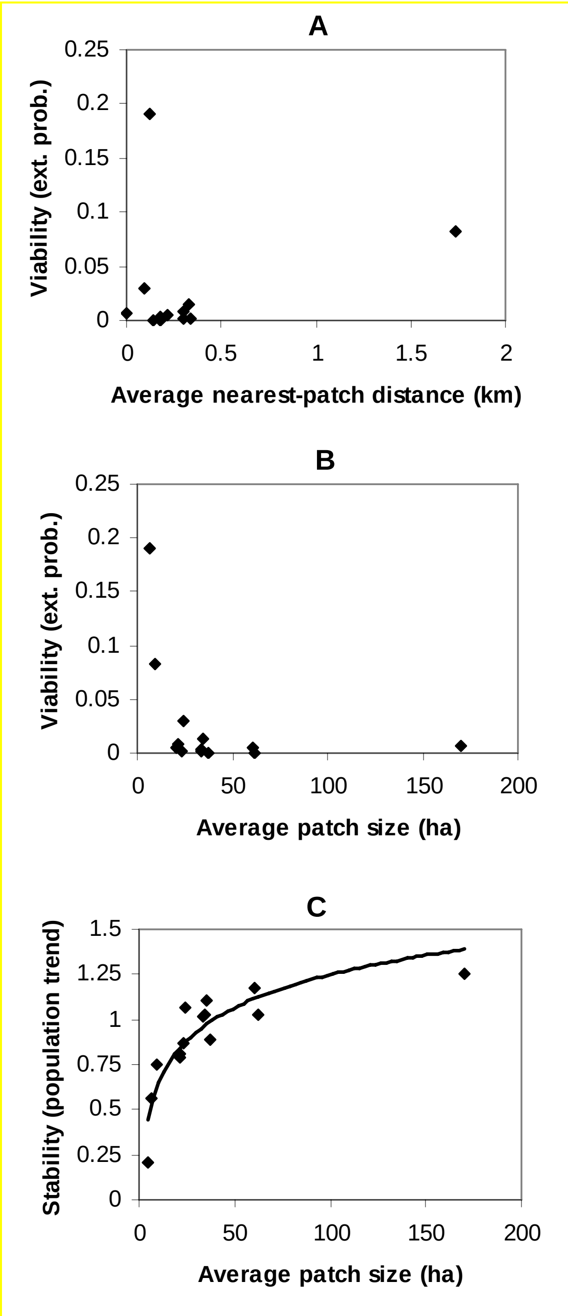


Table 4: Results from the Marsh Wren patch analysis for 14 landscape subset (100 km^2).

Area	# of populations	K (total)	Average habitat suitability	Average patch size (ha)	Average distance to nearest patch (km)	Habitat amount (%)
1	25	15189	0.86	62.0	0.14	18.71
2	37	13142	0.85	37.0	0.18	13.52
3	25	5327	0.86	23.0	0.30	5.62
4	6	310	0.72	6.8	0.12	0.41
5	4	134	0.66	4.7	0.06	0.19
6	16	3175	0.85	21.7	0.30	3.40
7	11	3402	0.87	33.5	0.18	3.66
8	2	1159	0.95	60.7	8.26	1.21
9	6	473	0.81	9.3	1.74	0.55
10	18	5732	0.88	34.1	0.34	6.07
11	21	4081	0.89	21.0	0.22	4.37
12	4	1213	0.76	34.9	0.33	1.39
13	1	1654	0.97	170.4	0.06	1.68
14	3	703	0.95	24.4	0.09	0.73

Table 5: Results from the spatial Marsh Wren PVA based on 14 landscape subsets as model input. Population trend was calculated as the ratio of average final population size to initial population size (50 years). Risk of decline refers to the risk of decline to 50% of the initial population abundance in any given year over the course of a simulation trajectory. Relative EMA is the ratio of EMA to initial population size.

Area	Extinction probability	Initial abundance	Average final abundance	Population trend	Risk of decline	Expected minimum abundance (EMA)	Relative EMA
1	0.000	7594	7772	1.02	0.643	3152	0.415
2	0.000	6572	5828	0.88	0.690	2586	0.393
3	0.002	2665	2316	0.86	0.660	1067	0.400
4	0.190	154	86	0.55	0.827	41	0.266
5	0.669	67	14	0.20	0.935	7	0.104
6	0.008	1587	1250	0.78	0.724	575	0.362
7	0.004	1699	1731	1.01	0.645	700	0.412
8	0.005	579	682	1.17	0.534	282	0.487
9	0.082	237	178	0.75	0.732	81	0.341
10	0.001	2869	2933	1.02	0.607	1263	0.440
11	0.005	2042	1651	0.80	0.689	789	0.386
12	0.014	606	671	1.10	0.582	277	0.457
13	0.006	827	1039	1.25	0.549	395	0.477
14	0.039	352	376	1.06	0.630	150	0.426

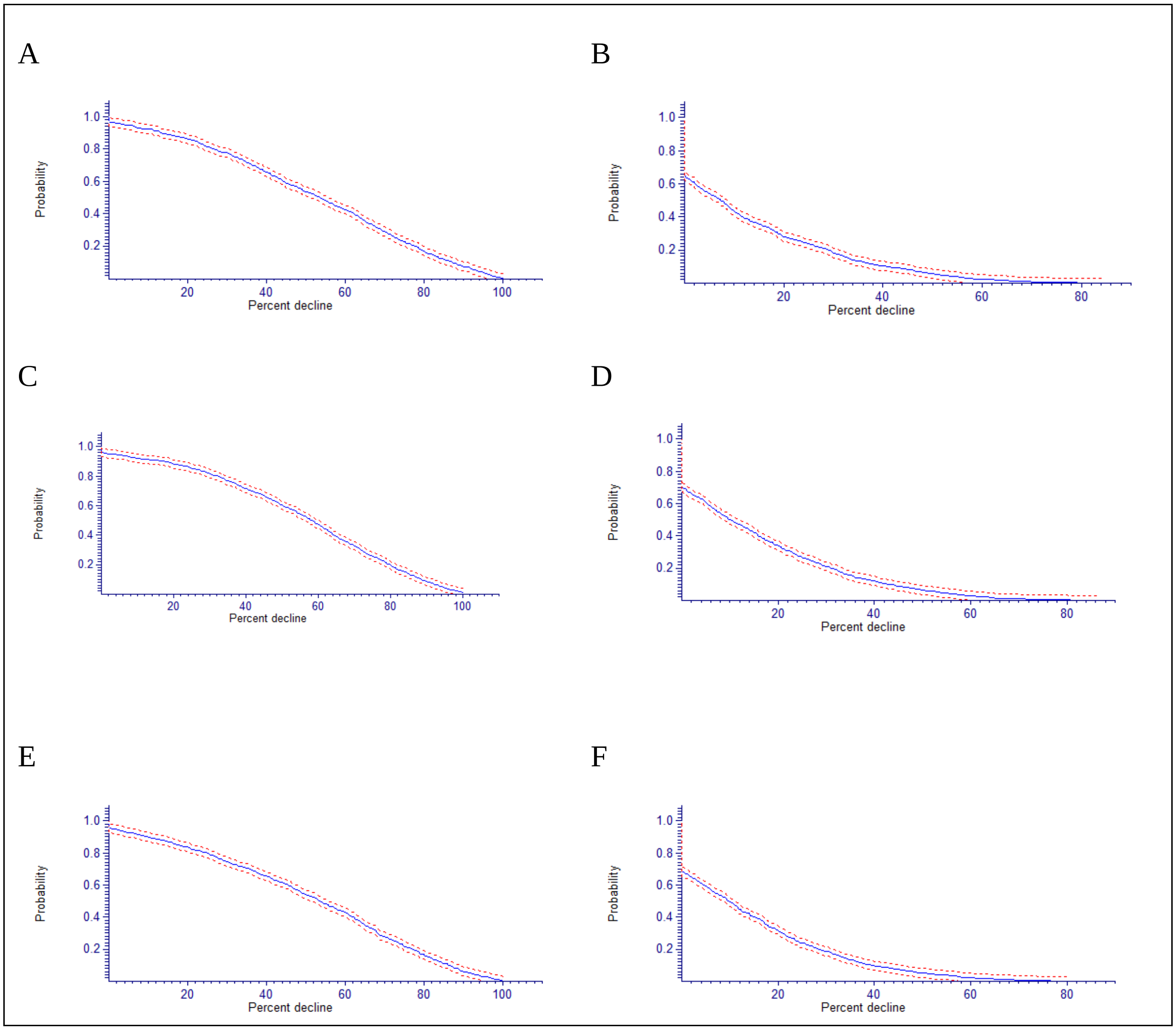
As none of the landscape subsets showed sufficient levels of ‘functionality’ (i.e., <5% risk of decline to 50% of initial abundance), we were interested under which model assumptions a ‘functional’ metapopulation may be achieved.

In general, the probability that a population declines to below a certain threshold (at least once during the simulation trajectory) is correlated with the degree of stochastic population fluctuations. We hypothesized that environmental stochasticity (besides habitat conditions) is important (demographic) driver for levels of functionality. We therefore decreased standard deviations in the stage matrix to analyze the resulting effects and see whether our hypothesis can be supported. For this purpose we reduced the stage matrix standard deviations by 10%, 20%, 30%, and 40% for three landscape subsets which had the best ‘functionality’ performance in the original data set (#8, #12, #13). Results from this simulation experiment show that desired levels of functionality (i.e., <5%) can only be achieved if standard deviations are reduced to as much as 40% of the assumed default value (Table 6 and Figure 10). However, even though base levels of standard deviations of the vital rates (i.e., fecundity and survival) are rough estimates based on field data, it can be assumed that such strongly reduced levels of environmental fluctuations are unlikely to occur as marshes are often subject to changes in water levels and these, in turn, can affect egg mortality and reproduction substantially. In essence, the performance goal of functional presence was not achieved for any of the landscape subset scenarios unless standard deviations of the stage matrix (i.e., biologically speaking, environmental fluctuations that affect reproduction and survival) were strongly reduced.

Table 6: Results from the spatial Marsh Wren PVA based on proportional (%) changes in the standard deviation (SD) of the stage matrix. The population trend was calculated as the ratio of average final population size to initial population size (50 years). Risk of decline refers to the risk of decline to 50% of the initial population abundance in any given year over the course of a simulation trajectory.

Area	Change in SD (%)	Population trend	Risk of decline	Habitat amount (%)	# of pop.	K
8	0	1.17	0.534	1.21	2	1159
8	-10	1.28	0.430	-	-	-
8	-20	1.43	0.253	-	-	-
8	-30	1.59	0.140	-	-	-
8	-40	1.73	0.058	-	-	-
12	0	1.10	0.582	1.39	4	1213
12	-10	1.24	0.471	-	-	-
12	-20	1.39	0.296	-	-	-
12	-30	1.54	0.169	-	-	-
12	-40	1.67	0.064	-	-	-
13	0	1.25	0.549	1.68	1	1654
13	-10	1.35	0.427	-	-	-
13	-20	1.47	0.274	-	-	-
13	-30	1.62	0.144	-	-	-
13	-40	1.75	0.049	-	-	-

Figure 11: Probability of risk of decline for the default (A, C, E) and a 40% reduction (B, D, F) in standard deviations of the Marsh Wren stage matrix. Figures A-B: area # 8, C-D: area # 12, E-F: area # 13. The probability of risk of decline refers to the risk of decline to a given proportion of the initial population abundance in any given year over the course of a simulation trajectory.



3.3 Recommended habitat-based standards

Based on the model assumptions and a simulation trajectory of 50 years the following habitat-based standards were recommended in the previous analysis (Tews, 2008): (i) a minimum patch size of 2 - 10 ha to avoid patches being a strong population sink (depending on habitat quality),

(ii) a minimum patch size of 65 ha of suitable habitat (based on an average population density of 0.25 ha per male) to support a single, viable population, (iii) a maximum inter-patch distance of 2 km to allow sufficient natal and breeding dispersal, and (iv) a minimum amount of 0.9% suitable marsh habitat to support a viable, and stable metapopulation. These standards were based on a spatial population model linked with a habitat suitability map of the entire NAESI Québec study area (4869 km^2). With this in-depth population modeling analysis we provide a detailed re-assessment, in particular for standard #4. Based on empirical data, the assumptions of the population model and its application in the NAESI Québec pilot study area we finally suggest the following habitat-based standards for the Marsh Wren:

- a minimum patch size of 10 ha to reduce possible population sink dynamics
- a minimum patch size of ~65 ha of suitable habitat (based on an average population density of 0.25 ha per male) to support a single, viable population over 50 years with 95% confidence
- a maximum inter-patch distance of ~2 km to facilitate sufficient natal and breeding dispersal
- a minimum amount of ~1% (~100 ha) suitable habitat and an average patch size of more than 20 ha to support a viable metapopulation on a spatial scale of 100 km2
- a minimum amount of 15% (~15 km2) suitable habitat and an average patch size of more than 50 ha to support a stable metapopulation on a spatial scale of 100 km2

We were not able to detect specific habitat thresholds for ‘functionality’ (i.e., < 5% risk of decline to 50% of initial abundance in any year over 50 years). Functional presence was only achieved for significantly lower standard deviations of the vital rates. However, based on the simulations it appears that for desired levels of functionality minimum habitat requirements ought to be present that would at least support ‘stable’ metapopulations.

The above habitat-based standards are subject to changes in the model assumptions. Particularly, as indicated by the sensitivity analysis, any deviations from the assumed survival rates of females would require a re-assessment of the recommended standards. Moreover, absolute minimum habitat amount (km^2) will most likely be higher if larger spatial scales are considered (due to declines in average inter-patch distance with increase in area).

4 OVENBIRD

The Ovenbird (*Seiurus aurocapillus* L.) is a common long-distance neotropical migratory passerine that breeds across Canada from northeast British Columbia to Newfoundland and south to North Carolina in the United States. Ovenbirds typically breed in large, mature deciduous forests where they build a domed nest of leaves and grass on the ground. Due to current fragmentation and loss of habitat in the St. Laurence Lowlands Ecoregion previous population modeling analyses showed relatively high risks of extinctions for a wide range of model scenarios (Noreca Consulting and Elutis Modeling and Consulting Inc., 2007; Tews, 2008). Extinction risk was high and population trends negative for all sampled sub-populations in the eastern Ontario pilot region (Noreca Consulting and Elutis Modeling and Consulting Inc., 2007). A summary of demographic and spatial model parameters used in this population analysis is given in Table 7. Literature references for the model parameters are given in Noreca Consulting and Elutis Modeling and Consulting Inc. (2007) and Tews (2008).

A population analysis conducted for the Québec pilot study area (Tews, 2008) suggested the following habitat-based standards: (i) a minimum patch size of 200 ha of highly suitable forest habitat to provide a population source (based on the assumed stage matrix and a minimum of

87% pairing success resulting in a minimum intrinsic rate of increase of 1.0), (ii) a minimum patch size of 850 ha of suitable habitat (based on an average population density of 0.24 individuals per ha) to support a single, viable population, (iii) a minimum amount of 20% - 40% suitable forest habitat at a spatial scale of 250 km^2 to support a viable metapopulation, (iv) a minimum of 80-90% of the total population abundance distributed across large, self-sustainable forest patches (lambda>1.0, > approx. 200 ha) to support near stable population trends. With this in-depth population analysis we will re-assess and further extend these habitat-based standards.

In the following two sections we will discuss the results of the sensitivity analysis and 'moving window' analysis. The relatively large number of landscape subsets (compared to the previous study, see Tews, 2008) will facilitate a more thorough assessment of habitat amount standards. That is, it allows to specifically assess under which specific habitat conditions 'viable', 'stable' and 'functional' levels of metapopulation dynamics can be achieved. For the moving window analysis we chose a spatial scale of 250 km^2 (25,000 ha) to remain consistent with the landscape subset size in the previous study (Tews, 2008) and also to accommodate the large minimum viable patch size of 850 ha. Further enlargement of the landscape size would have increased the degree of 'noise' for model interpretation as the 'regional' metapopulation may then be comprised of subsets (or compartments) of 'local' metapopulations.

Table 7: Summary of demographic and spatial model parameters used in the Ovenbird PVA. Literature references for parameters are given in Noreca Consulting and Elutis Modeling and Consulting Inc. (2007) and Tews (2008).

Parameter	Value / Comment
Replications	1000
Duration	50 years
Stage 1	Juveniles
Stage 2	Adults
Vital rate 1	0.434 (juvenile fecundity)

Table 7: Summary of demographic and spatial model parameters used in the Ovenbird PVA. Literature references for parameters are given in Noreca Consulting and Elutis Modeling and Consulting Inc. (2007) and Tews (2008).

Parameter	Value / Comment
Vital rate 2	0.434 (adult fecundity)
Vital rate 3	0.623 (juvenile survival)
Vital rate 4	0.623 (adult survival)
SD of vital rates (fecundity)	30% coefficient of variation (CV)
SD of vital rates (survival)	15% coefficient of variation (CV)
SD of vital rate 1	0.1302
SD of vital rate 2	0.1302
SD of vital rate 3	0.0934
SD of vital rate 4	0.0934
Sex structure	Female-only model
Density Dependence type	Ceiling (affects all stages)
Sex ratio	0.5 (males) : 0.5 (females)
Carrying capacity K	1 female per ha
SD of K	10% CV
Initial abundance	50% of K
HSI threshold	0.5
Neighborhood distance	90 m (based on average home range sizes of 0.61 – 1.6 ha)
Patch size threshold	To avoid overestimates of carrying capacity a patch needs to support at least 5 breeding pairs
Demographic stochasticity	Included
Environmental stochasticity	Lognormal distribution
Within population correlation	All vital rates are correlated
Correlation distance function	Increases linearly from 50% to 100% from maximum (edge to edge) to minimum (adjacent cells) distance within landscape subset (a=1.0; b=30.0; c=1.0)
Dispersal distance function	a = 0.1; b = 1.0; c = 1.0; Dmax = 5.0;
Size of landscape subsets	250 km^2

4.1 Sensitivity analysis

We generated a set of 1000 model scenarios by randomly varying 6 demographic parameters. The parameters included all vital rates of the stage matrix (vital rate 1-4) as well as the carrying capacity and the initial abundance. This set of 1000 model scenarios was then executed in Ramas©MetaPop each with 50 stochastic runs over 50 years. That is, a total of 50,000 simulations were analyzed for the Ovenbird SA.

The most important parameter was adult survival rate both when abundance (after 25 years) and extinction risk (after 20 years) were output variables (R^2 = 0.4111 and R^2 = 0.5711, respectively) (Figures 12 and 13). That is, changes in adult survival explained most of the variation of the randomized parameter set (Table 8). When abundance or extinction risk after 50 years was used as the output variable parameter comparison was impracticable due to the relatively low persistence probability of the standard demographic model (intrinsic rate of increase or eigenvalue of the stage matrix = 1.05). Hence, a shorter time period was chosen with the majority of final abundances > 1.

For both abundance and extinction risk as model output the second and third most important parameters were juvenile survival and adult fecundity, respectively (Table 8). Although increases in the carrying capacity slightly increased average final abundance (Figure 12) and the density dependence function in the Ovenbird population model was 'ceiling' type, the overall importance of the carrying capacity was low indicated by a low R-squared value. Initial abundances did not show any effect on the model output as abundance over time is driven by the stage matrix and the population ceiling which is set by the carrying capacity.

Table 8: Results from the sensitivity analysis (randomized parameter set) with R squared values for each demographic model parameter. The R-squared of the regression is the fraction of the variation in abundance or extinction predicted by each independent variable (i.e., demographic parameter). The number of stars indicates ranking of the third most important parameters, respectively (* highest effect). Vital rates are represented by the following parameters: vital rate 1 = juvenile fecundity; vital rate 2 = adult fecundity; vital rate 3 = juvenile survival; vital rate 4 = adult survival.**

	Default value	R^2 (Abundance 25 yrs)	R^2 (Ext. prob.20 yrs)
Carrying capacity	102	0.0641	0.0059
Initial abundance	102	0.0003	0.0005
Vital rate 1	0.434	0.0505	0.0649
Vital rate 2	0.434	0.0675*	0.1028*
Vital rate 3	0.623	0.1071**	0.1155**
Vital rate 4	0.623	0.4111***	0.5711***

Figure 12: Average abundances (50 stochastic replicates) after 25 years as a function of six different demographic parameters included in the Ovenbird sensitivity analysis (1000 random parameter combinations). Vital rate 1 = juvenile fecundity; vital rate 2 = adult fecundity; vital rate 3 = juvenile survival; vital rate 4 = adult survival.

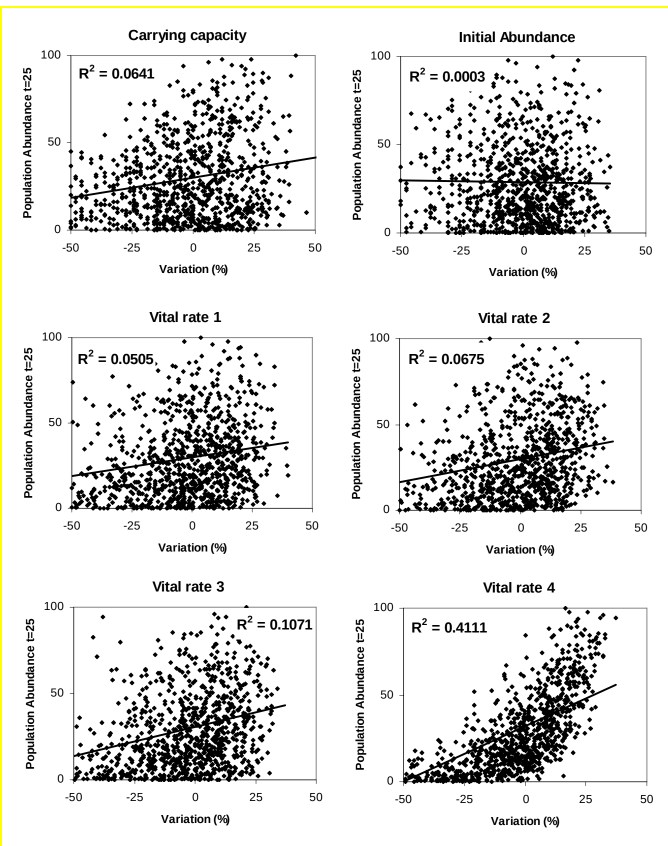
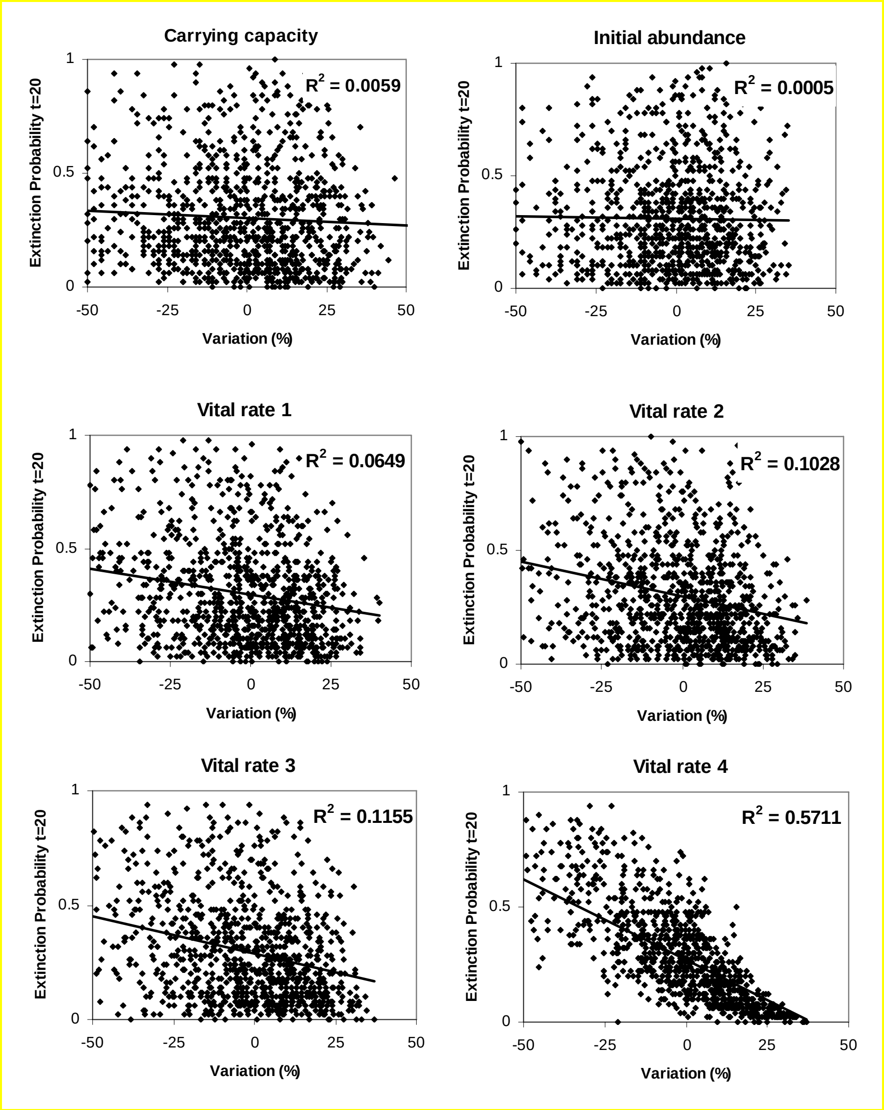


Figure 13: Average extinction risks (50 stochastic replicates) after 20 years as a function of six different demographic parameters included in the Ovenbird sensitivity analysis (1000 random parameter combinations). Vital rate 1 = juvenile fecundity; vital rate 2 = adult fecundity; vital rate 3 = juvenile survival; vital rate 4 = adult survival.

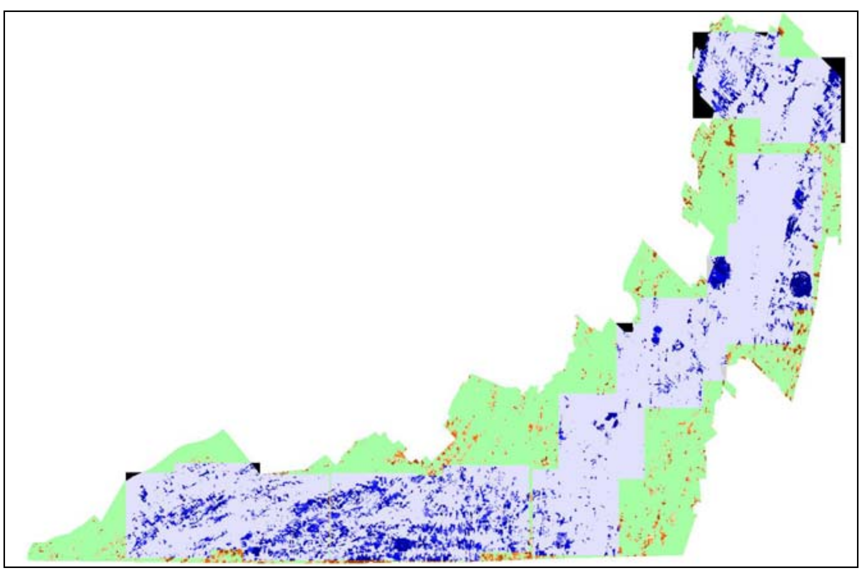


4.2 Moving window analysis

For the Ovenbird population analysis we conducted a ‘moving window’ analysis where a ‘moving’ spatial grid (250 km^2) was dynamically placed across the habitat suitability map in the Québec pilot study area. Subsequently, these landscape subsets were used as spatial inputs for the population analysis.

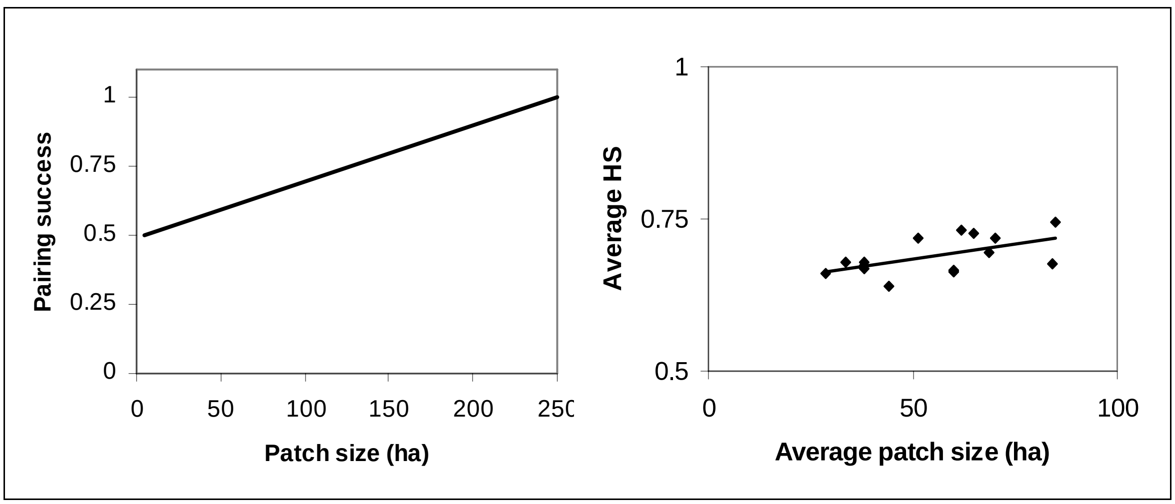
Figure 14 shows the placement of 15 landscape subsets across the study region. Landscape subsets were placed so that most of the habitat in the pilot study area was included and a maximum sampling variation in regional habitat conditions achieved. The habitat suitability model was based on the model presented in Tews (2008) with index values ranging from 0.0 (unsuitable) to 1.0 (highest suitability). For creating the patch import maps for Ramas©MetaPop we assumed a habitat suitability threshold of 0.5 and a neighborhood distance of 3 cells, i.e., 90 m (Table 7). The habitat suitability index (HSI) threshold defines the numerical boundary above which habitat cells are considered suitable. The neighborhood distance was based on average home range sizes of 0.61-1.6 ha (see references in Tews, 2008) and functions as a virtual 'glue' that aggregates suitable habitat cells into a single habitat patch. That is, if suitable cells are within 90 m of each other they will be considered as one continuous patch. The total habitat suitability of a patch then defines the carrying capacity of that patch (see calculation example in section 3.2)

Figure 14: Habitat suitability map for the Ovenbird in the Québec pilot study area based on the HS model in Tews (2008). HSI values range from 0.0 (no suitability) to 1.0 (highest suitability). A series of 15 landscape subsets (250 km^2, in blue) were placed over suitable habitat patches (HS threshold>0.5) and used for spatial population analysis.



For the Ovenbird HS model it was assumed that base fecundity rates of the stage matrix apply only for patches larger than 250 ha. For smaller patches a scaling factor is used to represent lower pairing success (see Tews, 2008). In other words, pairing success is a function of the size of a patch, i.e., fecundity increases with patch size (Figure 15). Forest patches smaller than 5 ha were considered to be unsuitable (Tews, 2008). As evident in Figure 15 (right figure) average habitat suitability increases with average patch size because index values are reduced by 50% if a cell is identified as an edge cell (a smaller patch contains more edge habitat). Smaller patches therefore lower the habitat suitability value but also have reduced pairing success.

Figure 15: Assumed Ovenbird pairing success as a function of patch size as implemented in the habitat suitability model (left figure) and average habitat suitability plotted against average patch size for each landscape subset (right figure).



The Ovenbird patch analysis for 15 landscape subsets in the NAESI Québec pilot study area showed habitat amounts varying between 2.91% to 23.68% on a 250 km^2 scale (i.e., 7.27 km^2 to 59.2 km^2) (Table 9). Average patch size varied between 28.5 ha to 84.0 ha. Total carrying capacity varied between a maximum of 4,183 for landscape subset #4 and 533 females for #7 (Table 4). Besides habitat amount (which co-determines total carrying capacity, in concert with the frequency distribution of habitat suitability classes), average patch size is an important habitat measure. Average patch size in a landscape subset is an indicator for the degree of self-sustainability. The minimum viable patch size for Ovenbird is relatively large (850 ha), however, even smaller differences in average patch size are of importance for metapopulation persistence probability as they directly influence patch-specific fecundity rates. We did not plot average inter-patch distances among nearest neighbors as the maximum dispersal distance (see Table 7) is larger than most of the average inter-patch distances and therefore dispersal was regarded as not a limiting factor in the population analysis.

Table 9: Results from the patch analysis for each 250 km^2 landscape subset.

Area	# of populations	K (total)	Average habitat suitability	Average patch size (ha)	Habitat amount (%)
1	67	1506	0.678	33.5	9.11
2	57	1491	0.673	38.2	8.73
3	69	2818	0.665	60.0	16.65
4	72	4183	0.677	84.0	23.68
5	88	3570	0.664	60.0	21.05
6	79	2245	0.638	44.0	13.80
7	14	533	0.718	51.3	2.91
8	28	729	0.680	38.0	4.38
9	36	1962	0.719	70.0	9.83
10	31	2298	0.744	85.0	10.6
11	24	1250	0.726	65.0	6.25
12	41	2018	0.694	68.5	11.18
13	36	1691	0.731	62.0	9.19
14	44	818	0.660	28.5	4.97
15	27	698	0.668	38.0	4.13

In the following step we then used all 15 landscape subsets as a spatial input for the Ovenbird population analysis. The results from this analysis are given in Table 10 and visualized in Figures 16 and 17. Plotting habitat amount (%) versus viability (extinction probability) (Figure 16A) shows that landscapes with more than 10% habitat amount were viable (i.e., <5% extinction risk) over the course of 50 years. All landscape scenarios resulted in unstable (i.e., >10% population decline) metapopulations (Figure 16B). All landscape subsets also showed risks of 50% decline of larger than 60% (Figure 16C). A similar measure is relative expected minimum abundance (EMA) (Figure D) (see variable explanation in section 3.1). Relative EMA was below 50% for all habitat scenarios (Figure 16D). Viability and stability also declined with decrease in average patch size (Figures 17A and B). Landscape subsets with an average patch size larger than ~60 ha and a habitat amount of more than 10% did show less then 5% extinction risk over 50 years. With increase in average patch size risk of decline and relative EMA decreased and increased, respectively (Figures 17C and D).

Table 10: Results from the spatial Ovenbird population analysis based on each landscape subset as a model input. Population trend was calculated as the ratio of average final population size to initial population size. Risk of decline refers to the risk of decline to 50% of the initial population abundance in any given year over the course of a simulation trajectory. Relative EMA is the ratio of EMA to initial population size.

Area	Extinction probability	Initial abundance	Average final abundance	Population trend	Risk of decline	Expected minimum abundance (EMA)	Relative EMA
1	0.764	754	1.58	0.002	1.000	1	0.001
2	0.442	745	11.46	0.015	1.000	8	0.010
3	0.026	1405	182	0.129	0.999	115	0.081
4	0.002	2091	675	0.322	0.958	397	0.189
5	0.004	1780	432	0.242	0.985	252	0.141
6	0.038	1123	166.7	0.148	1.000	85	0.075
7	0.264	268	28.8	0.107	1.000	16	0.061
8	0.032	354	142	0.401	0.983	65	0.184
9	0.000	978	809	0.827	0.693	386	0.395
10	0.002	1149	827	0.719	0.749	400	0.347
11	0.002	626	398	0.635	0.808	195	0.311
12	0.017	1006	205	0.203	0.983	124	0.123
13	0.007	847	336	0.396	0.957	178	0.210
14	0.949	414	0.3	0.000	1.000	0	0.000
15	0.025	350	141	0.402	0.973	67	0.190

Figure 16: Simulation results of the spatial-explicit Ovenbird PVA based on 15 case study areas (250 km^2) in the Québec pilot study area. Figures A to D show extinction probability (A), trend in abundance from initial to final year 50 (B), functionality measured as risk of decline to 50% of the initial abundance (C), and relative expected minimum abundance (EMA) (i.e., lowest abundance over the course of a simulation trajectory averaged over all simulation replicates relative to the initial population size) (D). All performance measures are plotted against percent habitat amount in each landscape subset. Red dots indicate simulation results from Tews (2008).

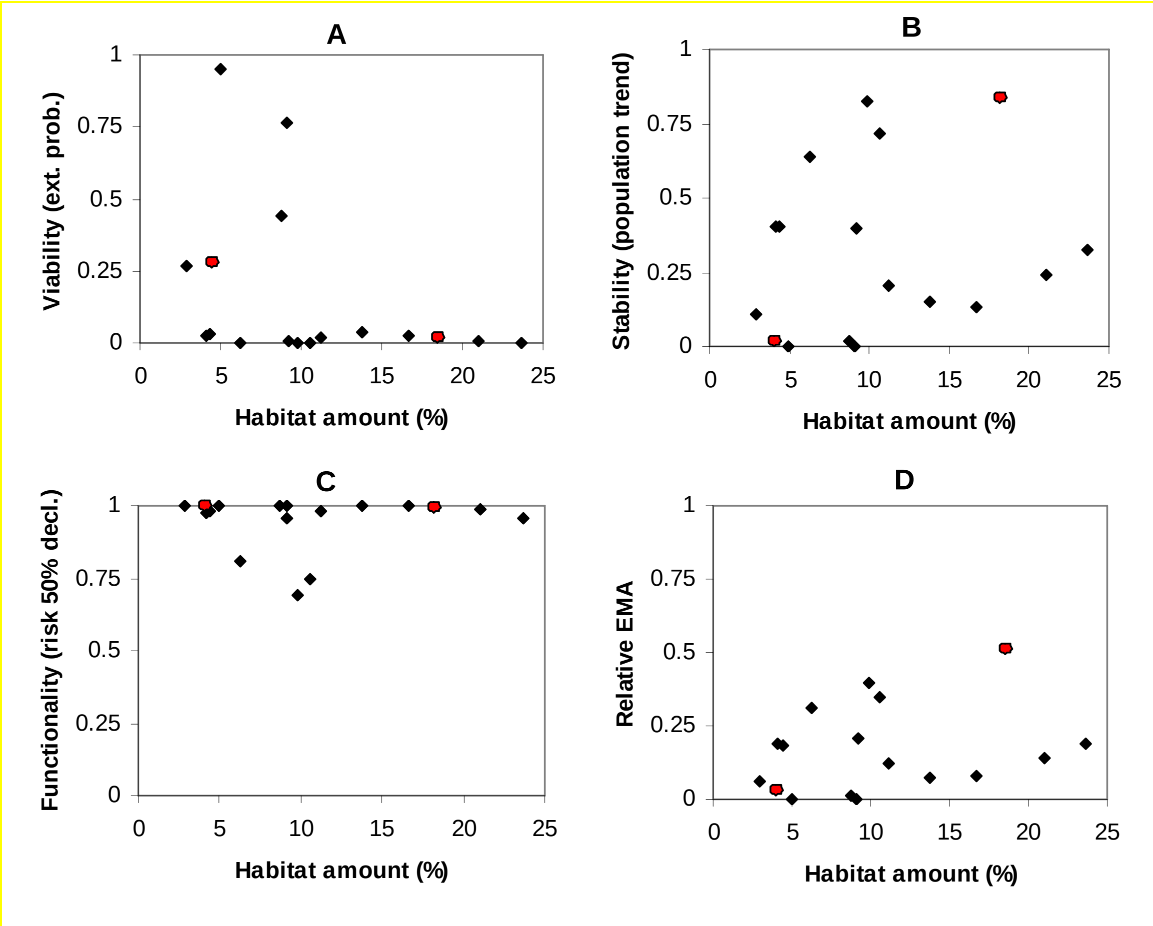
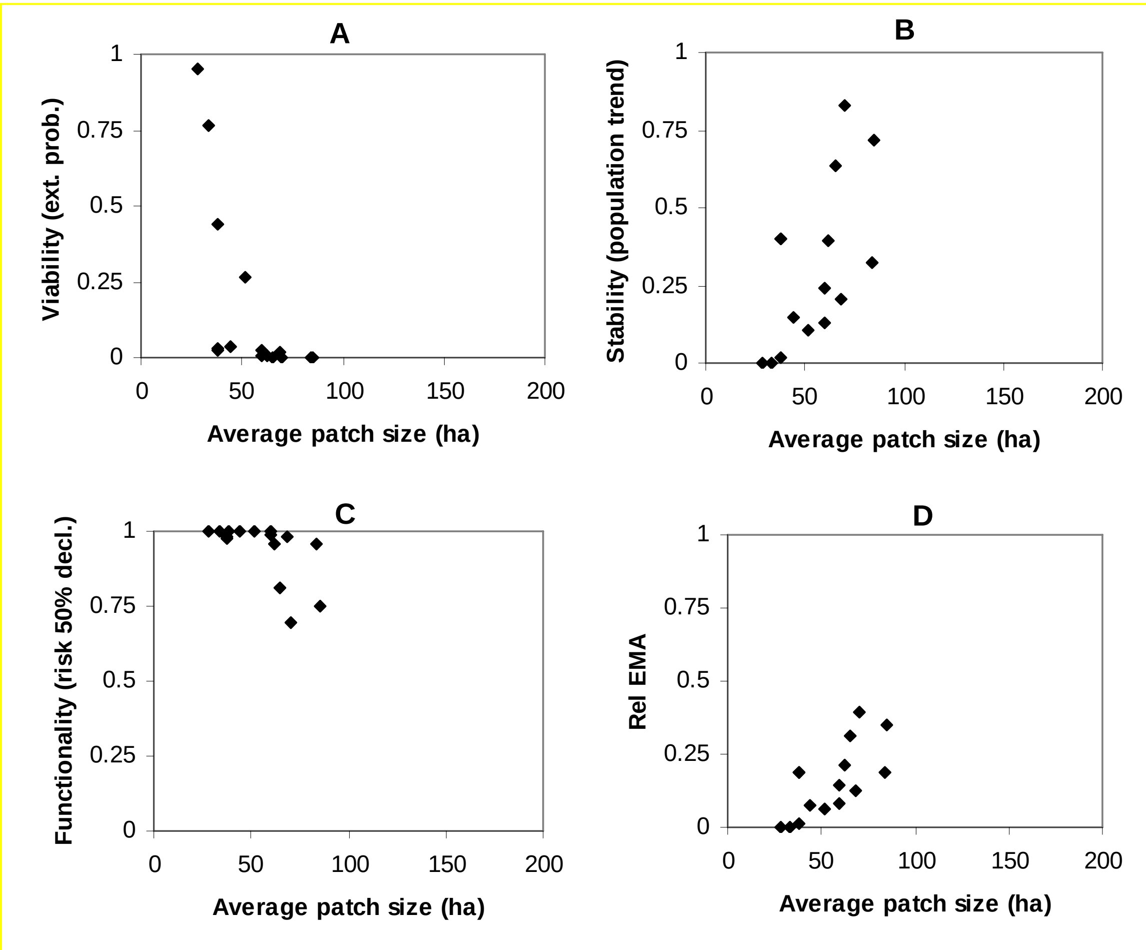
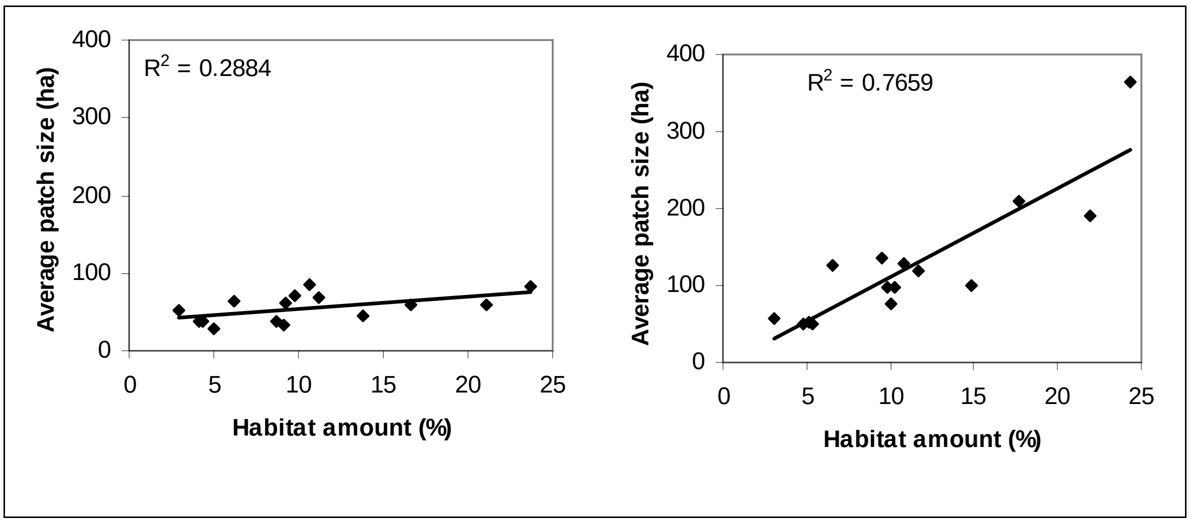


Figure 17: Simulation results of the spatial-explicit Ovenbird PVA based on 15 case study areas (250 km^2) in the Québec pilot study area. Figures A to D show extinction probability (A), trend in abundance from initial to final year 50 (B), functionality measured as risk of decline to 50% of the initial abundance (C), and relative expected minimum abundance (EMA) (i.e., lowest abundance over the course of a simulation trajectory averaged over all simulation replicates relative to the initial population size) (D). The performance measures in figure panels A to D are plotted against the average size (ha) of suitable Ovenbird habitat patches in each landscape subset.



As none of the landscape subsets showed sufficient levels of ‘stability’ and ‘functionality’, we were interested under which model assumptions a ‘functional’ and/or ‘stable’ metapopulation may be achieved. In a first step we decided to modify the patch structure of all 15 landscape subsets so that average patch sizes were larger (note, that the original amount of habitat in each landscape remained the same). We achieved this by ‘artificially’ increasing the neighborhood distance from 90 to 300 m, i.e., through this procedure smaller patches being less than 300 m apart were aggregated into larger patches. This can be seen in Figure 18 which shows the relationship between average patch size and habitat amount in each landscape. For the 300 m neighborhood scenario (right figure) we can see that average patch size generally increases as more patches are aggregated.

Figure 18: Relationship between average patch size and habitat amount based on simulated data of 15 landscape subsets in the Québec pilot study area (left figure: neighborhood distance = 90 m; right figure neighborhood distance = 300 m).



With this modification we were able to simulate pseudo-real landscapes with larger average patch sizes than the current landscape in the NAESI Québec pilot study area (total habitat amount in each landscape remained the same). For this scenario model performances in terms of stability and functionality increased substantially. Tables 11 and 12 and Figure 19 show that, in order to achieve stability (i.e., <10% decline in abundance over 50 years) a 250 km^2 landscape needs to have at least 17.5% habitat amount with an average patch size of at least 200 ha. If average patch sizes are smaller minimum habitat amounts are most likely to be higher. Although levels of functionality were significantly increased none of the modified landscape subsets did show desired levels of risk of decline (i.e., <5% risk of decline to 50% of initial abundance). However, when we used the logarithmic and linear trends (Figure 19) as predictors we calculated a minimum required habitat amount of 40% and a minimum average patch size of 850 ha (minimum viable patch size).

Figure 19: Ovenbird PVA simulation results based on 15 case study areas (250 km^2) with an increased neighborhood distance of 300 m. The upper left figure shows the trend in abundance from initial to final year 50 as a function of habitat amount. The upper right figure the same plotted against average patch size. The bottom left figure shows functionality (measured as the risk of decline to 50% of the initial abundance) as a function of habitat amount. The figure at the right bottom shows the same for average patch size.

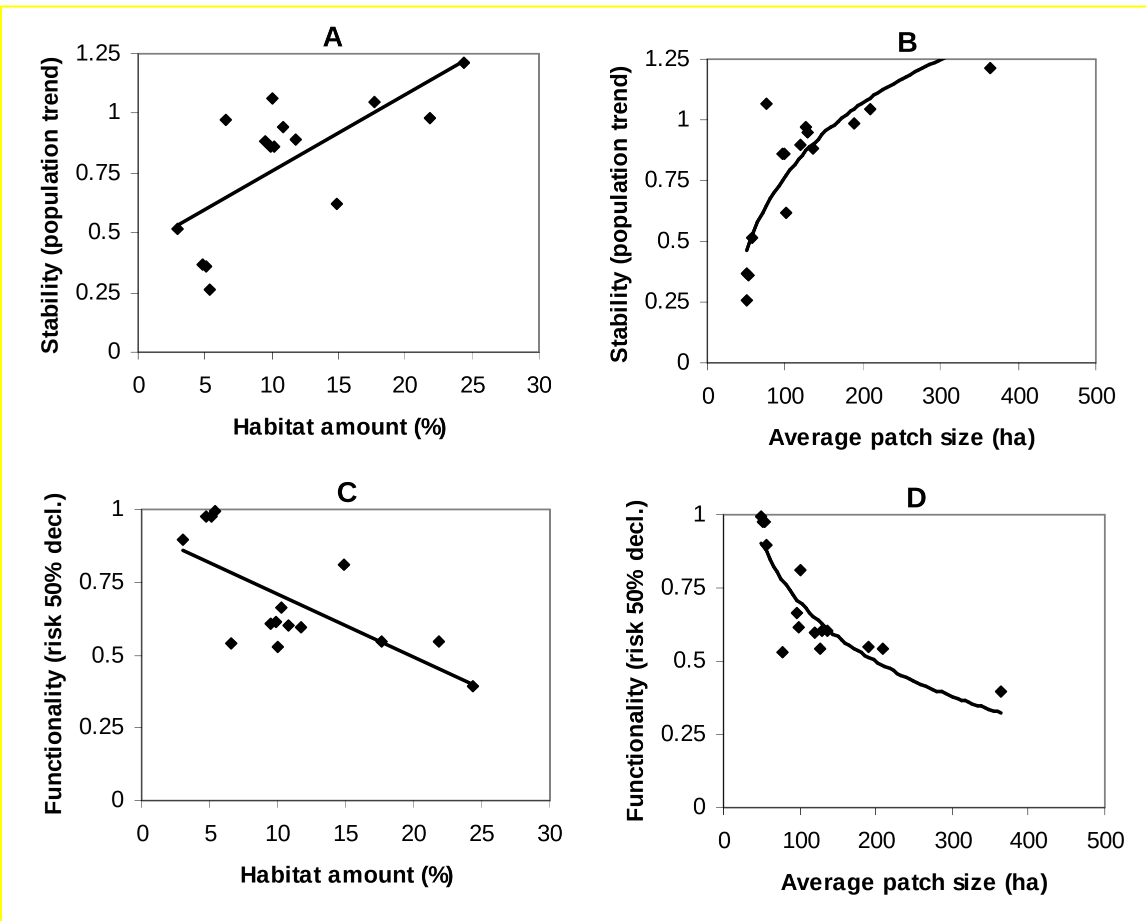


Table 11: Results from the patch analysis for each 250 km^2 landscape subset when the neighborhood distance for the patch calculation was increased from 90 to 300 m. This modification resulted in larger habitat patches (while keeping habitat amount constant).

Area	# of populations	K (total)	Average habitat suitability	Average patch size (ha)	Habitat amount (%)
1	21	2972	0.670	210	17.68
2	17	4277	0.685	364	24.33
3	29	3694	0.676	190	21.89
4	21	2326	0.762	128	10.79
5	23	2102	0.698	120	11.72
6	32	1635	0.682	77	10.01
7	25	1658	0.666	98	9.85
8	37	2402	0.637	101	14.83
9	13	548	0.707	57	3.01
10	23	834	0.677	53	5.09
11	27	2022	0.723	97	10.21
12	13	1304	0.744	127	6.59
13	17	1737	0.735	136	9.48
14	27	880	0.659	50	5.36
15	23	797	0.675	51	4.77

Table 12: Results from the spatial-explicit Ovenbird PVA based on modified landscape subsets with a neighborhood distance of 300 m.

Area	Extinction probability	Initial abundance	Average final abundance	Population trend	Risk of decline	Expected minimum abundance (EMA)	Relative EMA
1	0.000	1485	1554	1.046	0.544	709	0.477
2	0.000	2138	2595	1.213	0.394	1239	0.579
3	0.000	1844	1815	0.984	0.547	868	0.470
4	0.000	1162	1098	0.944	0.602	523	0.450
5	0.000	1051	940	0.894	0.595	474	0.450
6	0.000	1485	1582	1.065	0.530	719	0.484
7	0.001	829	713	0.860	0.614	355	0.428
8	0.000	1200	743	0.619	0.811	385	0.320
9	0.028	274	142	0.518	0.895	71	0.259
10	0.021	418	151	0.361	0.978	78	0.186
11	0.000	1010	871	0.862	0.663	414	0.409
12	0.001	654	635	0.970	0.541	305	0.466
13	0.000	867	766	0.883	0.606	387	0.446
14	0.062	440	114	0.259	0.994	58	0.131
15	0.022	399	146	0.365	0.976	74	0.185

Although functionality seems to be positively influenced by increasing patch size (Figure 19), desired levels of functionality were only achieved indirectly through modifying the neighborhood distances. As in the case with the Marsh Wren, we hypothesized that reduced standard deviations of the vital rates in the stage matrix (i.e., lower levels of environmental fluctuations) may support sufficient levels of functional presence. We therefore decreased all standard deviations in vital rates to 10% of the mean (SD fecundity = 0.0434, SD survival = 0.0623) to analyze the resulting effects and see whether our hypothesis can be supported. Original estimated standard deviations in the stage matrix were 30% for fecundity and 15% for survival and we believe that 10% is the lowest 'realistic' level of environmental stochasticity.

Results from this experiment show that desired levels of functionality could only be directly generated if standard deviations of vital rates (i.e., biologically speaking, environmental fluctuations that affect reproduction and survival) were reduced to as much as 10% of the mean. Figure 20 and Table 13 show that for a CV of 10% in vital rates landscape subsets with more than 7.5% habitat amount and 100 ha average patch size were able to generate <5% risk of decline to 50% of the initial population size (in any year over the course of a 50-year simulation run). However, based on available empirical data, it remains speculative whether 10% CV is a realistic 'optimistic' estimate. It is most likely that stochastic variations are higher and we therefore believe that our estimates based on linear and logarithmic trends represent a more suitable assessment (Figure 19).

Figure 20: Simulation results based on 15 modified landscape subsets (250 km^2) with a neighborhood distance of 300 m and a 10% standard deviation of survival and fecundity rates. Figure A shows functionality (measured as the risk of decline to 50% of the initial abundance) as a function of habitat amount. Figure B shows the same as a function of average patch size.

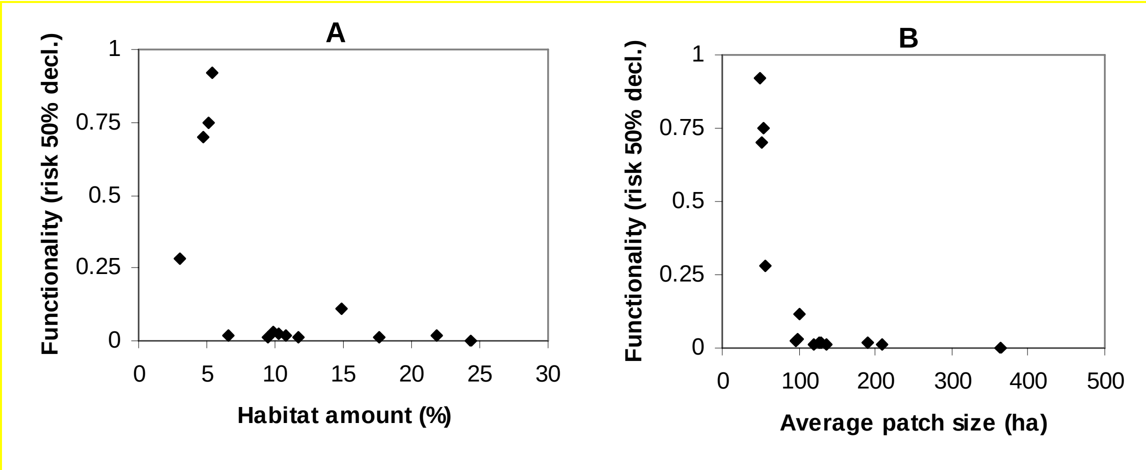


Table 13: Simulation results for each modified 250 km^2 landscape subset when the neighborhood distance was increased to 300 m and standard deviations of fecundity and survival rates were reduced to a CV of 10%.

Area	# of populations	K (total)	Average patch size (ha)	Habitat amount (%)	Population trend	Risk of decline
1	21	2972	210	17.68	1.60	0.011
2	17	4277	364	24.33	1.75	0.000
3	29	3694	190	21.89	1.39	0.016
4	21	2326	128	10.79	1.51	0.019
5	23	2102	120	11.72	1.38	0.011
6	32	1635	77	10.01	1.25	0.090
7	25	1658	98	9.85	1.36	0.028
8	37	2402	101	14.83	1.04	0.113
9	13	548	57	3.01	0.89	0.283
10	23	834	53	5.09	0.59	0.747
11	27	2022	97	10.21	1.21	0.022
12	13	1304	127	6.59	1.42	0.020
13	17	1737	136	9.48	1.38	0.013
14	27	880	50	5.36	0.46	0.920
15	23	797	51	4.77	0.61	0.700

4.3 Recommended habitat-based standards

Based on the model assumptions and a simulation trajectory of 50 years the following habitat-based standards were recommended in the previous analysis (Tews, 2008): (i) a minimum patch size of 200 ha of highly suitable forest habitat to provide a population source (based on the assumed stage matrix and a minimum of 87% pairing success resulting in a minimum intrinsic rate of increase of 1.0), (ii) a minimum patch size of 850 ha of suitable habitat (based on an average population density of 0.24 individuals per ha) to support a single, viable population, (iii) a minimum amount of 20% - 40% suitable forest habitat at a spatial scale of 250 km^2 to support a viable metapopulation, (iv) a minimum of 80-90% of the total population abundance distributed across large, self-sustainable forest patches (lambda>1.0, > approx. 200 ha) to support near stable population trends. With this in-depth population modeling analysis we provide a detailed re-assessment, in particular for standard #3 and #4. Based on empirical data, the assumptions of the population model and its application in the NAESI Québec pilot study area we finally suggest the following habitat-based standards for the Ovenbird:

- a minimum patch size of ~200 ha to facilitate population source dynamics
- a minimum patch size of ~850 ha of suitable habitat (based on an average population density of 0.24 individuals per ha) to support a single, viable population over 50 years with 95% confidence
- a minimum amount of ~10% (~2500 ha) suitable habitat and an average patch size of more than 60 ha to support a viable metapopulation on a spatial scale of 250 km^2
- a minimum amount of 17.5% (~4375 ha) suitable habitat and an average patch size of more than 200 ha to support a stable metapopulation on a spatial scale of 250 km^2; for smaller average patch sizes total habitat amount will be significantly higher

- a minimum amount of 40% (~100 km^2) suitable habitat and an average patch size larger than the minimum viable patch size (i.e., 850 ha) to support a functional metapopulation on a spatial of 250 km^2; both habitat amount and average patch size may be significantly smaller for lower standard deviations in vital rates (i.e., lower degrees of environmental stochasticity).

The above functionality standards are based on estimates from trends of simulated landscape sets. Standards of functional presence (i.e., < 5% risk of decline to 50% of initial abundance) for the current landscape conditions in the Quebec pilot study area could only be detected for simulation scenarios with significantly lower standard deviations in the vital rates.

The above habitat-based standards are subject to changes in the model assumptions. Particularly, as indicated by the sensitivity analysis, any deviations from the assumed adult survival rates would require a re-assessment of the recommended standards. Moreover, absolute minimum habitat amount (km^2) will most likely be higher if larger spatial scales are considered (due to declines in average inter-patch distance with increase in area).

5 BOBOLINK

Bobolinks (*Dolichonyx oryzivorus*) originally inhabited tall-grass and mixed-grass prairies of midwestern and south central Canada. However, today they primarily use hay-fields and meadows and consequently are readily impacted by farm management practices. A PVA study conducted for the Eastern Ontario pilot study area (see Pearce et al., 2007) suggested a viable, stable and ecologically functional metapopulation irrespective of estimates of habitat amount and quality. However, the bobolink population cannot withstand more than a 20% reduction in fledging rates annually; consequently widespread annual disturbance because of haying during the nesting season would reduce the viability of this population.

A modified version of the population model developed for the Eastern Ontario pilot study area was applied for the NAESI Québec pilot study area (Tews, 2008) and suggested the following habitat-based standards: (i) a minimum patch size of 20 ha for patch occupancy, (ii) a minimum patch size of 135 ha (based on an average population density of 1.5 individuals per ha) to support a single, viable population, (iii) a maximum inter-patch distance of 15 km, (iv) a minimum amount of 0.75% of high quality habitat to support a viable, stable and functional metapopulation, (v) no hayfield harvesting prior to the first week in July.

With this in-depth population analysis we will conduct a detailed demographic sensitivity analysis and re-assess the above habitat-based standards. As opposed to the previous analysis for the Québec pilot study area this analysis is based on a set of smaller landscape samples to better assess under which specific habitat conditions (i.e., minimum thresholds) 'viable', 'stable' and 'functional' levels of metapopulation dynamics can be achieved. For the moving window analysis we chose a spatial scale of 100 km^2 to accommodate the operational scale of the Bobolink. We chose this spatial scale in order to be consistent with the Marsh Wren model which had a 65 ha minimum viable patch size (as opposed to the Ovenbird model which had a minimum viable patch size of 850 ha and a moving window scale of 250 km^2 spatial scale). A summary of demographic and spatial model parameters used in this population analysis is given in Table 14. Literature references for parameters in the Bobolink model are given in Noreca Consulting and Elutis Modeling and Consulting Inc. (2007) and Tews (2008).

Table 14: Summary of demographic and spatial model parameters used in the Bobolink population model. Literature references for parameters are given in Noreca Consulting and Elutis Modeling and Consulting Inc. (2007) and Tews (2008).

Parameter	Value / Comment
Replications	1000
Duration	50 years
Stage 1	Female juveniles
Stage 2	Female adults
Stage 3	Male juveniles
Stage 4	Male adults
Vital rate 1	0.651 (juvenile fecundity, female offspring per juvenile female)
Vital rate 2	0.651 (adult fecundity, female offspring per adult female)
Vital rate 3	0.34 (juvenile survival, females)
Vital rate 4	0.49 (adult survival, females)
Vital rate 5	0.532 (juvenile fecundity, male offspring per juvenile female)
Vital rate 6	0.532 (adult fecundity, male offspring per adult female)
Vital rate 7	0.34 (juvenile survival, males)
Vital rate 8	0.49 (adult survival, males)
SD of vital rates	10% coefficient of variation (CV)
SD of vital rate 1	0.065
SD of vital rate 2	0.065
SD of vital rate 3	0.034
SD of vital rate 4	0.049
SD of vital rate 5	0.053
SD of vital rate 6	0.053
SD of vital rate 7	0.034
SD of vital rate 8	0.049
Density Dependence type	Contest (affects all stages)
Maximum growth rate	1.1
Sex ratio	0.45 (males) : 0.55 (females)
Mating system	Polygynous: each male can mate with up to 1.23 females
Carrying capacity K	2.68 individuals per ha
SD of K	10% CV
Initial abundance	50% of K
HSI threshold	0.5
Neighborhood distance	60 m (2 cells)
Demographic stochasticity	Included
Environmental stochasticity	Lognormal distribution
Within population correlation	All vital rates correlated
Correlation distance function	Increases linearly from 75% to 100% from maximum (edge to edge) to minimum (adjacent cells) distance within landscape subset (a=1.0; b=30.0; c=1.0)
Dispersal distance function	a = 0.0024; b = 3.0; c = 1.0; Dmax = 14.2;
Size of landscape subsets	100 km^2

5.1 Sensitivity analysis

We generated a set of 1000 parameter scenarios by randomly varying 10 demographic parameters of the Bobolink population model. The parameters included fecundity and survival rates of the stage matrix (vital rate 1-8) as well as the carrying capacity and the initial abundance. This parameter scenario set was then executed in Ramas©MetaPop each with 50 stochastic runs over 50 years. That is, a total of 50,000 simulations were analyzed for the Bobolink sensitivity analysis.

First and foremost, extinction risk (50 years) proved to be a better dependent model variable then abundance (50 years) (Figures 21 and 22). By looking at the R-squared values for extinction risk in Table 15 we can see the following ranking: female juvenile fecundity (vital rate 1) showed the highest impact, followed by male adult survival (vital rate 8), followed by female adult fecundity as the third most important parameter (vital rate 2). All vital rates of females (especially vital rate 1-3) showed a negative impact, i.e., increases in female vital rates resulted in higher extinction risk (Figure 22).

At first sight this seems surprising as one would expect that increase in fecundity and survival independent of sex or stage type should decrease extinction risk. However, a closer look at the model structure explains this unexpected pattern. When the R-squared for vital rate 1 was only calculated for the data set below 0% variation the level of significance decreased substantially (R^2=0.067, not shown). This can be also seen by visually inspecting vital rate 1 in Figure 22 which shows a slightly stronger positive relationship between the variables above 0% variation. The explanation for the negative impact of proportional increase in female abundance is linked to the polygynous mating system and a sex ratio of 0.55 to 0.45 (female to males). According to our model assumptions each male can ‘only’ mate with up to 1.23 females (on average) and with the assumed sex ratio this results in a balance where the average number of males in a population (although lower in abundance than females) is large enough to mate all females. If female abundance is proportionally increased (via higher survival and/or fecundity rates) additional females do not actively contribute to reproduction, they rather 'negatively' affect the population by approaching the carrying capacity which then in turn decrease the population growth rate. The opposite effect results from a proportional increase in the abundance of males (see vital rate 8, Table 15 and Figure 22): a higher (average) proportion of male Bobolink in the population ensures that all females can successfully mate in all years.

Table 15: Results from the sensitivity analysis (randomized parameter set) with R squared values for each demographic model parameter. The R-squared of the regression is the fraction of the variation in abundance (after 50 years) or extinction (after 50 years) predicted by each independent variable (i.e., demographic parameter). The number of stars indicates ranking of the third most important parameters, respectively (* highest effect). Vital rates are represented by the following parameters: vital rate 1 = juvenile fecundity (female offspring per juvenile female); vital rate 2 = adult fecundity (female offspring per adult female); vital rate 3 = juvenile survival (females); vital rate 4 = adult survival (females); vital rate 5 = (juvenile fecundity (male offspring per juvenile female); vital rate 6 = adult fecundity (male offspring per adult female); vital rate 7 = juvenile survival (males); vital rate 8 = adult survival (males).**

	Default value	**R^2 (Abundance 50 yrs)**	**R^2 (Ext. prob.50 yrs)**
Carrying capacity	90	0.0402	0.0296
Initial abundance	90	0.0006	0.0092
Vital rate 1	0.6507	0.1449***	0.2683***
Vital rate 2	0.6507	0.0509**	0.0933*
Vital rate 3	0.3400	0.0405*	0.0521
Vital rate 4	0.4900	0.0005	0.0031
Vital rate 5	0.5324	0.0046	0.0347
Vital rate 6	0.5324	0.0107	0.0301
Vital rate 7	0.3400	0.0156	0.0363
Vital rate 8	0.4900	0.0397	0.1159**

Figure 21: Average abundances (50 stochastic replicates) after 50 years as a function of ten different demographic parameters included in the Bobolink sensitivity analysis (1000 random parameter combinations). Vital rate 1 = juvenile fecundity (female offspring per juvenile female); vital rate 2 = adult fecundity (female offspring per adult female); vital rate 3 = juvenile survival (females); vital rate 4 = adult survival (females); vital rate 5 = (juvenile fecundity (male offspring per juvenile female); vital rate 6 = adult fecundity (male offspring per adult female); vital rate 7 = juvenile survival (males); vital rate 8 = adult survival (males).

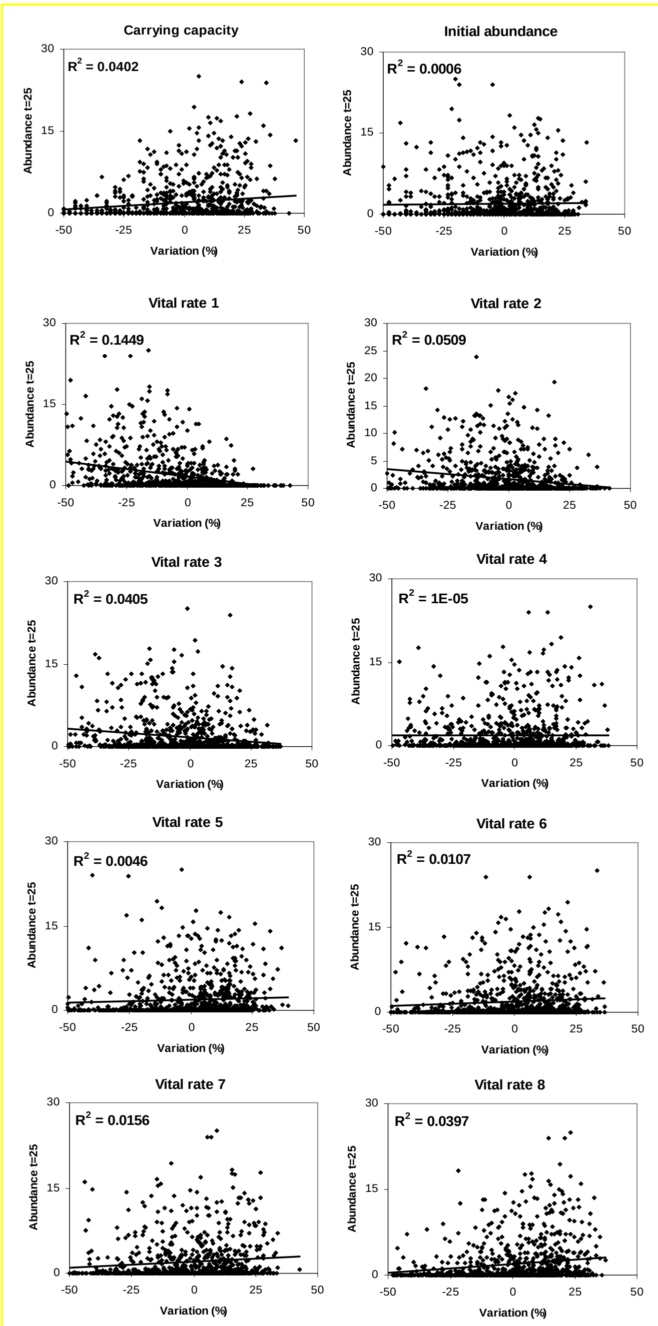
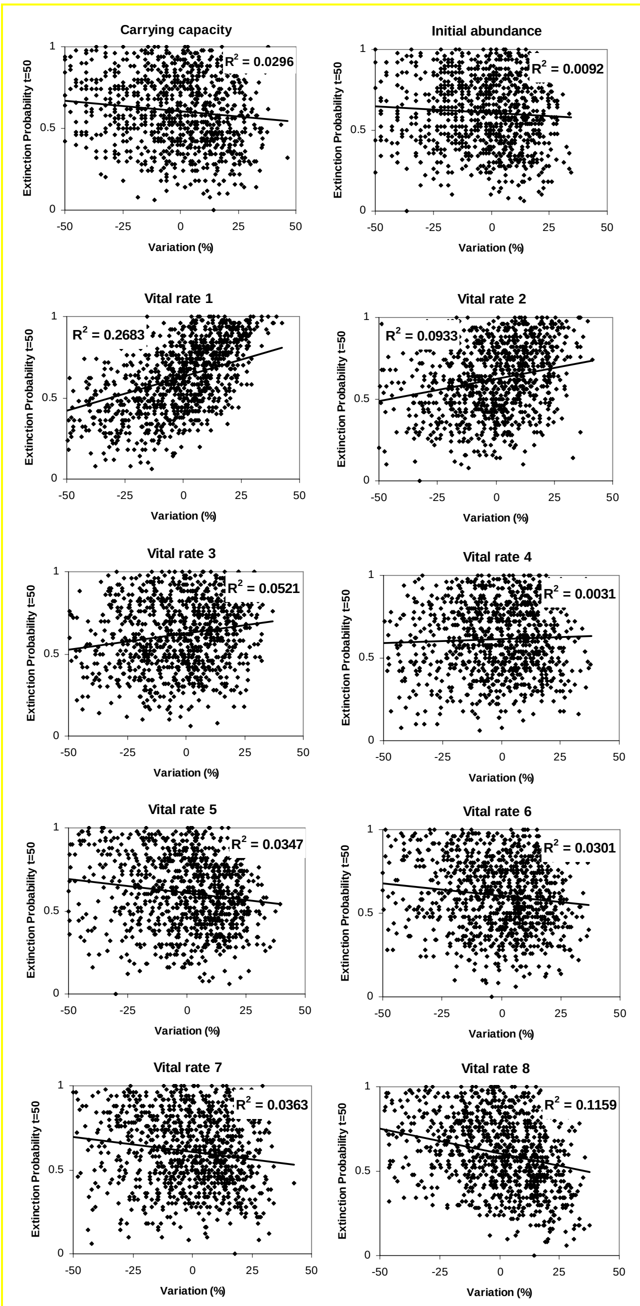


Figure 22: Average extinction risks (50 stochastic replicates) after 50 years as a function of ten different demographic parameters included in the Bobolink sensitivity analysis (1000 random parameter combinations). Vital rate 1 = juvenile fecundity (female offspring per juvenile female); vital rate 2 = adult fecundity (female offspring per adult female); vital rate 3 = juvenile survival (females); vital rate 4 = adult survival (females); vital rate 5 = (juvenile fecundity (male offspring per juvenile female); vital rate 6 = adult fecundity (male offspring per adult female); vital rate 7 = juvenile survival (males); vital rate 8 = adult survival (males).



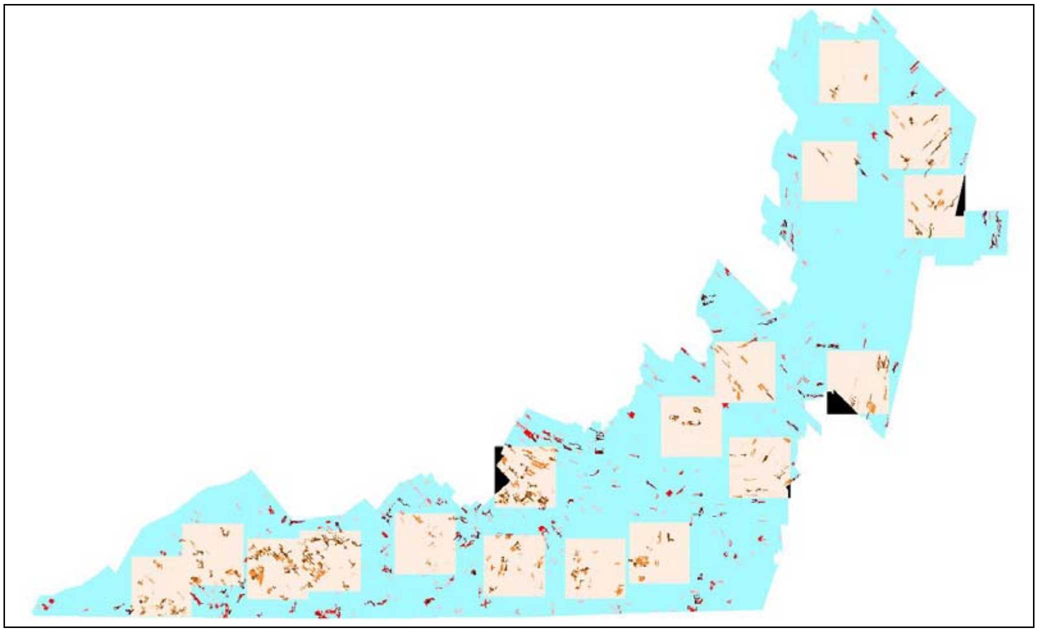
5.2 Moving window analysis

For the Bobolink population analysis we conducted a ‘moving window’ analysis where a ‘moving’ spatial grid (100 km^2) was dynamically placed across the habitat suitability map in the Québec pilot study area. Subsequently, these grids were used as landscape subsets for the population analysis.

Figure 23 shows the placement of the 17 landscape subsets across the study region. Landscape subsets were placed so that most of the suitable habitat in the pilot study area was included and a maximum sampling variation in regional habitat conditions achieved. The habitat suitability model was based on the model of Maheu-Giroux (2007) with index values ranging from 0.0 (unsuitable) to 1.0 (highest suitability).

For creating the patch import maps for Ramas©MetaPop we assumed a habitat suitability threshold of 0.5 and a neighborhood distance of 2 cells, i.e., 60 m (Table 14). The habitat suitability index (HSI) threshold defines the numerical boundary above which habitat cells are considered suitable. The neighborhood distance (required for patch aggregation) was based on average territory sizes at six tame hayfields in New York (Bollinger, 1988).

Figure 23: Habitat suitability map for the Bobolink in the Québec pilot study area based on the HS model of Maheu-Giroux (2007). HSI values range from 0.0 (no suitability) to 1.0 (highest suitability). A series of 17 landscape subsets (100 km^2) were randomly placed over suitable habitat patches and used for spatial population analysis.

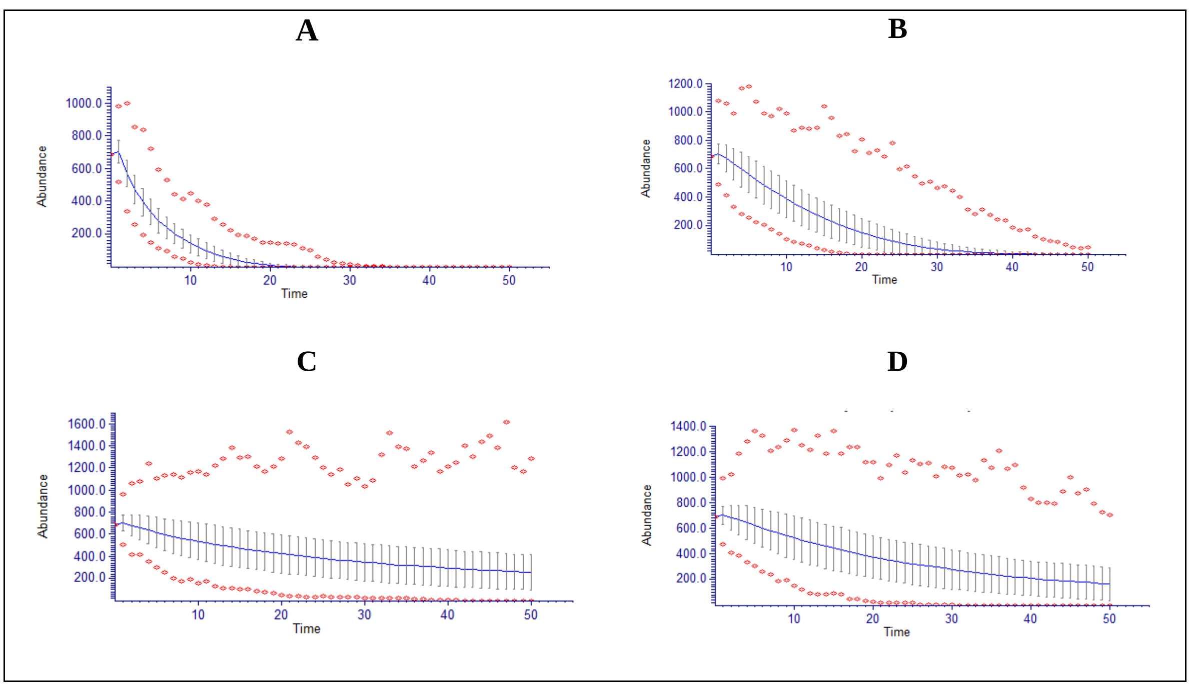


Based on empirical data a maximum dispersal distance of 14.2 km (24% maximum dispersal rate, see dispersal distance function in Table 14) was previously assumed (see Pearce et al., 2007; Tews, 2008). However, when the model was parameterized with the above dispersal kernel metapopulations in all simulation scenarios were deterministically going extinct (for a scenario set with different dispersal rates see Figure 24). This is a result of the interacting effects of carrying capacity, abundance and dispersal rate. To illustrate this: if a population A (source) with 80 individuals (carrying capacity = 100) and a population B (sink) with 10 individuals (carrying capacity = 20) are in close proximity and 20% of the population in population A emigrates to population B, (each year) population B increases to 50 individuals due to immigration. However, due to the effect of the carrying capacity population B will be reduced down to 20 and, thus, 30 individuals are lost (each year).

This process of source-sink dynamics may be realistic for specific cases, however, in most 'real world' cases, emigrating individuals from population A will move on to another (larger) patch where enough suitable territories are available. To our knowledge, it is not possible to introduce so called 'global' dispersal into Ramas©Metapop which would only allow immigration into a patch up to the level of the carrying capacity and remaining individuals would be distributed across remaining 'free' patches (note that this 'global' dispersal type only applies to metapopulations were dispersal is not limiting for population dynamics).

In order to avoid severe population loss through the above described sink dynamics we therefore reduced the dispersal rate (dispersal parameter a, Table 14) to a very low level (a = 0.0024). As effects of dispersal limitation can be neglected (the largest distance on a spatial scale of 10*10 km is within the assumed maximum dispersal distance) we believe that this step is adequate in order to avoid unrealistic population loss through dispersal.

Figure 24: Population trajectories (1000 replicates) for four dispersal rate scenarios in the spatial Bobolink PVA (A = 0.24; B = 0.024; C = 0.0024; D = 0.0).



The patch analysis for 17 landscape subsets in the NAESI Québec pilot study area showed habitat amounts varying between 1.55% to 18.96% on a 100 km^2 scale (i.e., 1.55 km^2 to 18.96 km^2) (Table 16). Average patch size varied between 24.4 ha to 123 ha. Total carrying capacity varied between a maximum of 3,311 individuals (both male and female) for landscape subset #7 and 254 individuals for #16. Besides habitat amount (which co-determines total carrying capacity, in concert with the frequency distribution of habitat suitability classes), average patch size is an important indicator for the degree of self-sustainability. The minimum viable patch size for Bobolink was estimated at 135 ha. Thus, a few of the landscape subsets provide average patch sizes that approach this threshold. As discussed above we did not plot average inter-patch distances among nearest neighbors as average dispersal distances (maximum dispersal distance = 14.2 km) were larger than average inter-patch distances and therefore dispersal was regarded as not a limiting factor in the population analysis.

Table 16: Results from the patch analysis for each 100 km^2 landscape subset in the Bobolink PVA.

Area	# of populations	K (total)	Average habitat suitability	Average patch size (ha)	Habitat amount (%)
1	23	1368	0.435	41.9	9.59
2	21	1548	0.441	43.5	8.93
3	15	3290	0.624	123.0	18.05
4	16	3214	0.594	102.0	16.10
5	22	588	0.328	24.4	5.25
6	19	1292	0.404	46.6	8.72
7	23	3311	0.829	83.0	18.96
8	8	1068	0.501	86.9	6.92
9	8	964	0.482	79.0	6.30
10	3	601	0.833	88.7	2.62
11	18	1213	0.482	43.9	7.77
12	10	917	0.473	66.1	6.52
13	9	1179	0.474	82.0	6.93
14	11	1193	0.56	63.4	6.61
15	21	1408	0.465	42.4	8.34
16	5	254	0.404	42.7	2.05
17	4	266	0.577	35.7	1.55

In the following step we then imported all 17 landscape subsets for spatial population analysis.

The results from this analysis are given in Table 17 and visualized in Figures 25 and 26. Plotting habitat amount (%) versus viability (extinction probability) (Figure 25A) shows that landscapes with more than 6.5% habitat amount were viable (i.e., <5% extinction risk) over the course of 50 years. All landscape scenarios resulted in unstable (i.e., >10% population decline) metapopulations (Figure 25B). All landscape subsets also showed risks of 50% decline of larger than 29% (Figure 25C). Relative EMA was below 61% for all habitat scenarios (Figure 25D).

Population viability and stability also increased with increase in average patch size (Figures 26A and B). Landscape subsets with an average patch size larger than ~50 ha and a habitat amount of more than 6.5% did show less then 5% extinction risk over 50 years. With increase in average patch size risk of decline and relative EMA decreased and increased, respectively (Figures 17C and D).

None of the simulated landscape subsets provided ‘stable’ or ‘functional’ metapopulations (Figures 25B and C; Figures 26B and C). It was also not feasible to detect such thresholds for lower environmental stochasticity scenarios as estimated standard deviations in vital rates of the stage matrix were 10% and we believe that this represents the lower boundary for ‘realistic’ variations in fecundity and survival rates. Another option would have been to increase neighborhood distance (such as in the Ovenbird population analysis). However, average patch sizes in landscape subsets of near-stability and -functionality (Figure 26) are already approaching minimum viable patch sizes. We therefore used the plotted trend to estimate thresholds of habitat conditions. Based on the linear trends we estimated minimum habitat amount for functional presence and stability to be 23% and 30%, respectively (Figures 25B and C). Estimated minimum patch sizes were 125 ha and 150 ha for stability and functionality, respectively (Figures 26 B and C).

Table 17: Results from the spatial Bobolink population analysis based on 17 landscape subsets. Population trend was calculated as the ratio of average final population size to initial population size. Risk of decline refers to the risk of decline to 50% of the initial population abundance in any given year over the course of a simulation trajectory. Relative EMA is the ratio of EMA to initial population size.

Area	Extinction probability	Initial abundance	Average final abundance	Population trend	Risk of decline	Expected minimum abundance (EMA)	Relative EMA
1	0.019	687	179	0.260	0.948	144	0.209
2	0.005	777	314	0.404	0.824	248	0.319
3	0.000	1648	1389	0.842	0.300	997	0.604
4	0.000	1605	1383	0.861	0.290	987	0.614
5	0.512	294	16	0.054	1.000	12	0.040
6	0.008	646	244	0.377	0.892	191	0.295
7	0.000	1656	1167	0.704	0.479	859	0.518
8	0.000	535	308	0.575	0.662	226	0.422
9	0.001	482	291	0.603	0.674	205	0.425
10	0.028	300	174	0.580	0.638	152	0.506
11	0.031	608	158	0.259	0.946	123	0.202
12	0.041	459	123	0.267	0.947	97	0.211
13	0.000	589	392	0.665	0.557	284	0.482
14	0.005	597	247	0.413	0.807	194	0.324
15	0.023	701	187	0.266	0.942	154	0.219
16	0.641	128	9	0.070	0.996	6	0.046
17	0.391	123	24	0.195	0.955	17	0.138

Figure 25: Simulation results of the spatial-explicit Bobolink PVA based on 17 case study areas (100 km²) in the Québec pilot study area. Figures A to D show extinction probability (A), trend in abundance from initial to final year 50 (B), functionality measured as risk of decline to 50% of the initial abundance (C), and relative expected minimum abundance (EMA) (i.e., lowest abundance over the course of a simulation trajectory averaged over all simulation replicates relative to the initial population size) (D). All performance measures are plotted against percent habitat amount in each landscape subset.

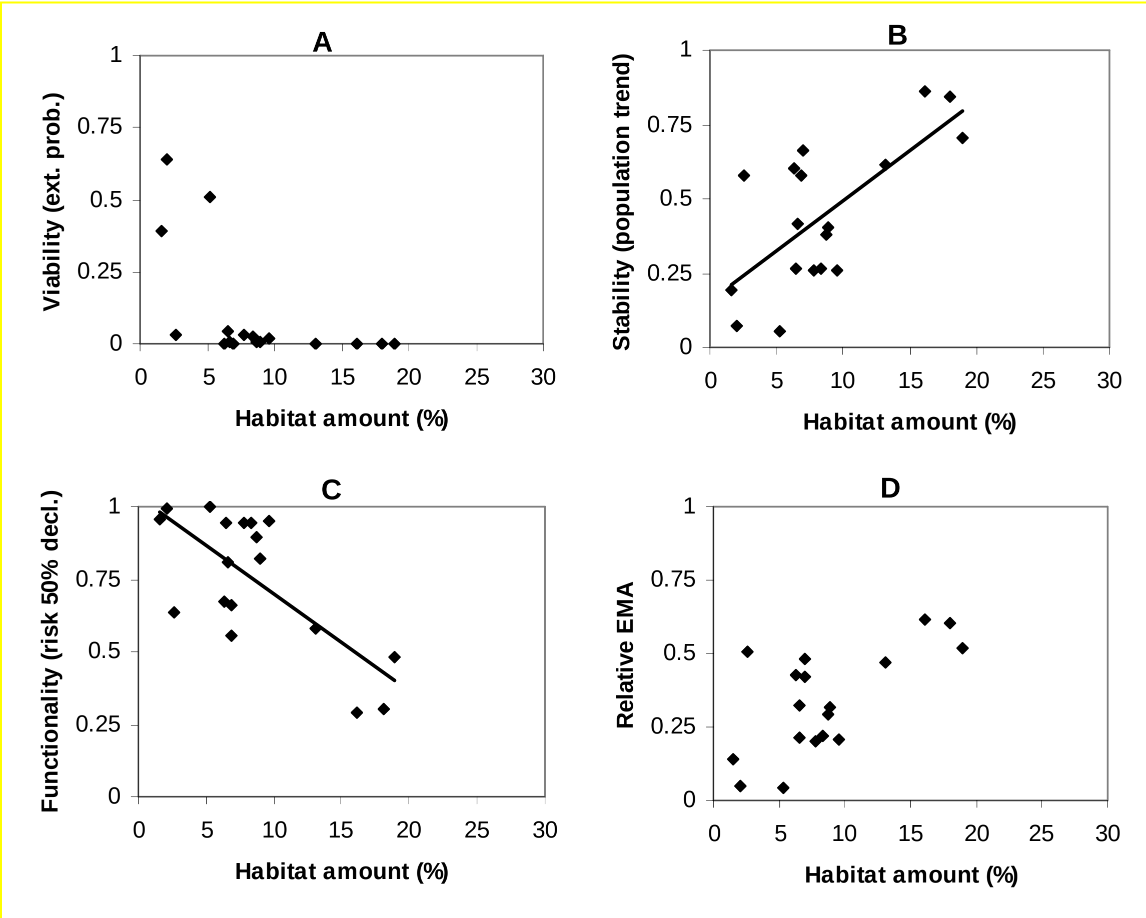
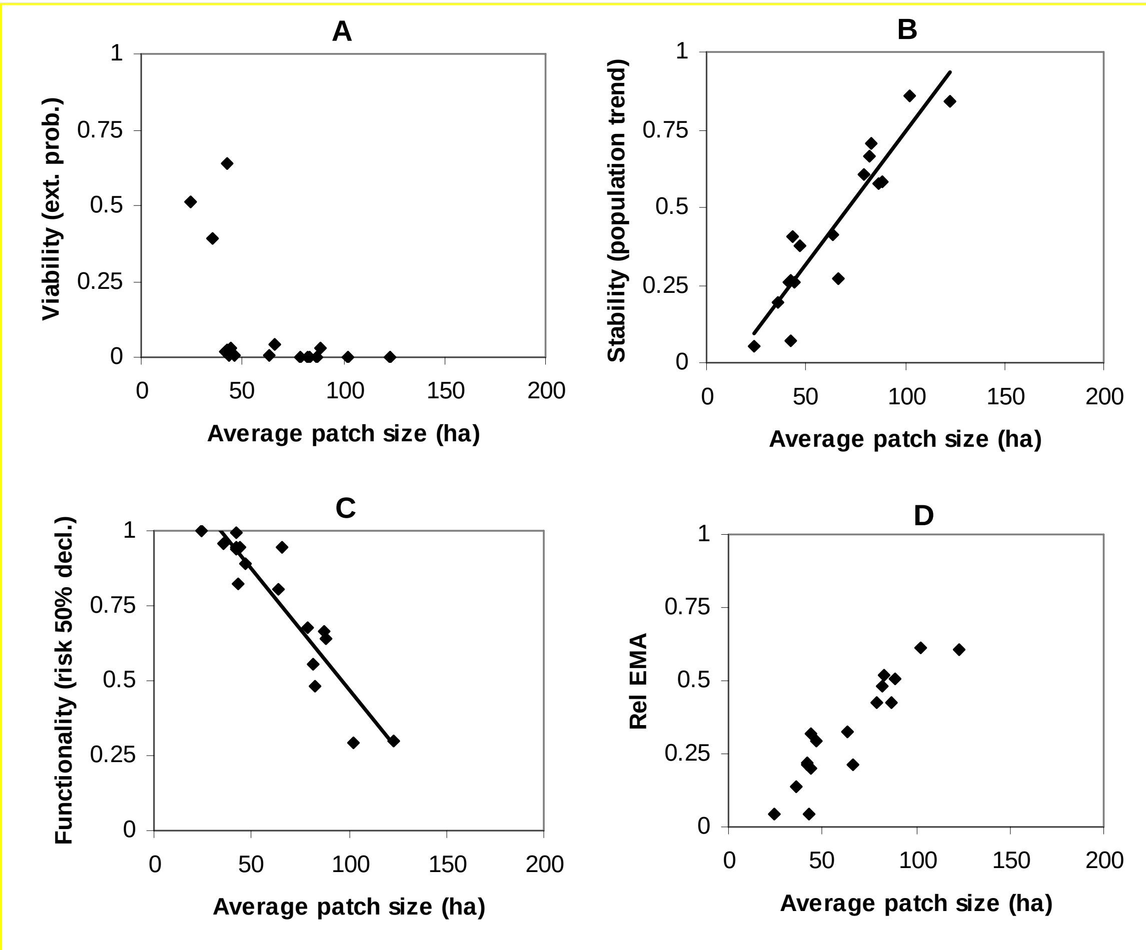


Figure 26: Simulation results of the spatial-explicit Bobolink PVA based on 17 case study areas (100 km²) in the Québec pilot study area. Figures A to D show extinction probability (A), trend in abundance from initial to final year 50 (B), functionality measured as risk of decline to 50% of the initial abundance (C), and relative expected minimum abundance (EMA) (i.e., lowest abundance over the course of a simulation trajectory averaged over all simulation replicates relative to the initial population size) (D). The performance measures in figure panels A to D are plotted against the average size (ha) of suitable habitat patches in each landscape subset.



5.3 Recommended habitat-based standards

Based on the model assumptions and a simulation trajectory of 50 years the following habitat-based standards were recommended in the previous analysis (Tews, 2008): (i) a minimum patch size of 20 ha for patch occupancy, (ii) a minimum patch size of 135 ha (based on an average population density of 1.5 individuals per ha) to support a single, viable population, (iii) a maximum inter-patch distance of 15 km, (iv) a minimum amount of 0.75% of high quality habitat to support a viable, stable and functional metapopulation, (v) no hayfield harvesting prior to the first week in July. With this in-depth population modeling analysis we provide a detailed re-assessment for standard #4. Based on the assumptions of the population model we suggest the following habitat-based standards for the Bobolink:

- a minimum patch size of ~20 ha for patch occupancy
- a minimum patch size of ~135 ha of suitable habitat (based on an average population density of 1.5 individuals per ha) to support a single, viable population over 50 years with 95% confidence
- a maximum inter-patch distance of 15 km to facilitate sufficient natal and breeding dispersal
- no hayfield harvesting prior to the first week in July
- a minimum amount of ~6.5% (~650 ha) suitable habitat and an average patch size of more than 50 ha to support a viable metapopulation on a spatial scale of 100 km^2
- a minimum amount of 23% (~2300 ha) suitable habitat and an average patch size of more than 125 ha to support a stable metapopulation on a spatial scale of 100 km^2; for smaller average patch sizes total habitat amount will be significantly higher
- a minimum amount of 30% (~3,000 ha) suitable habitat and an average patch size larger than 150 ha to support a functional metapopulation on a spatial of 100 km^2; both habitat amount and average patch size may be significantly smaller for lower standard deviations in vital rates (i.e., lower degrees of environmental stochasticity).

For a spatial scale of 100 km^2 we were not able to detect current habitat conditions that support desired levels of functionality (i.e., < 5% risk of decline to 50% of initial abundance) and stability (<10% population decline over 50 years). For the above estimates (i.e., thresholds) of functional presence and population stability we therefore used trend data based on simulated landscape sets.

All of the above habitat-based standards are subject to changes in the model assumptions. Particularly, as indicated by the sensitivity analysis, any deviations from the assumed female juvenile fecundity, male adult survival, as well as sex ratio and polygyny rate would require a re-assessment of the recommended standards. Absolute minimum habitat amount (km^2) will most likely be higher if larger spatial scales are considered (due to declines in average inter-patch distance with increase in area).

6 RED-SHOULDERED HAWK

The Red-shouldered Hawk (*Buteo lineatus*) is a raptor species that nests in mature forest stands, but depends on riparian areas, woody swamps, and wetland margins for foraging activities. The Red-shouldered Hawk was selected as a surrogate species for the NAESI Québec pilot study area due to its habitat area requirements, large home range, and dependence on forest interiors.

A modified version of the population model developed for the Eastern Ontario pilot study area was applied for the NAESI Québec pilot study area (Tews, 2008) and suggested the following habitat-based standards: (i) a minimum patch size of 26 km^2 of suitable habitat (based on an average population density of 1.7 breeding individuals per km^2) to support a single, viable population, (ii) a minimum amount of 6.6% of suitable habitat to support a viable and stable metapopulation under optimal patch size distribution; if the metapopulation contains a significant proportion of smaller patches with low connectivity (with the total area below the minimum viable patch size) the recommended habitat amount may be significantly higher.

With this population analysis we will conduct an in-depth sensitivity analysis and re-assess the above habitat-based standards by applying a wide range of different habitat suitability thresholds. A moving window analysis was not feasible due to the large home range, dispersal distance, and minimum viable population size. A summary of demographic and spatial model parameters is given in Table 18. Literature references for model parameters are given in Noreca Consulting and Elutis Modeling and Consulting Inc. (2007) and Tews (2008).

Table 18: Summary of demographic and spatial model parameters used in the Red-shouldered Hawk population analysis. Literature references for parameters are given in Noreca Consulting and Elutis Modeling and Consulting Inc. (2007) and Tews (2008).

Parameter	Value / Comment
Replications	1000
Duration	50 years
Stage 1	Female juveniles
Stage 2	Female adults
Stage 3	Male juveniles
Stage 4	Male adults
Vital rate 1	0.01948 (juvenile fecundity, female offspring per juvenile female)
Vital rate 2	0.3564 (adult fecundity, female offspring per adult female)
Vital rate 3	0.75485 (juvenile survival, females)
Vital rate 4	0.75485 (adult survival, females)
Vital rate 5	0.01948 (juvenile fecundity, male offspring per juvenile female)
Vital rate 6	0.3564 (adult fecundity, male offspring per adult female)
Vital rate 7	0.75485 (juvenile survival, males)
Vital rate 8	0.75485 (adult survival, males)
SD of vital rates	Survival: 10% CV, Fecundity: ~66.4% CV
SD of vital rate 1	0.012935
SD of vital rate 2	0.2367
SD of vital rate 3	0.0245
SD of vital rate 4	0.0245
SD of vital rate 5	0.012935
SD of vital rate 6	0.2367
SD of vital rate 7	0.0245
SD of vital rate 8	0.0245
Density Dependence type	Contest (affects only adult stage)
Stage-specific breeding	Stage 1 (0.053), Stage 2 (0.97), Stage 3 (0), Stage 4 (0.97)
Maximum growth rate	1.1

Table 18: Summary of demographic and spatial model parameters used in the Red-shouldered Hawk population analysis. Literature references for parameters are given in Noreca Consulting and Elutis Modeling and Consulting Inc. (2007) and Tews (2008).

Parameter	Value / Comment
Mating system	Monogamous
Carrying capacity K	0.036 individuals per ha (males and females)
SD of K	0%
Initial abundance	50% of K
HSI threshold	0.1-0.9
Neighborhood distance	1700 m
Demographic stochasticity	Included
Environmental stochasticity	Lognormal distribution
Within population correlation	All vital rates correlated
Correlation distance function	Increases linearly from ~20% to 100% from maximum (edge to edge) to minimum (adjacent cells) distance within landscape subset (a=1.0; b=80; c=1.0)
Dispersal distance function	a = 0.17; b = 20.0; c = 1.0; Dmax = 100; (dispersal applies to juveniles only)
Size of landscape	Entire Québec study area

6.1 Sensitivity analysis

We generated a set of 1000 scenarios by randomly varying eight vital rates (i.e., fecundity and survival) as well as the carrying capacity and the initial abundance. This parameter scenario set was then executed in Ramas©MetaPop and each parameterization was replicated 50 times over 50 years. Note that survival rates can not exceed 1.0, i.e., maximum variation could not be sampled for all demographic rates (see e.g., vital rate 3, 4, 7 and 8 in Figure 27).

When abundance after 50 years was selected as the dependent variable the three most important parameters were male adult survival (vital rate 8), female adult survival (vital rate 4), and the carrying capacity (Table 19; Figure 27). When extinction risk after 50 years was selected the third most important parameter was vital rate 2 (juvenile females per adult female) instead (Figure 28).

Higher male adult survival rates have a significant positive impact on population performance because it allows mating of otherwise unmated females (note, that there is always a 5.3% surplus of unmated females due to a small proportion of breeding juvenile females, see stage-specific breeding in Table 18). Interestingly, three of the four vital rates of females (vital rate 2-4) showed a negative impact, i.e., increases in female vital rates resulted in higher extinction probabilities or lower abundances (Figures 27 and 28). This seems to be surprising as one would expect that increase in fecundity and survival independent of sex or stage type should decrease extinction probabilities or increase abundance. However, additional unmated females do not actively contribute to reproduction; they affect the population ‘negatively’ by approaching the carrying capacity which then in turn reduces the growth rate of the whole population.

Table 19: Results from the sensitivity analysis (randomized parameter set) with R squared values for each demographic model parameter. The R-squared of the regression is the fraction of the variation in abundance or extinction predicted by each independent variable (i.e., demographic parameter). The number of stars indicates ranking of the third most important parameters, respectively (* highest effect). Vital rates are represented by the following parameters: vital rate 1 = juvenile fecundity (female offspring per juvenile female); vital rate 2 = adult fecundity (female offspring per adult female); vital rate 3 = juvenile survival (females); vital rate 4 = adult survival (females); vital rate 5 = juvenile fecundity (male offspring per juvenile female); vital rate 6 = adult fecundity (male offspring per adult female); vital rate 7 = juvenile survival (males); vital rate 8 = adult survival (males).**

	Default value	**R^2 (Abundance 50 yrs)**	**R^2 (Ext. prob.50 yrs)**
Initial abundance	60	0.0002	0.0001
Vital rate 1	0.1948	0.0011	0.0001
Vital rate 2	0.3564	0.0593	0.0901*
Vital rate 3	0.7548	0.0456	0.0756
Vital rate 4	0.7548	0.1856**	0.1762**
Vital rate 5	0.0194	0.0003	0.0021
Vital rate 6	0.3564	0.0074	0.0029
Vital rate 7	0.7548	0.0053	0.0028
Vital rate 8	0.7548	0.2106***	0.3665***

Figure 27: Average abundances (50 stochastic replicates) after 50 years as a function of ten different demographic parameters included in the Red-shouldered Hawk sensitivity analysis (1000 random parameter combinations). Vital rate 1 = juvenile fecundity (female offspring per juvenile female); vital rate 2 = adult fecundity (female offspring per adult female); vital rate 3 = juvenile survival (females); vital rate 4 = adult survival (females); vital rate 5 = (juvenile fecundity (male offspring per juvenile female); vital rate 6 = adult fecundity (male offspring per adult female); vital rate 7 = juvenile survival (males); vital rate 8 = adult survival (males).

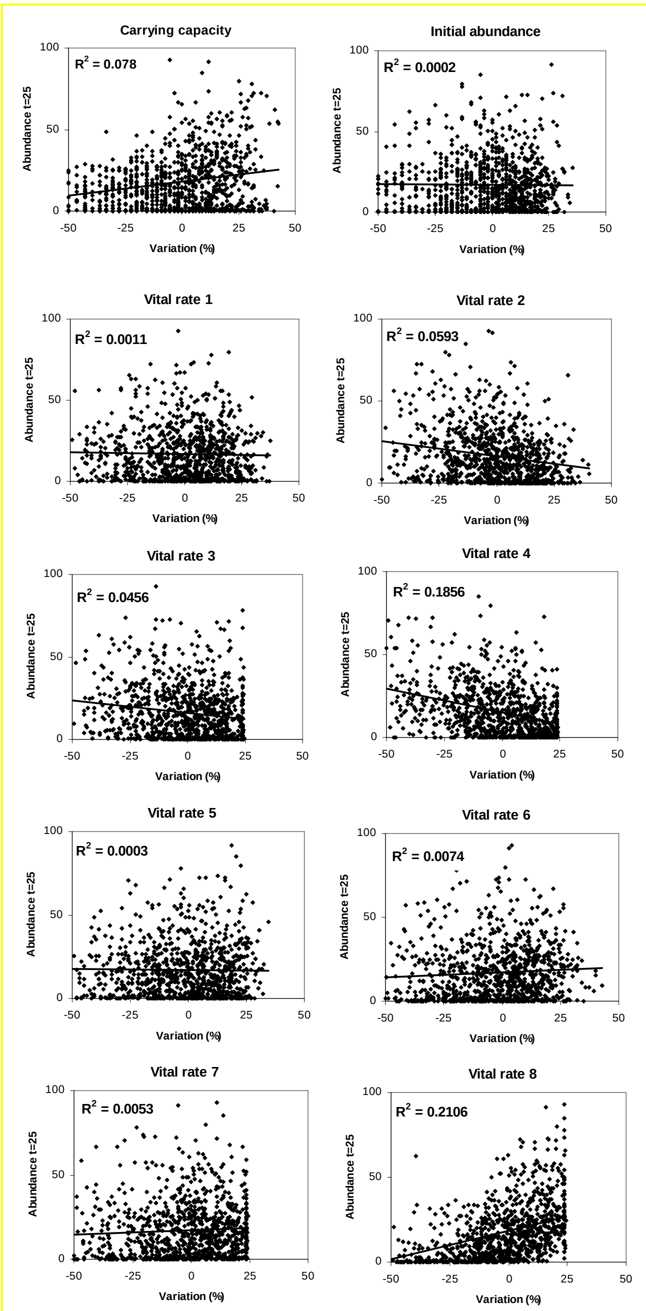
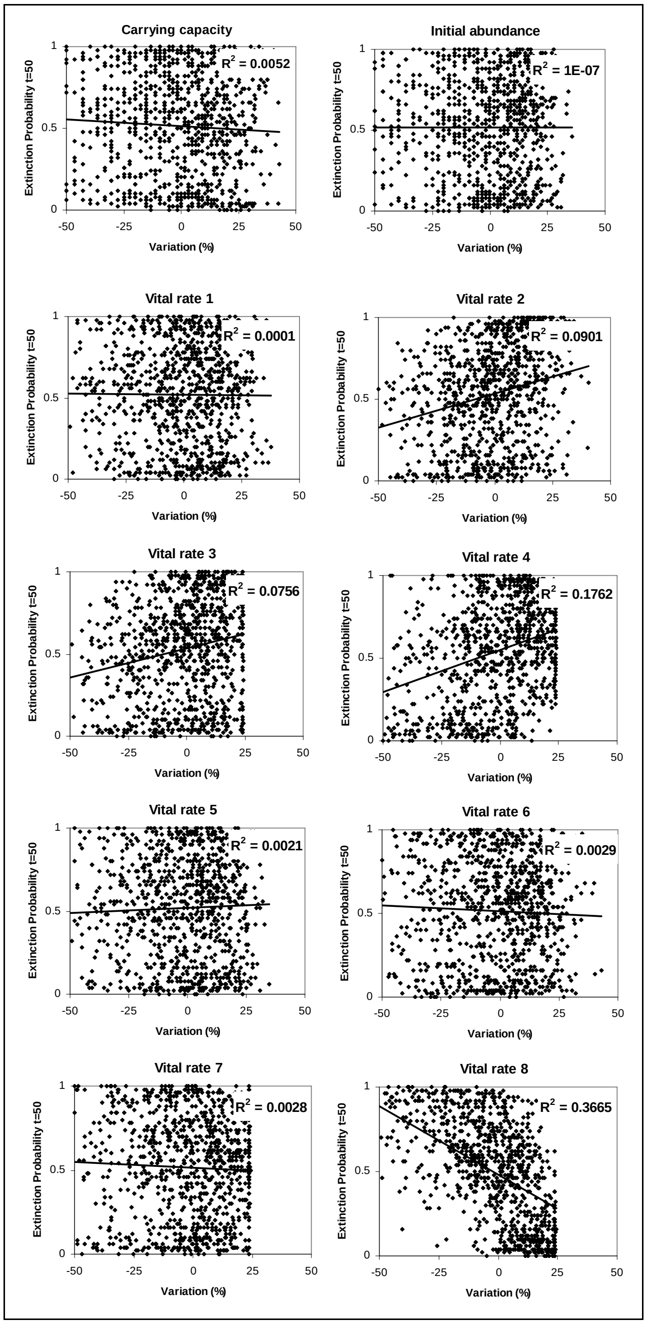


Figure 28: Average extinction risks (50 stochastic replicates) after 50 years as a function of ten different demographic parameters included in the Red-shouldered Hawk sensitivity analysis (1000 random parameter combinations). Vital rate 1 = juvenile fecundity (female offspring per juvenile female); vital rate 2 = adult fecundity (female offspring per adult female); vital rate 3 = juvenile survival (females); vital rate 4 = adult survival (females); vital rate 5 = (juvenile fecundity (male offspring per juvenile female); vital rate 6 = adult fecundity (male offspring per adult female); vital rate 7 = juvenile survival (males); vital rate 8 = adult survival (males).



6.2 Spatial population analysis

The habitat suitability model for the Red-shouldered Hawk analysis was based on the Eastern Ontario habitat suitability model presented in Akçakaya et al. (2007) (Figure 29). For the Red-shouldered Hawk it was not feasible to conduct a moving-window analysis due to its large operational scale. However, in order to simulate different scenarios of habitat supply we varied the habitat suitability threshold in the patch analysis. The habitat suitability index (HSI) threshold defines the numerical boundary above which habitat cells are considered suitable. Thus, by increasing the threshold value from low (e.g., 0.1) to high (e.g., 0.9) less suitable habitat is excluded and total habitat amount declines (Figure 30). For example, for a threshold of 0.1 almost all patches are considered suitable whereas for a value of 0.9 only highly suitable patches are included in the spatial population viability analysis. Thus, when habitat amount is plotted on the x-axis, increase in habitat amount will result in lower quality habitat being added and a saturation curve of the carrying capacity (see lower Figure in Figure 30).

Figure 29: HSI map for the Red-shouldered Hawk in the Québec pilot study area based on the modified eastern Ontario HS model. HSI values range from 0.0 (no suitability, pink) to 1.0 (highest suitability, brown).

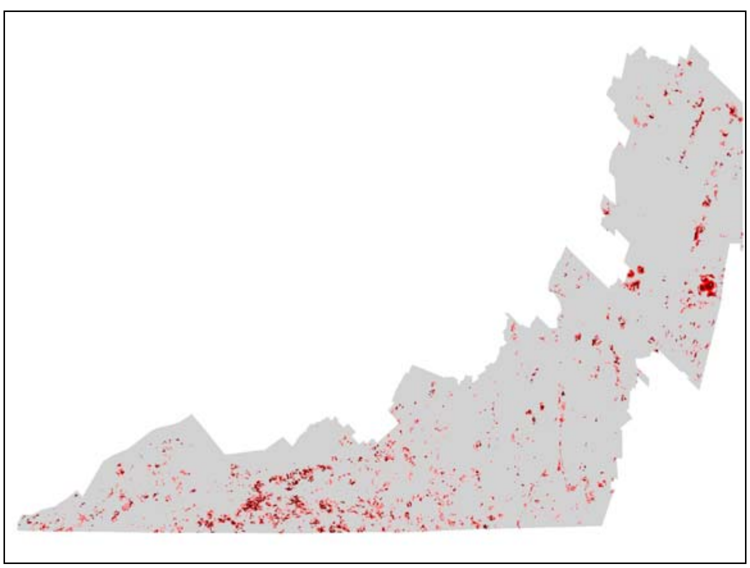
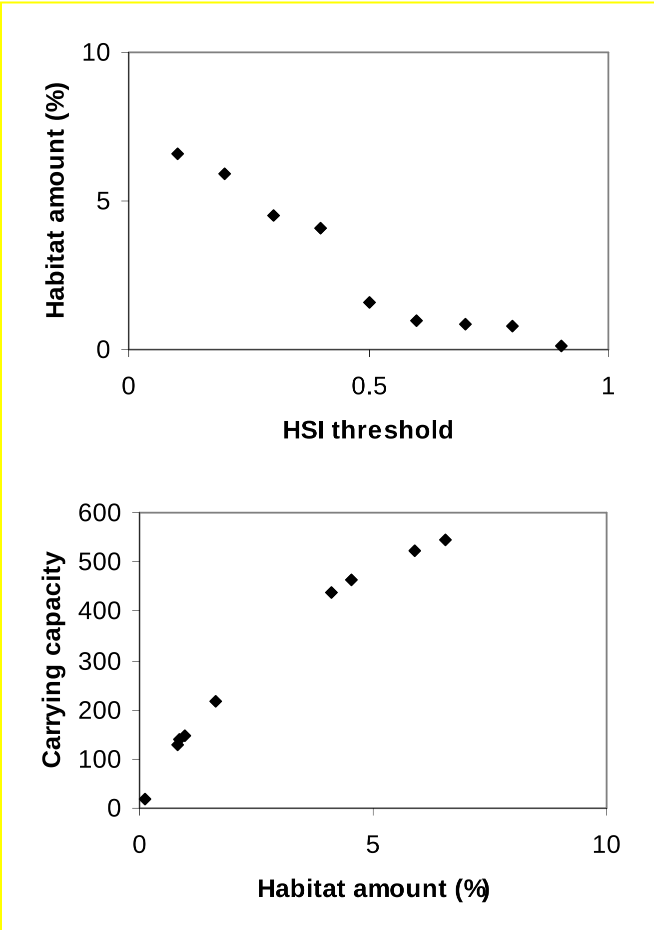


Figure 30: Results form the Red-shouldered Hawk patch analysis. The upper figure shows habitat amount (Québec pilot study area scale) as a function of the habitat suitability index threshold (which defines the boundary between suitable and unsuitable habitat). The lower figure shows how the total carrying capacity of the landscape reaches an asymptote with increase in habitat amount, i.e., decreases in the HSI value.



Due to the known issue of population loss through dispersal (see discussion in previous sections) and the fact that Red-shouldered Hawk can be considered as not dispersal limited on this spatial scale we reduced the dispersal rate by 50% (see Table 18). Note also that stage-specific dispersal only applies to juveniles. The results from the patch analysis (Table 20) show that habitat amount increased from 0.1% to 6.56%, the number of populations from 2 to 14 and the carrying capacity from 19 to 544 while decreasing the HSI threshold value from 0.1 to 0.9.

In the following step we then analyzed all HSI threshold scenarios in Ramas©MetaPop. The results from this analysis are given in Table 21 and Figure 31. Plotting habitat amount (%) versus viability (extinction probability) (Figure 31A) shows that landscapes with more than 0.81% habitat amount (on a spatial scale of 4869 km^2) were viable (i.e., <5% extinction risk) over the course of 50 years. Stability (i.e., <10% decline abundance over 50 years) was achieved with more than 1.61% habitat. Note that the above habitat amount standards are lower than the ones previously defined in the Tews (2008) study. This is due to the fact that dispersal rates where reduced by 50% to avoid population loss through 'unrealistic' sink dynamics. In the previous analysis population loss through dispersal did result both in higher minimum standards and a strong importance of patch size (presence of small patches/populations increased extinction risk).

The simulated data in Figure 31 show strong non-linear relationships whereas relationships in the other three case studies where more or less linear. This is due to the fact that under increasing habitat amount carrying capacities reach an asymptote and do not increase in a more or less linear fashion as opposed to when landscape scenarios are sampled from different areas (see discussion on page 63). This also means that habitat amount-based thresholds (i.e., standards) are more conservative, i.e., most likely larger than threshold derived from normally distributed habitat suitability classes. To illustrate this, decreasing the HSI threshold value from 0.3 to 0.1 would increase habitat amount. However, the amount of habitat added would only represent very low quality habitat (with low carrying capacity), and a standard derived from a scenario with a threshold value of 0.1 would encompass a strongly biased habitat suitability class distribution towards low suitability classes. Thus, a similarly sized different study area with a more normally distributed habitat suitability class distribution would yield a lower threshold for the same extinction risk.

Using the trend of the logarithmic function (Figure 31C) for calculation of functional presence we estimated that no habitat amount scenario for the standard demographic parameter set would be able to support functionality. Maximum optimal levels of functionality were generated for two spatial scenarios (>5% habitat) with an approximate risk of decline of 25% (see also Figure 32). However, when we decreased the relatively high standard deviations in fecundities from 66% to 30% we were able to generate acceptable risks of decline of less than 5% for four of the nine landscape scenarios with a minimum habitat amount of ~4% (Figure 33).

Average patch size was not included as an additional habitat-based standard as Red-shouldered Hawk have large home ranges. A large home range means that a large (here 1.7 km) neighborhood distance needs to be chosen for patch calculation in Ramas©HabDyn. Thus, patches in the model are significantly larger than ‘real’ habitat patches on the landscape (because patches are ‘glued’ together in the model’s patch calculation based on the neighborhood distance). This may lead to confusion in the applicability of standards and regarding the species’ and land use managers perception of what constitutes ‘a’ patch and its size.

Table 20: Habitat suitability thresholds scenarios for the spatial Red-shouldered Hawk model and their effects on area, habitat amount, number of patches, and carrying capacity (K).

HSI	Area (km^2)	Habitat amount (%)	# of pop.	K
0.1	319.60	6.56	14	544
0.2	287.20	5.89	12	521
0.3	221.40	4.54	11	462
0.4	200.30	4.11	11	437
0.5	78.50	1.61	9	219
0.6	46.80	0.96	6	148
0.7	43.10	0.85	6	139
0.8	39.56	0.81	6	129
0.9	4.97	0.10	2	19

Table 21: Simulation results from the spatial Red-shouldered Hawk population analysis based on changes in the habitat suitability threshold value.

HSI	Extinction probability	Initial abundance	Average final abundance	Population trend	Risk of decline	Expected minimum abundance (EMA)	Relative EMA
0.1	0.000	274	321	1.17	0.235	183	0.667
0.2	0.000	260	349	1.34	0.209	177	0.681
0.3	0.000	232	275	1.18	0.249	152	0.655
0.4	0.000	217	254	1.17	0.252	144	0.663
0.5	0.008	110	100	0.90	0.501	56	0.509
0.6	0.021	73	71	0.97	0.529	36	0.493
0.7	0.035	70	62	0.88	0.570	32	0.457
0.8	0.039	65	52	0.80	0.609	27	0.415
0.9	0.860	10	0	0.00	0.973	1	0.100

Figure 31: Red-shouldered Hawk PVA simulation results based on changes in the habitat suitability index threshold for the Québec pilot study area. Shown results are plotted against habitat amount: extinction probability (A), trend in abundance from initial to final year (B), functionality measured as the risk of decline to 50% of the initial abundance (C), and relative expected minimum abundance (D).

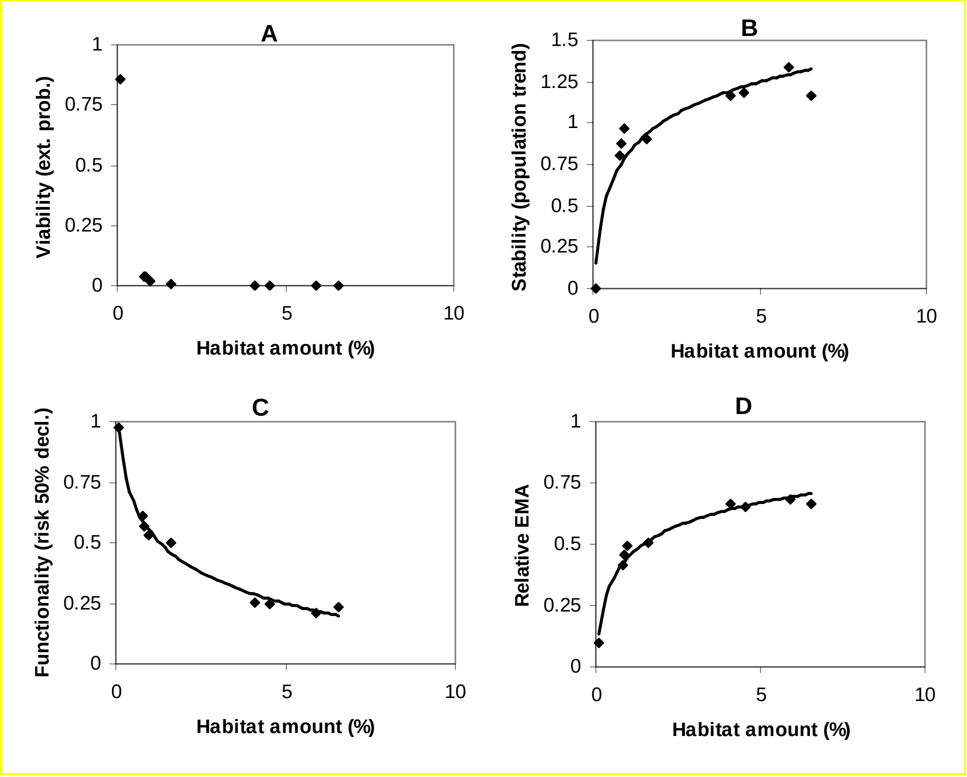


Figure 32: Average population trajectory (A, C, D) and risk of percent decline (B, D, F) for three different habitat suitability index scenarios in the patch analysis (A=0.3, B=0.6, C=0.9)

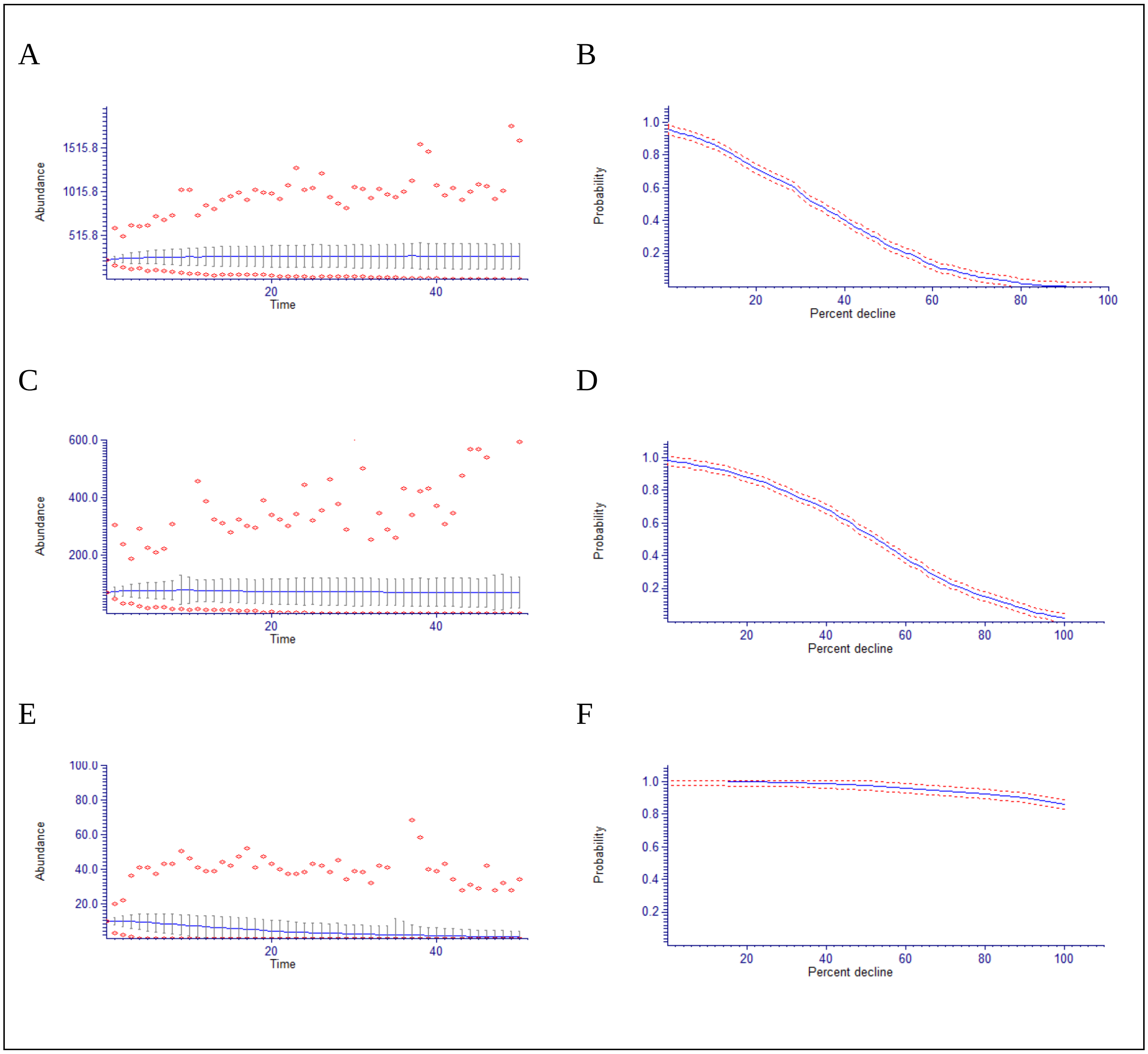
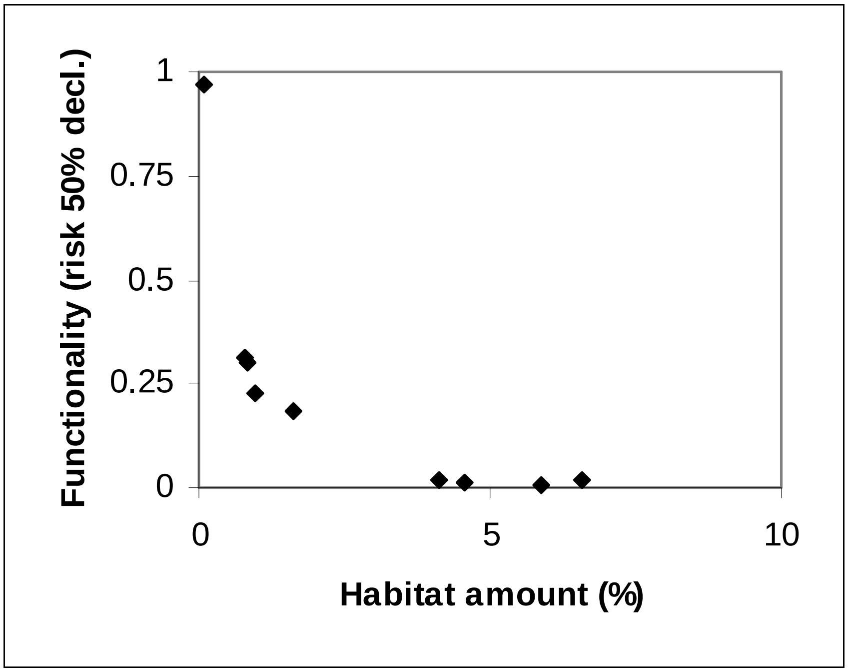


Figure 33: Functionality (measured as the risk of decline to 50% of the initial abundance) plotted against habitat amount (30% standard deviation in fecundities).



6.3 Recommended habitat-based standards

Based on the model assumptions and a simulation trajectory of 50 years the following habitat-based standards were recommended in the previous analysis (Tews, 2008): (i) a minimum patch size of 26 km^2 of suitable habitat (based on an average population density of 1.7 breeding individuals per km^2) to support a single, viable population, (ii) a minimum amount of 6.6% of suitable habitat to support a viable and stable metapopulation under optimal patch size distribution; if the metapopulation contains a significant proportion of smaller patches with low connectivity (with the total area below the minimum viable patch size) the recommended habitat amount may be significantly higher.

With this in-depth population modeling analysis we provide a re-assessment and a more detailed recommendation, in particular for standard #2. As discussed we also decided to exclude assessments with respect to patch size. The following recommended habitat-based standards represent conservative minimum thresholds based on a spatial analysis in the Québec pilot study area:

- a minimum patch size of ~26 km^2 of suitable habitat (based on an average population density of 1.7 individuals per km^2) to support a single, viable population over 50 years with 95% confidence (note that 'patch' may refer here to an aggregation of habitat patches with inter-patch distances smaller than the average home range size of Red-shouldered Hawks)
- a minimum amount of ~0.8% (~39 km^2) suitable habitat to support a viable metapopulation on a spatial scale of 4869 km^2
- a minimum amount of ~1.6% (~78 km^2) suitable habitat to support a stable metapopulation on a spatial scale of 4869 km^2
- a minimum amount of ~4% (~195 km^2) suitable habitat to support a functional metapopulation on a spatial scale of 4869 km^2 when standard deviations in fecundity rates are reduced to ~30% of the mean.

Note that the standard for functional presence is based on a modified version of the base demographic model presented in Akçakaya et al. (2007) and Tews (2008) (30% CV of fecundities). All of the above habitat-based standards are also subject to changes in the model assumptions. Particularly, as indicated by the sensitivity analysis, any deviations from the assumed male and female adult survival rates would require re-assessments of the recommended standards.

7 CONCLUSIONS

For the purpose of developing habitat-based biodiversity performance standards under NAESI we have conducted a detailed population modeling analysis for the Marsh Wren, Ovenbird, Bobolink, and Red-shouldered Hawk. Each population analysis included two main components: a sensitivity analysis of demographic parameters based on randomized parameter sets and a re-assessment of habitat-based standards by applying a spatial 'moving window' analysis for three of the four surrogate species. The moving window analysis was conducted by sampling 100 and 250 km^2 landscape subsets from the NAESI Québec pilot study area, respectively.

For each species and the performance targets 'viability' and 'stability' we developed a list of habitat-based minimum standards and associated minimum patch size requirements. For three of the four species we were also able to develop habitat-based biodiversity standards for 'functional' presence (i.e., <5% risk of decline to 50% of the initial population abundance in any year over the course of 50 years) (Table 22). Based on the simulation results we conclude that sufficient levels of functional presence are highly linked with lower levels of environmental stochasticity. In addition, we found that a species' metapopulation requires an average patch size at least the size of the minimum viable patch size in order to achieve functional presence.

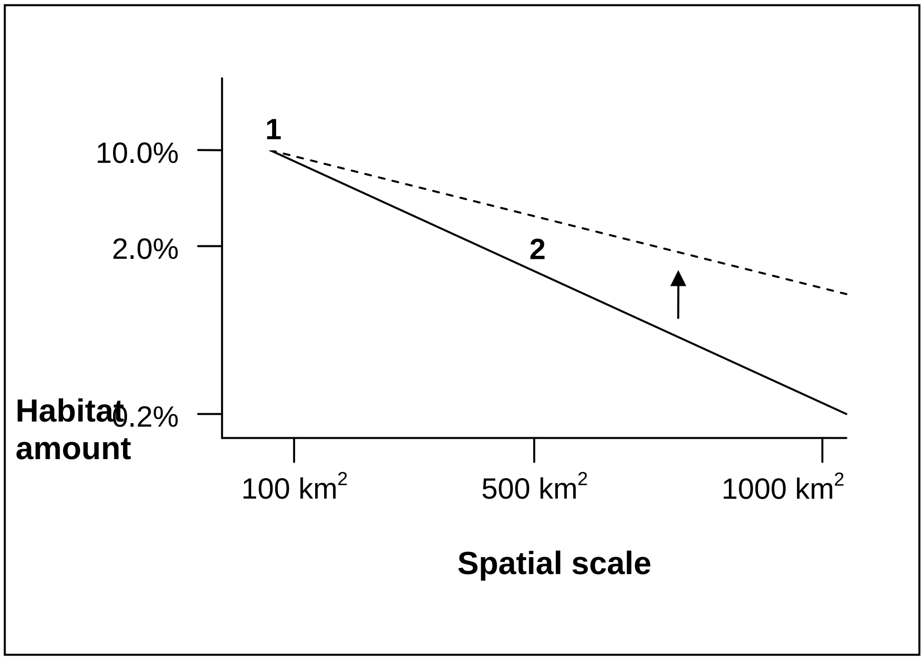
Our analysis indicates a close relationship between average patch size and amount of habitat in determining viability, stability and functionality and that the size of a population patch determines its degree of self-sustainability. This relationship is reflected in the fact that recommended minimum standards of habitat amount would need to be larger when smaller average patch sizes are considered. Also, as shown in Figure 34 the recommended relative habitat amounts (%) are smaller if applied for larger spatial scales whereas required absolute habitat amount (km^2) would need to be larger for larger spatial scales with increased average inter-patch distances (due to reduced connectivity).

The habitat-based standards recommended in this study are intended as broad guidelines to ensure a minimum supply of habitat so that metapopulations may be viable and near stable and that their ecological functions and processes are maintained at appropriate spatial and temporal scales. However, due to the stochastic nature of population models, such standards are subject to an unknown degree of uncertainty and may vary depending on spatial model parameters, demographic rates (as shown in the sensitivity analysis) and other factors. Thus, any changes in the model structure or parameterization will inevitably lead to variations in the recommended standards.

Table 22: Summary of recommended habitat-based standards for all four species, based on empirical data, the Québec pilot study area PVA (Tews, 2008) and series of spatial population analysis (100 km^2 scale) in the NAESI Québec study area (this study). MPS-O = minimum patch size required for occurrence; MPS-Si = minimum patch size required to avoid sink dynamics (lambda<1.0); MPS-So = minimum patch size required to ensure source dynamics (lambda >1.0); MPS-V = Minimum patch size for providing a viable (single) population; MIPD = minimum inter-patch distance to allow sufficient natal and breeding dispersal; MHA-V = minimum habitat amount required for viability (<5% extinction risk over 50 years); MHA-S = minimum habitat amount required for stability (<10% population decline over 50 years); MHA-F = minimum habitat amount required for functionality (<5% risk of decline to 50% of initial population abundance). Note that habitat amounts for Marsh Wren, Ovenbird, and Bobolink were derived on a 100 km^2 scale; standards for Red-shouldered Hawk were developed based on the Québec pilot study area scale (4869 km^2).

	MPS-O	MPS-Si	MPS-So	MPS-V	MIPD	MHA-V	MHA-S	MHA-F
Marsh Wren	-	10 ha	-	65 ha	2 km	1% (20 ha)	15% (50 ha)	-
Ovenbird	-	-	200 ha	850 ha	-	10% (60 ha)	17.5% (200 ha)	40% (850 ha)
Bobolink	20 ha	-	-	135 ha	15 km	6.5% (50 ha)	23% (125 ha)	30% (150 ha)
Red-shouldered Hawk	-	-	-	26 km^2	-	39 km^2	78 km^2	195 km^2

Figure 34: Relative habitat amount (%) as a function of spatial scale (1 and 2) if required absolute habitat amount (km^2) remains constant (solid line) or increases due to larger inter-patch distances and reduced connectivity (dotted line). The following rules apply: *(1)* If average inter-patch distance at scale 1 = 2 → absolute habitat amount (km^2) 1 = 2 (solid line); *(2)* If average inter-patch distance 2 < 1 → habitat amount (km^2) 2 > 1 (dotted line). *(3)* If average patch size 1 and 2 >= minimum viable patch size → average inter-patch distance unimportant and habitat amount (km^2) 1 = 2 (solid line).



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